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Impact on a Changing World

Program Report 1997-98

International Potato Center

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Program Report 1997-98

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Program Overview

Poverty eradication, increasing food productivity, and conservation of natural resources continue to be the primary goals of CIP's research. The last few years have brought revolutionary changes in the way our researchers can work towards those goals. Biological and information sciences have expanded explosively, providing new tools and new methods, both for conducting research and for managing and using the wealth of information that results. A heightened awareness of the wisdom and value of involving end-users early in the process of technology development has evolved. The resulting interactions increase the applicability and acceptance of our work, and help us to understand the sociological and economical context for appropriate technology development.

CIP has reacted to the changing world of research by redesigning its research program. We continue to concentrate on potatoes and sweetpotatoes, two of the world's most important food crops; management of natural resources, particularly in the high mountain areas of the world; and on the conservation and preservation of a group of underutilized but potentially valuable Andean root and tuber crops. Research is now organized in 17 well-designed projects that operate through a team approach and in close conjunction with partners in advanced research institutes, in national programs of developing countries, and in the field with farmer collaborators.

Research management is decentralized with most decisions made at the project level, increasing our flexibility to reach project goals. At one end of the spectrum, the new project structure allows us to take advantage of rapidly developing scientific and information innovations to shorten the technology development process. At the other end of the spectrum, we bring our research processes closer to the field and to farmers through participatory methods that involve them directly in the discovery process. These diverse partners provide us a wide range of expertise from lab to land and help us to use our limited resources to the best advantage. A mutual environment of cooperation and trust is the result. Project-level decision-making, guidance from the newly formed Program Management Team, and dialogue with our many research partners have created a synergy that greatly enhances CIP's research.

CIP's 1997-98 Program Report presents the first research progress reports from the 17 newly created projects. Forty-six research reports are grouped into the broad categories of Potato, Sweetpotato, Potato and Sweetpotato, Natural Resource Management in the Andes, and Andean Roots and Tubers. A full listing of the 17 projects contributing to this Program Report follows this overview.

In addition, we present a feature article "Incorporating Poverty in Priority Setting: CIP's 1998-2000 Medium Term Plan" by T. Walker and M. Collion. This article describes the

process by which CIP's projects were chosen based on a priority-setting mechanism that focuses on the poverty alleviation potential of each project.

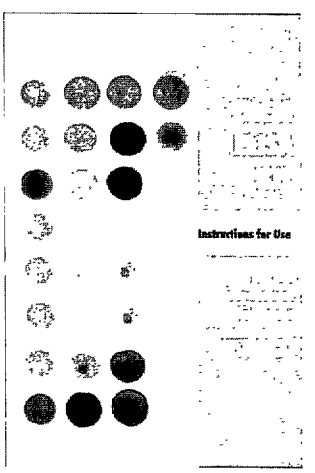
The following descriptions give a sketch of the research articles within this report.

Potato

Research in potatoes during 1997-98 emphasized finding a solution to the increasing late blight problem. Late blight is the world's most costly plant disease in terms of lost production, chemical inputs, and environmental contamination. It is particularly devastating to small, resource-poor farmers. CIP's research features an integrated approach: from highly technical molecular genetics to helping farmers learn in the field about recognizing and managing the disease; and from working with the microscopic pathogen which causes the disease to breeding new resistant cultivars. The integrated, full spectrum approach is necessary to provide solutions that farmers understand and use. Research reports cover pathogen biology and ecology, genetics of resistance to late blight, breeding for resistance, and integrated management of the disease. Progress in using molecular genetics, socio-economic perspectives, and geographic information systems, and participatory research methods are reported and lay the foundation for better control of late blight within the next few years.

While controlling the late blight disease became a very high priority in CIP because of the magnitude and urgency of the problem, research progress with other serious constraints facing small, poor producers is also covered in this volume, including:

- Development of a sensitive and affordable technology to detect *Ralstonia solanacearum*, the organism which causes bacterial wilt in soil and tubers.
- Taxonomic, population, and behavioral information critical for integrated management of three of the most serious potato pests in the world: Andean potato weevil, potato tuber moth, and leafminer fly.
- Establishment of a core collection of potato genetic resources so they can be used more efficiently.
- Using potato in intensified rice-wheat productions for diversity.
- Economic studies of potato research covering true potato utilization technologies, globalization of markets, and investing in potato breeding.



Improving Bacterial Wilt detection (see page 122).

Sweetpotato

Sweetpotato continues to be an important food crop in the world, and increasingly so in Africa after the reduction in cassava production due to disease outbreaks. CIP's highest priority for sweetpotato research is in developing and making available clones with the potential for yielding high levels of dry matter per hectare. High dry matter is essential in every area of the developing world for sweetpotato to reach its full potential for utilization, whether it is for animal feed, human consumption, or industrial processing.

Preliminary results indicate that rapid progress is being made in increasing dry matter. In this Program Report, progress is reported in a number of areas of direct importance to the introduction and utilization of new high dry matter clones. Research includes significant progress in the causes and controls of virus diseases and utilization to reduce nutritional deficits such as Vitamin A, especially among women and children. Trends in the production and utilization of sweetpotato in developing countries are reported as well as specific uses in food systems. Much of the research reported in this volume is focused on learning more about sweetpotato germplasm. Studies report molecular assessment of germplasm for diversity, surveying germplasm for food quality traits, and determining how farmers help to maintain diversity in the field. Knowledge of the diversity hidden in sweetpotato germplasm is essential for maximizing its potential use.

Harvesting in situ sweetpotato germplasmin the Phillippines (related story begins on page 317).

Natural Resource Management in the Andes

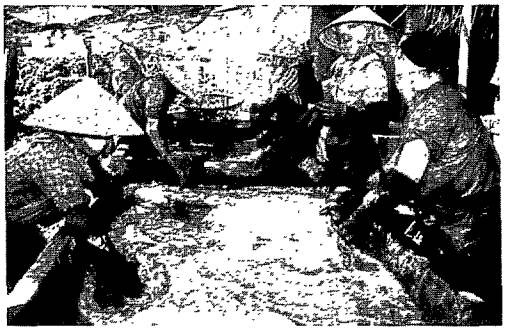
The Andean ecoregion is a particularly vulnerable ecosystem for agriculture. CIP's natural resource management program focuses on providing sound scientific, technical, and economic bases for policy and technology decisions. Research reported here focuses on assessing the risks associated with production in these fragile agricultural lands through the development and use of advanced technological modeling approaches. The development and application of tools and methods to enhance natural research management research capacity, including the use of microwave remote sensing, GIS, and multichannel radar imagery, is also reported. These tools and methods are applied at different spatial scales, from the field level to the landscape and regional levels.

Natural resource management in the Andes exemplifies an ecoregional approach to land use management for sustainable agriculture. This ecoregional approach, which uses the tools and methods mentioned above for research and development of management options, is implemented in the Andes through the Consortium for the Sustainable Development of the Andean Ecoregion (CONDESAN). CONDESAN is also the Andean Ecoregion partner of the Global Mountain Program, a more extensive research program for the high mountain areas of the world, convened and led by CIP. The Global Mountain Program represents the CGIAR's contribution to meeting the objectives of the UNCED accord for sustainable environmental development of mountain areas and involves other international agricultural research centers within the CGIAR conducting similar research in the African Highlands and the Himalayas.

CONDESAN works in the Andes, one of the most challenging agroecosystems on earth (see page 409).

Andean Roots and Tubers

A small but important part of CIP's research program is devoted to a group of underutilized high potential Andean root and tuber crops. The focus is on preserving the genetic diversity through both in-situ and ex-situ conservation methods, and by increasing the demand and utilization of the crops. Research results are included which explore the potential utilization of two of these crops: canna and yacon.



The first step in canna noodle production (see page 415).

CIP's continuing goal is to achieve its objectives of contributing to poverty eradication through the development of environmentally positive production technologies that increase productivity and sustainable livelihoods for developing country farmers. The research results reported in this edition of the CIP Program Report bring us closer to that goal and assure that CIP continues to have a strong and measurable impact on our changing world.

Wanda Collins
Deputy Director General
for Research

The Role of Regions in CIP's Research

Research through Partnership: CIP's Regional and Liaison Offices Increase Impact

The potential impact of CIP research is magnified by the posting of scientists in five regional and nine liaison offices* throughout the developing world. Working side by side with developing country research partners and keeping a users' perspective in mind enables new technologies to be user driven and quickly adopted, decreasing the time lag for impact to be seen, felt, and measured. It also allows priority setting to be a dynamic and participatory process reflecting local needs and constraints.

Potatoes and sweetpotatoes are grown in many developing countries of the world. Ecosystems, production systems, and food systems vary tremendously, however, making the adaptation of technology to local conditions both necessary and valuable. Additionally, in its natural resource management work, CIP researchers work on a scale that encompasses a wide range of site specificities. Characterizing these systems and specificities and understanding underlying mechanisms is a necessary part of technology development and implementing change. However, the impact of new management technologies for this resource base will only be realized through working with communities and local agencies who can bring about the large-scale and inter-related changes necessary to protect and conserve these very fragile production zones. This would not be possible without regional- and liaison office-based researchers.

CIP's decentralized organization enables researchers to develop technologies where they will be most readily used, and with the people who will most quickly adopt them. Increasingly, this includes farmers, communities, and local nongovernmental organizations. However, interchange of technologies also occurs across regions. The new team-oriented project structure creates an environment for rapid spillover to share successes.

* The Vietnam liaison office opened in mid-1999, and does not appear in the accompanying map.

The importance of CIP's regional and liaison office locations is obvious in this Program Report. More than half of the papers report on research conducted where CIP has regional and country offices, and many local collaborators are included as authors.

Location and contact information for all CIP offices are included below.

CIP Headquarters
Lima, Peru
E-mail: cip@cgiar.org
Website: www.cipotato.org

Latin America and the Caribbean (LAC) Regional Office
Lima, Peru
Fernando Ezeta, Regional Representative
E-mail: cip@cipa.org.pe

LAC Liaison Offices
Ecuador (Quito)
Charles Crissman, Liaison Scientist
E-mail: cip-quito@cgiar.org

Bolivia (Cochabamba)
Graham Thiele, Andean Potato Project, hosted by Fundación PROINPA
E-mail: g.thiele@cgiar.org

Sub-Saharan Africa (SSA) Regional Office
Nairobi, Kenya
Peter Ewell, Regional Representative
E-mail: cip-nbo@cgiar.org

SSA Liaison Offices
Cameroon (Bamenda)
Joseph Koi, Liaison Office Manager
E-mail: cip-bamenda@cgiar.org

Uganda (Kampala)
J. O. Otieno
E-mail: jotieno@imul.com

South and West Asia (SWA) Regional Office
New Delhi, India
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SWA Liaison Offices
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East and Southeast Asia and the Pacific (ESEAP) Regional Office
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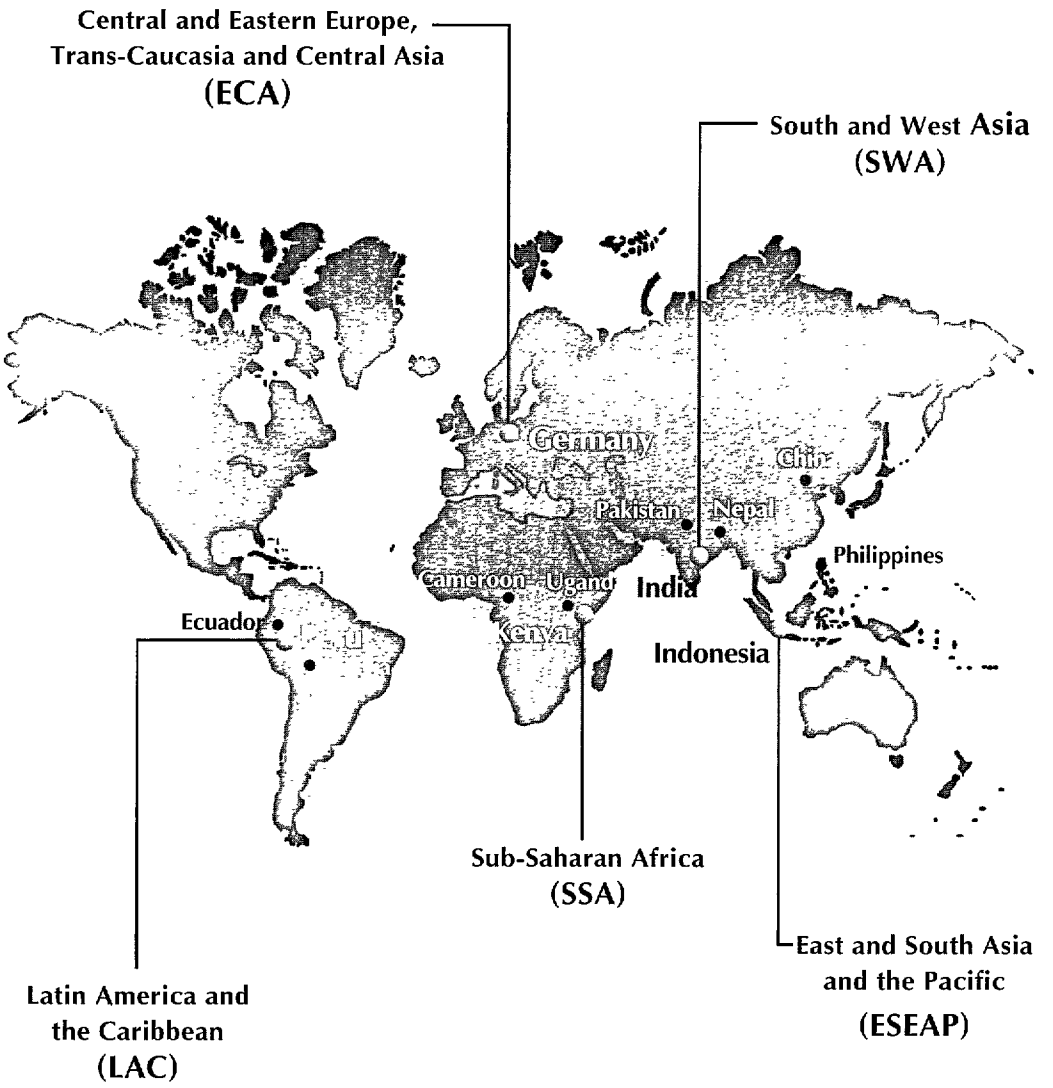
Vietnam (Hanoi)
Dai Peters, Liaison Scientist
E-mail: cip-hanoi@fpt.vn

Central and Eastern Europe, Transcaucasia and Central Asia (ECA) Regional Office
Berlin, Germany
Peter Schmiediche, Coordinator
E-mail: p.schmiediche@cgiar.org

CIP Regional and Liaison Offices



CIP's Research Project Portfolio

1 Integrated control of late blight (R. Nelson)

Late Blight is CIP's highest priority at the moment and this project is highly focused on developing, adapting, and integrating technologies for the management of the world's worst agricultural crop disease. The project integrates biotechnological tools for pathogen epidemiology and developing disease resistance with disease management and control in farmers' fields through the Farmer Field School concept.

- Pathogen population biology and ecology (G. Forbes)
- Development and application of methods for phenotypic characterization of resistance (G. Forbes)
- Development of tools: maps, markers, genes, and databases (M. Bonierbale)
- Marker-assisted genetic analysis of resistance (M. Ghislain)
- Diploid pre-breeding for LB resistance (B. Trognitz)
- Intermediate breeding for LB resistance at the tetraploid level (J. Landeo)
- Genetic engineering for resistance to late blight (M. Ghislain)
- Analysis of genotype by environment interactions (M. Bonierbale)
- Utilization of improved populations for late blight resistance (J. Landeo)
- Development of component technologies for integrated management of late blight (G. Forbes)
- Farmer participatory research and implementation for integrated late blight management (R. Nelson)

2 Integrated control of bacterial wilt (E. Chujoy)

Bacterial wilt is the second worst potato disease in the world. As resistance is difficult to develop and maintain, CIP's program concentrates on understanding and diagnosing the presence of bacteria in the soil and in tubers. This is used to improve site management, seed systems, and utilization of available resistant material. Decreased transmission of the disease is a key target in control.

- Characterization, detection, and ecology of *P. solanacearum* (S. Priou)
- Integrated management of bacterial wilt of potato in Southeast Asia (E. Chujoy)
- Integrated control of potato bacterial wilt in East Africa (E. Chujoy)
- Integrated management of bacterial wilt of potato in China (Y. Wang)
- Development of components of bacterial wilt control and IDM (S. Priou)
- Integrated control of diseases of potato: bacterial wilt in South West Asia (O. Hidalgo)

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3 Control of potato viruses (M. Querci)

Viruses cause serious losses in potato and impede movement of seed and genetic resources. The project concentrates on sensitive, low-cost detection and epidemiological factors affecting spread. Genetic engineering is used to identify, clone, and transfer genes of related species to potato for resistance; this is combined with traditional methods of breeding for maximum efficiency in incorporating resistance to a range of viruses.

- Studies on potato phytoplasmas and their vectors (L. Salazar)
- Development of serological techniques for potato virus diagnosis (L. Salazar)
- Molecular techniques for detection and control of viruses and viroids in potato (M. Querci)
- Molecular characterization of genetic resistance to viruses and use of natural genes for transgenic resistance (M. Querci)
- Breeding for virus resistance (M. Bonierbale)
- Adaptation and utilization of advanced virus-resistant clones and progenitors (M. Bonierbale)
- In-vitro eradication of potato viruses and multiplication of materials for distribution (A. Golmirzaie)

4 Integrated management of potato pests (A. Lagnaoui)

Key pests are potato tuber moth (a rapidly growing threat), Andean potato weevil, leafminer flies, and whiteflies. The project objective is to combine management practices into locally adapted packages to reduce chemical pesticide use and increase overall benefits for farmers. Components include biological, cultural, and resistance aspects of control.

- Management of potato tuber moth complex (A. Lagnaoui)
- Management of leafminer fly and other foliage insects (F. Cisneros)
- Management of Andean potato weevil and other soils pests (F. Cisneros)
- Management of insect vectors (A. Lagnaoui)
- Management of potato nematodes (M. Canto)
- Entomopathogens as integrated pest management components (F. Cisneros)

5 Propagation of clonal potato planting materials (U. Jayasinghe)

Increasing efficiency and effectiveness of both informal and formal seed systems is the target of this project. Varietal introduction and diffusion is dependent on the informal system, but it must be linked with the formal and it must emphasize high quality planting material. The project accomplishes this with farmer training and establishment of pilot seed systems.

- Impact of innovations in links between formal and informal seed systems in Ecuador, Kenya, and the Philippines (C. Crissman)
- Strengthening research and production of seed potato in Bolivia (A. Devaux)
- Seed multiplication and varietal diffusion through the development of a farmer-based seed system (H. Kidane Mariam)
- Diffusion and production of quality seed through informal participatory seed systems in Bangladesh and Sri Lanka (S. Ilangantileke)

- Research and technical assistance for the improvement of seed technologies and the development of seed programs (O. Hidalgo)
- Seed multiplication and varietal diffusion of new potato varieties through the farmer-based seed system in the Philippines, and Vietnam (U. Jayasinghe)
- Seed degeneration studies in Southern Peru (L. Salazar)

6 Sexual potato propagation (True Potato Seed) (M. Upadhya)

True potato seed (TPS) has growing potential in specific areas of the world where the more traditional production systems fail. CIP concentrates on the researchable areas of improving parental performance in hybrids and in certain constraints (late blight resistance, earliness, seed set, etc.). Backstopping is being done by local organizations (private sector, NGOs, and NARs) in efforts to commercialize TPS systems and thus underpin the developing of small industries.

- Breeding TPS parental lines: production and evaluation of hybrid TPS families (M. Upadhya)
- Breeding TPS parental lines: production and evaluation of hybrid TPS families (S. Ilangantileke)
- Evaluation of hybrid TPS families for adaptation and yield (R. El Bedewy, S. Ilangantileke, G. Prain, and M. Upadhya)
- Physiological studies on TPS quality postharvest handling and storage (N. Pallais)
- Evaluation of parental lines and hybrid TPS families for reaction to late blight (B. Trognitz)
- Evaluation of parental lines and hybrid TPS families for total glycoalkaloids (M. Upadhya)

7 Global sector commodity analysis and impact assessment for potato (T. Walker)

The lack of consistent and reliable statistics covering the agronomic, economic, social, and environmental aspects of new and improved technologies in potato decreases the ability to document effectiveness and guide investment. This project is providing that information and determining rates of returns on CIP research. Price and production databases are established for constant reference and priority setting. Commodity analysis is improving domestic potato marketing and international trade prospects for developing countries.

- Impact assessment (T. Walker)
- Global characterization (T. Walker)
- Characterizing consumption, markets, and trade (G. Scott)

8 Control of sweetpotato viruses (L. Salazar)

Although sweetpotato viruses cause significant production losses, especially in sub-Saharan Africa, there is still a lack of research in this area. This project is developing methods of detection and control for the virus complex known as WBV. It also seeks to identify resistance to this virus complex.

- Identification and characterization of sweetpotato viruses and search for resistance (L. Salazar)
- Eradication of sweetpotato viruses (A. Golmirzaie)

- Evaluation of virus diseases (L. Salazar)
- Test of sweetpotato cultivars resistant to sweetpotato virus disease (L. Salazar)
- Propagation of clean planting material (N. Pallais)

9 Integrated management of sweetpotato pests (F. Cisneros)

Integrated pest management for sweetpotato depends on good knowledge of the biology and incidence of the target pests. IPM components are then developed and evaluated against site-specific ecological, economical, and social factors. Pilot units and Farmer Field Schools (FFS) are used as the mechanisms for testing and implementing IPM components.

- Institutionalizing sweetpotato FFS in Indonesia (E. van de Fliert)
- Institutionalizing sweetpotato FFS in Vietnam (E. van de Fliert)
- ICM for sweetpotato in Uganda (N. Smit)
- Management of sweetpotato pests in Latin America (F. Cisneros)

10 Postharvest utilization of sweetpotato (G. Scott)

This project studies a range of technologies and technology adoptions to improve the sustainable livelihoods of rural poor through diversification and expansion of sweetpotato use. In the various countries, the main beneficiaries are women and children and poor households. The project goal is to improve nutrition and income and reduce poverty.

- Expanding utilization of sweetpotato starch (C. Oates)
- Facilitating consumption of sweetpotato flour (V. Hagenimana)
- Increasing use of sweetpotato for livestock feed (D. Peters)
- New uses for fresh sweetpotato (G. Scott)

11 Breeding for high dry matter in sweetpotato (D.P. Zhang)

This project provides the raw material for increases in both fresh and processed use of sweetpotato. Dry matter, the essential component in both types of use, has been increased and genetic material made available. The new clones are being adapted to low-input subsistence systems in targeted environments to feed into the developing markets.

- Sweetpotato breeding and germplasm evaluation for SSA (E. Carey)
- Breeding high dry matter sweetpotato adaptable to Southeast Asia (I.G. Mok)
- Breeding dual purpose and early maturing varieties for SW Asia (T.R. Dayal)
- Introgression of exotic germplasm into the Chinese breeding program (Y. Wang)
- Germplasm evaluation for abiotic stresses (N. Pallais)
- Germplasm enhancement through population improvement and biotechnology (D.P. Zhang)

12 Global sector commodity analysis and impact assessment for sweetpotato (G. Scott)

Commodity analysis and impact assessment data are difficult to locate and to generate. This project is providing much-needed information through country case studies, local and regional literature review, and data to develop the analyses necessary to study constraints

as well as the potential for developing country production and postharvest sweetpotato systems.

- Global Characterization (G. Scott)
- Impact studies (J. Otieno)
- Projections/database (G. Scott)

13 Potato production in rice-wheat systems (T. Walker)

The assessment of opportunity for potato to fit into the cool dry season cropping systems following rice in the rainy season has been completed. Potential is good for increasing the efficiency of this cropping ecology through the addition of potato. Current work concentrates on diagnosing the constraints to and increasing the productivity of the full potato-rice-based system. Ecosystem resource management is particularly critical, and the project is developing models to provide natural resource management options.

- Productivity and sustainability of the rice-potato-rice cropping system (T. Walker)
- Characterizing the feasibility and desirability of intensifying potato production in cereal-based cropping systems (W. Bowen)

14 Sustainable land use in the Andes (R. Quiroz)

The Andean ecoregion is a particularly vulnerable ecosystem for sustainable agriculture. The project is providing a sound scientific, technical, and economic base for both policy and technology recommendations. Innovative tools for ecoregional research are developed through the integration of process-based crop growth models, remote sensing, economic decision models, and geographic information systems (GIS). Such integrated tools are also applicable to other global mountain ecosystems.

- Characterization of land use in the Andean ecoregion (R. Hijmans)
- Methodology development for ecoregional research in mountain environments (W. Bowen)
- Land use intensification and natural resource management in the Andean ecoregion (C.L. Velarde)
- Policy intervention in the high Andes (R. Estrada)
- Linking research and development activities with CONDESAN and GMP (J. Posner)

15 Conservation and characterization of potato genetic resources (Z. Huaman)

This project conserves the most comprehensive collection of wild and cultivated potatoes in the world. Characterization (both molecular and morphological) is the key objective, along with database development and availability. Significant activities focus on identifying key desirable traits and distributing healthy material throughout the world for utilization in potato improvement projects. The project provides key input into CIP's own breeding efforts.

- Conservation of potato genetic resources (Z. Huaman)
- Molecular and agronomic evaluation of potato genetic resources (M. Bonierbale)
- In vitro culture, conservation and cryopreservation of potato cultivars (A. Golmirzaie)

16 Conservation and characterization of sweetpotato genetic resources (M. Hermann)

This project conserves the most comprehensive collection of wild and cultivated Ipomoea *species (including cultivated sweetpotato). New and more efficient methods of conservation are being studied (e.g., cryopreservation). The collection is being characterized for a core collection to make it more accessible to breeders. Virus eradication is a key component. Desirable traits are being identified for more efficient use of the collection.*

- Conservation of sweetpotato genetic resources (Z. Huaman)
- DNA fingerprinting for the selection of a core sweetpotato collection (D. Zhang)
- In vitro conservation and cryopreservation of sweetpotato genetic resources (A. Golmirzaie)

17 Conservation and characterization of Andean root and tuber crops (M. Holle)

The activities of this project assist national programs in the Andes in rationalizing strategies in conservation of Andean roots and tubers (ARTC). Nine genera are included for collection, study, and conservation of biodiversity. The potential for ARTC use on a wider basis is also studied through market and consumption patterns, and identification of poorly documented demand. Healthy planting material is produced for farmers. This project is perhaps the only one with a significant effort toward developing virus identification and eradication procedures for these important, underutilized crops.

- Conservation methods (C. Arbizu)
- ARTC diversity: Characterization and classification of ARTC variability (M. Hermann)
- ARTC biotic constraints: Clean planting material (viruses emphasized) (L. Salazar)
- Product development of ARTC for specific characters (e.g., starch) and sites to increase competitiveness (S. Salas)
- Links with CONDESAN partners (M. Holle)

Incorporating Poverty in Priority Setting: CIP's 1998-2000 Medium Term Plan

T. Walker[1] and M. Collion[2]

Alleviating poverty is increasingly regarded as an important objective of public-sector agricultural research in developing countries. Indeed, the mission statement of the Consultative Group on International Agricultural Research (CGIAR) has evolved over the last 15 years from an emphasis on "improving the economic well-being of low-income people" to "contributing to poverty eradication."

The role of agricultural research in increasing productivity and in priming the pump for economic growth is well known, but agricultural research is also viewed as a blunt instrument to improve inequality. Poverty is often associated with inequality, but the two are not the same. A strong positive relationship between economic growth and reduction in absolute poverty has been documented in comprehensive empirical studies of the World Bank (Deininger and Squire, 1996). But the same research does not find a statistically significant relationship between economic growth and inequality. Therefore, while we are confident that agricultural research will contribute to poverty alleviation in developing countries, it would be too much to expect that agricultural research will be a vehicle for redistributing assets and income from the rich to the poor.

Almost always, agricultural research that increases the productivity of food crops will favor the poor of developing countries. Those below the poverty line will reap a substantial share of the net benefits of technological change. But quantifying the size of such benefits is a complex empirical undertaking. To what extent do the rural poor produce, consume, and market potatoes and sweetpotatoes? To what extent do the urban poor consume potatoes and sweetpotatoes? To what extent is the economy open or closed? To what extent are project technologies labor saving or labor using? To what extent do policies and institutions reinforce incentives for the adoption of potato and sweetpotato technologies? These are usually only a subset of the questions that need to be answered before the effects of agricultural research on the poor can be quantified with some degree of precision.

In this article, we address only one dimension of the relationship between agricultural research and poverty: does adjusting for the spatial distribution of poverty lead to substantial changes in the project rankings in priority setting? In our application, project rankings adjusted for poverty depend heavily on estimates of poverty in China, the largest growing potato and sweetpotato country in the world.

The Geography of Poverty and CIP's Projects

In priority setting for its 1998-2000 Medium-Term Plan, CIP scientists and management evaluated 15 projects in a conventional format of economic project appraisal (CIP, 1997). Project benefits depended on the size of the recommendation domain (in target and spill-over countries), probabilities of technological success, per hectare benefits of adopted technology, and ceiling levels of adoption in 2015 (Walker and Collion, 1997). Estimates for these four

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2 World Bank, Washington, D.C., USA.

parameters were elicited from scientists in group discussions.

Calculating the weighted average incidence of poverty for each of the projects was the first step in assessing the potential leverage each project has on poverty. A headcount index is the most common way to measure absolute or "threshold" poverty. It shows the proportion of the population falling below a poverty line that reflects a minimum standard of living or consumption. In the TAC database that was used for priority setting (Gryseels et al., 1996), the poverty line is roughly equivalent to a standard of living at $1 per day in purchasing power parity income that adjusts for differences in price levels across countries. Data on the population of the rural and urban poor were presented for 118 developing countries. The estimated national incidence of poverty in the early 1990s ranged from 86% in Rwanda and Bhutan to 4% in South Korea. For the developing countries as a whole, the weighted average incidence of poverty was 31%, about three persons in ten.

These national poverty estimates were combined with regional estimates in China and India to generate project-specific mean estimates weighted by the geographic distribution of benefits (Table 1). Most of the projects are characterized by a poverty intensity that exceeds the weighted global average of 31%. Four projects fall below this threshold. Three pertain to sweetpotato, and all are geographically concentrated in China. In general, projects with benefits more heavily concentrated in China rank at the lower end of the scale on poverty intensity.

Table 1. The average poverty rating of CIP's projects by measure.

Project	Poverty measure			
	Head-count index (%)[a]		TAC projected[b]	
	Original	Revised[c]	Original	Revised[c]
Potato Sustainable Intensive Cropping (PSIC)	52.0	52.0	0.787	0.787
Sweetpotato Planting Material (SPM)	50.4	50.4	0.644	0.644
Potato Seed Systems (PSS)	47.6	47.6	0.587	0.587
NRM in Tropical Mountains (NRM)	44.2	44.2	0.560	0.560
Sweetpotato IPM (SIPM)	43.4	43.4	0.585	0.585
Potato Utilization (PU)	40.7	40.7	0.694	0.694
IPM Potato Insects (PIPM)	39.7	39.7	0.367	0.367
ARTC Postharvest (ARTC)	35.1	42.6	0.452	0.561
Potato Late Blight (PLB)	34.3	34.3	0.426	0.548
True Potato Seed (TPS)	32.8	32.8	0.466	0.572
Potato Viruses (PV)	31.4	44.3	0.326	0.514
Sweetpotato Dry Matter and Adaptation (SDM)	29.6	41.2	0.372	0.540
Potato Bacterial Wilt (PBW)	25.8	38.0	0.321	0.498
Sweetpotato Product Development (SPD)	22.5	37.4	0.272	0.489
Sweetpotato Virus (SV)	16.7	28.6	0.197	0.370

[a] Percentage of people that fall below the poverty line in countries and provinces where the project is expected to have results

[b] Poverty measure that combines a poverty line with an estimate of income inequality (TAC, 1996).

[c] Authors' revisions based on recent estimates of poverty in China.

Poverty in China

The consequences of poverty in China for the project rankings warrant more discussion. First, the use of a national average in TAC's own priority setting for the CGIAR as a whole hides a great deal of interregional variation in poverty (TAC, 1996). For example, potatoes in China are mainly produced in the poorer interior mountainous provinces distant from the richer coast (Figure 1). Weighting growing area by provincial estimates of poverty shows that potatoes are cultivated in regions that are two to three orders of magnitude poorer than comparable regions where rice is produced.

Low growth and adverse distributional effects have dampened growth in the poorer inland provinces (Chen and Ravallion, 1996). In four provinces in southern China, reliable household survey data on rural living standards suggested a range in the incidence of rural poverty of from 3% to 5% (depending on the method used) in prosperous coastal Guangdong to 27% to 42% in poor inland Guizhou. These interregional differences appear to be sharper among rural rather than urban households (World Bank, 1993). In part, these differences reflect competitive advantages of the coastal provinces. Government policies have also contributed to these differences. Several coastal zones receive preferential treatment for foreign investment. The government also enforces a registration system that increases the cost of interregional migration. Geographic poverty traps are becoming more evident.

Second, the national headcount index for China looked surprisingly low compared with estimates for other developing countries. In descending order of the incidence of poverty in the TAC database, China occupies position 116, with mean estimated poverty lower than that of all other developing countries except Oman and South Korea. Estimated poverty is greater in many upper-middle-income economies, such as Malaysia, Uruguay, and Cyprus, than in China. As an extreme example, per-person income adjusted for purchasing power parity was about eight times higher in high-income Singapore than in China, yet 15% of the population of Singapore was estimated to be poor compared with 11% for China.

The World Bank has revised upward estimates of poverty in China (The Economist, 1996). The use of this more recent estimate, which we call the revised headcount index, results in a tighter grouping of projects than the use of the lower estimate. For most projects, the mean incidence of poverty lies between 37% and 47% (Table 1).

Ideally, a poverty measure should also convey information on the severity of poverty, and a class of "higher-order" poverty measures is preferred in the literature (Ravallion, 1994a). In the TAC priority-setting exercise, an "inclusive" higher-order measure of poverty was used (Ravallion, 1994b). The proportion of poor below a threshold poverty line was not the sole focus in measuring social welfare. Some notion of the severity of poverty was approximated by the degree of income inequality in the TAC exercise. The poverty weight is also based on a projection of income in purchasing power parity to 2010. Income inequality was assumed to be positively related to absolute poverty. In other words, even if base purchasing power parity income and projected economic growth were assumed to be the same for Brazil and Bangladesh, the estimated TAC poverty weight would be larger for Brazil than for Bangladesh because of Brazil's greater income inequality. In practice, differences in inequality across countries are not that important in contributing to the national variation in TAC estimated poverty weights, which are influenced heavily by the variation in base purchasing power parity income and projected growth rates.

Like the headcount index, we use two versions of the TAC poverty measure: the

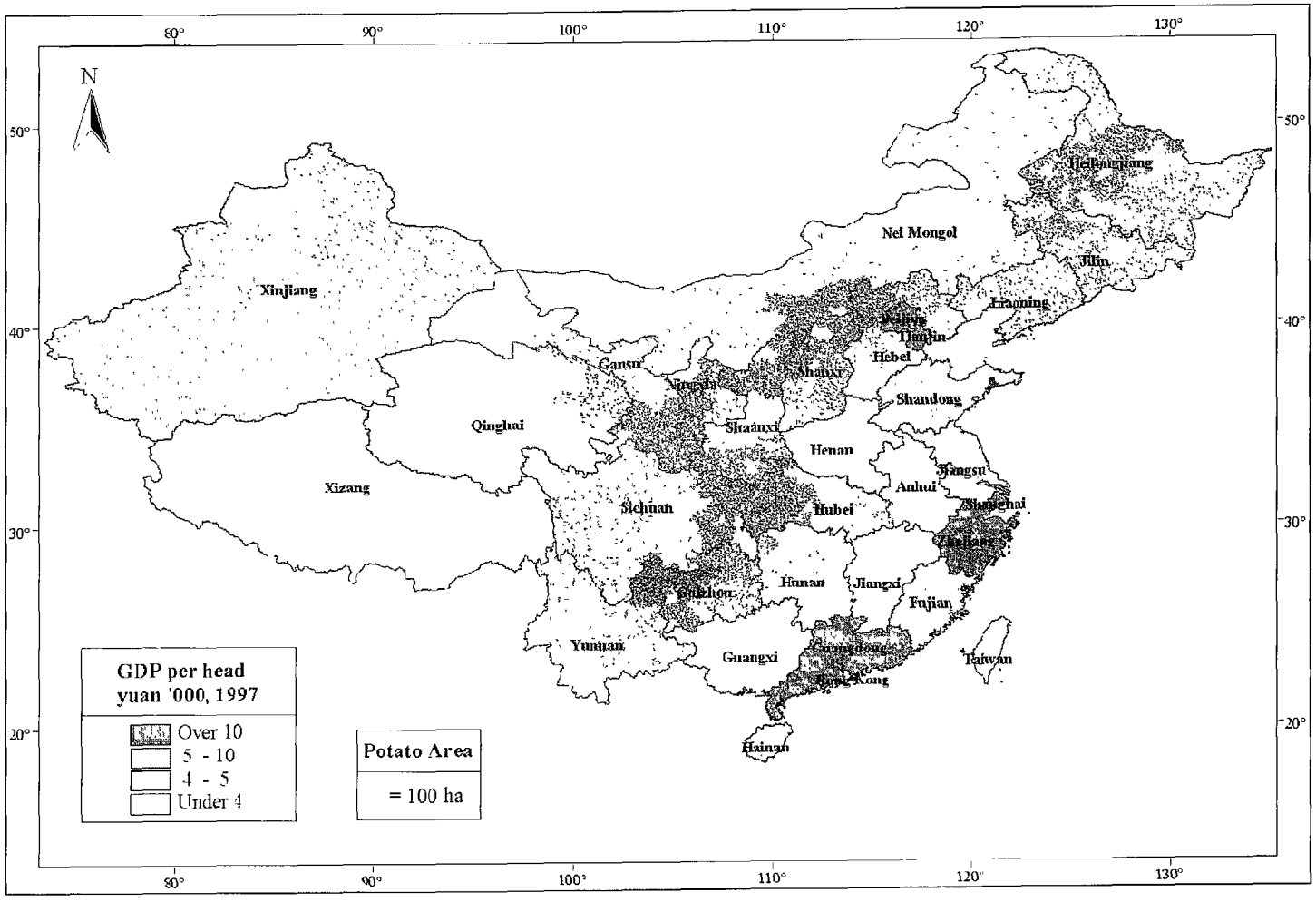

Figure 1. The geography of potato area and poverty in China.

"original," based on a purchasing power parity per capita income of $2,946 in 1991 prices for China; and the "revised," based on $1,800 in 1994 which is consistent with the recent World Bank revisions. Both measures use the same robust projected growth rates for China given in the TAC database.

Project results, generated with the original TAC projected poverty measure, are strongly associated with those from the initial headcount index (Table 1). Similar results are not surprising because the estimate of the TAC projected poverty measure for China as a whole is 0.106 which is only slightly lower than the initial national headcount index of 0.112 (expressed as a proportion) for China. In the same vein, the revised TAC poverty weights give results quite similar to the revised headcount index. China's per capita income of $1,800 in purchasing power poverty in 1994 combined with the projected growth rates results in a poverty weight of 0.432, which is about four times higher than the earlier estimate of 0.106.

Assessing the Impact of Poverty on the Project Rankings

In conventional scoring models for priority setting, weights would be applied to criteria to arrive at a project score. In our application, we essentially have two criteria: efficiency in the form of net present value and equity in the form of poverty intensity. For a comparative treatment, both of these variables would be rescaled (or normalized) between 0 and 1, representing the lowest and highest project values for each criterion. Arbitrary weights would then be assigned to each criterion to rank the projects. Changing the weights allows the analyst to relate the sensitivity of the project rankings to judgments about what is desirable.

This procedure for assessing the effects of different objectives on project rankings in a scoring model of priority setting is tricky (Alston et al., 1996). In our application, blind adherence to conventional practice can lead to distorted results because issues related to the breadth of coverage of the project are not considered. The size of project net benefits in the form of Net Present Value (NPV) should mirror the size of the opportunity to be grasped or the problem to be solved. Therefore, the cost of the project reflects considerations of critical mass to get the job done. Because of a fixed size of the problem to be solved or opportunity to be exploited, doubling the size of the project is unlikely to lead to a twofold increase in NPV. Hence, multiplying net benefits by the poverty measures in Table 1 and estimating a poverty-weighted NPV is perhaps the most informative way to evaluate how the projects rate on the equity dimension while preserving the reality of project size.

The effects of incorporating a poverty criterion are graphed in Figure 2, which contains three versions of the composition of NPV in CIP's research portfolio. The first, on the left-hand side, is based on average project NPV. The second and third entries show the composition of poverty-weighted NPV with the two versions of the TAC measure given in Table 1.

In going from efficiency to the two poverty-modified rankings in Figure 2, several findings emerge. As expected from Table 1, the project that loses the most ground is sweetpotato viruses. Its contribution to total NPV drops from 5.5% to 2% to 3% depending on the poverty measure we use to weigh benefits by. In other words, the project loses about 50% of its importance. Integrated pest management (IPM) of sweetpotato is the main beneficiary of modifying the results for poverty. Its value share rises by 40% from 5% to 7%. Some other projects, including late blight, true potato seed, natural resource management in tropical mountains, and several of the smaller projects, contribute more to the value of CIP's portfolio when benefits are adjusted to reflect the poverty intensity of the recommendation domain.

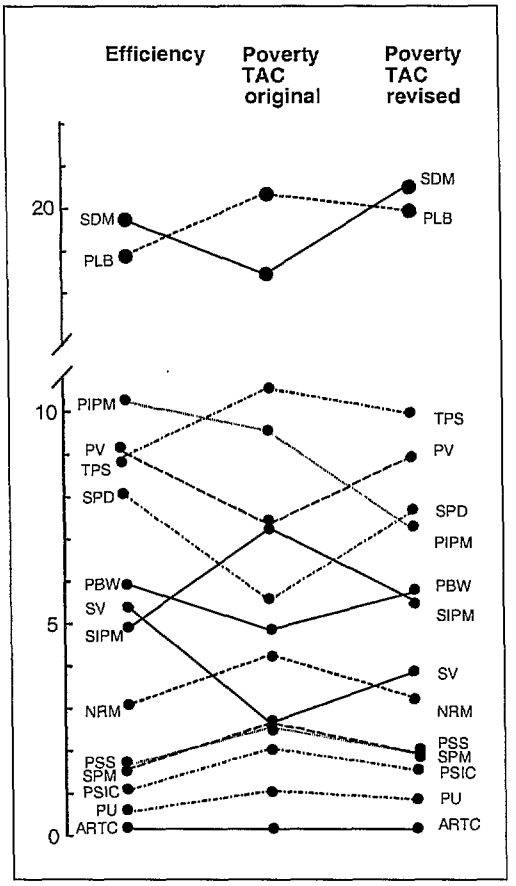

Figure 2. Composition of project benefits (in % of NPV) by one efficiency and two poverty scenarios.

Almost all projects for which China does not figure as a target or spillover country gain in importance when benefits are weighted by the original TAC poverty measure. Potato integrated pest management is the exception because of high projected growth rates in Colombia, which contributes about 30% to project benefits. Strong projected growth results in an estimated poverty weight of only 0.180 for Colombia.

In general, the use of the revised poverty estimates in the third column of Figure 2 leads to the reestablishment of the efficiency ranking. In other words, poverty matters as a modifier when the earlier lower estimates on its incidence in China are used. We prefer to use our revised TAC poverty weight that incorporates the recent rethinking on a higher incidence of poverty in China together with the projected high rates of economic growth.

Concluding Comments

In our application, modifying priority setting for the geographic incidence of poverty did not appreciably change the efficiency-based results in terms of project rankings. The extent to which poverty matters to project outcomes depends on the incidence and severity of poverty in China.

Estimates of the geographic incidence of poverty provide only a rough guideline of the impact of technical change on poor people. For example, poorer farmers grow proportionally more sweetpotato than richer farmers in Shandong Province, and the former have benefited disproportionately more than the latter from a new virus-free propagation program related to research and training in the sweetpotato virus project (Fuglie et al., 1999).

Targeting for the rural poor has been difficult to implement at a more disaggregate spatial level within a country because increasing geographic specificity is usually accompanied by larger sampling errors in national surveys measuring standards of living. Some innovative approaches to poverty mapping, such as combining census data with information from national living standards surveys, show promise in enhancing the resolution of geographic poverty traps (Minot, 1998). These developments should lead to increased precision in factoring the geography of poverty into priority setting in agricultural research.

Computationally, modifying the results of priority setting for poverty is an easy, albeit uncertain, exercise. Disentangling the effects of technological change on the rural and urban poor is considerably more difficult. We plan to draw as many lessons

as possible from our case study research (Walker and Crissman, 1996) to improve the poverty focus of our research and training.

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Research on Potato

Impact on a Changing World

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Characterization of *Phytophthora infestans* Populations in Peru

W. Pérez[1], S. Gamboa[1], M. Coca[2], R. Raymundo[1], R. Hijmans[1], and R. Nelson[1]

The late blight (LB) pathogen (*Phytophthora infestans*) is widely believed to have originated in the Toluca Valley of Mexico and to have spread around the world through two major migrations. The first of these occurred in the nineteenth century and led to the Irish Potato Famine. DNA fingerprinting of global collections of the pathogen has indicated that this pathogen migration led to the worldwide dissemination a single lineage of the pathogen, designated US-1 (the "old" lineage). More recent worldwide migrations of diverse, aggressive and fungicide-resistant strains of *P. infestans* ("new" populations) have made management of the disease increasingly difficult since the 1970's (Fry et al., 1993).

Relatively little is known about contemporary populations of *P. infestans* in Peru; systematic studies have not been conducted since the 1980s. Much of CIP's work on breeding potato (*Solanum tuberosum*) for improved resistance to LB is conducted in Peru, and national programs around the world use the products of this breeding program. It is therefore important to know whether the pathogen populations in Peru are representative of the new pathogen populations that are currently predominant in many countries.

Available data on *P. infestans* populations in Ecuador and Bolivia suggest that both the A1 and A2 mating types might be present in Peru. Recent pathogen population analyses demonstrated that Ecuadorian *P. infestans* populations belonged to the new migration, but showed the A1 mating type (Forbes et al., 1997), while Bolivian *P. infestans* populations belonged to the A2 mating type (Fundación PROINPA [Promoción e Investigación de los Productos Andinos] Bolivia, pers. comm.). Sexual recombination between A1 and A2 strains could lead to increases in pathogen diversity and aggressiveness. It is important, therefore, to know if recombination occurs, and where, and to document the consequences.

The present study was undertaken to characterize Peruvian populations of *P. infestans*. Samples were taken from Pasco, Junin, Cusco, and Puno departments, which cover the central to southern highlands. The sampling sites included CIP's screening sites at Comas and Oxapampa.

Materials and Methods

Sampling

The sampling strategy was designed to allow assessment of the dominant pathogen populations at two sites in the central highlands of Peru (Comas and Oxapampa), and to determine the population structure in the two southernmost departments of Peru (Puno and Cusco). The specific sampling route was based on maps constructed using geographic systems, indicating zones of high estimated LB severity.

Approximately 30 samples each were taken from Oxapampa and Comas. For the departments of Puno and Cusco, a hierarchical sampling strategy was used to allow analysis of diversity within and between fields, sites, and regions. For each department, several localities (neighboring

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villages) were sampled. For each locality, 3 or 4 fields were sampled, with 10 samples taken per field (unless fewer than 10 were found because the level of LB was low).

Each infected leaflet was maintained after collection in a sealed Petri dish containing a layer of 1.5% water agar. Using this method, infected tissue could be maintained for 7-10 days between collection in the field and isolation in the laboratory.

Control DNA samples were used to allow comparison with populations of *P. infestans* elsewhere. G. Forbes (CIP-Quito) and W. Fry (Cornell University, USA) provided these samples.

Pathogen isolation, culture, and storage. Plates with infected tissue were incubated for 7 d at 15-18°C, and sporangia were collected and rinsed on a 10-µm filter. The filter system allowed recovery of isolates, even when the infected tissue was several days old and contaminated with bacteria and saprophytes.

The sporangial suspension was refrigerated at 5-8°C to promote the liberation of zoospores, which were then used to inoculate potato slices (var. Huayro). Tuber slices were incubated at 18°C for 5-7 d in moist chambers. Mycelial fragments were transferred aseptically to Rye B agar and V-8 agar plates. After 1 to 2 wk, growing colonies were transferred to Rye A agar and maintained at 15°C.

Determination of mating type. The mating type of 287 different isolates was determined by pairing each unknown with two isolates of a known A1 mating type (Peruvian isolates 228 and 1696) on 10% clarified V-8 agar. Plates were placed in an incubator at 15°C in the dark and examined for the presence of oospores after 4 wk. A subset (n = 78) of the isolates was tested for a polymerase chain reaction (PCR)-based marker linked to the mating type locus (Judelson, 1996; see below for DNA methods).

Virulence assays

The specific virulence of 114 isolates was determined by inoculation of detached leaflets of a differential set of potato cultivars carrying the 11 known major (R) genes for resistance. Differentials were obtained from the Research Institute for Plant Protection, Wageningen, the Netherlands. Leaflets collected from the middle part of each differential cultivar at 45-60 days of age were inoculated in inverted Petri dishes lined with 1.5% agar water, such that leaflets lay in the lids below the agar layer. Inocula for virulence tests were obtained from tuber slices incubated for 6 to 7 d at 18°C in a moist chamber. A 20-µL drop of a sporangia (approx. 5×10^3 sporangia/mL) was placed on the abaxial surface of each leaflet. Each test included the susceptible cultivar Chata Blanca (containing no known R genes) as a control. The virulence assays were repeated at least twice.

Metalaxyl resistance. A subset (n = 276) of isolates was plated on 10% V-8 agar containing metalaxyl at concentrations of 0, 5, 50, and 100 ppm. Isolates were considered resistant to the systemic fungicide if growth was ≥ 40% of the 0-ppm control at any metalaxyl concentration. Isolates were considered moderately resistant if growth was reduced to <40% of the control value at 100 ppm, but not at 5 ppm. Isolates were considered susceptible if growth was retarded at 5 ppm to <40% of the 0-ppm control.

Isolation of DNA. Cultures of *P. infestans* were grown in pea broth (filtrate from 120-g autoclaved frozen peas per liter) in 5-6 disposable Petri dishes at 18°C in a dark incubator without shaking. Each Petri dish was inoculated with mycelium from an actively growing colony in Rye B agar. After 10 days, the fungal tissue was harvested by vacuum filtration, frozen at -70°C for several hours, and then lyophilized for 4-5 d. Lyophilized tissue was then ground in liquid N_2. DNA was extracted from the powdered mycelium (De Paulo and Powell, 1995).

Polymerase chain reaction (PCR). A subset of the isolates from Puno and Cusco (n = 78) was analyzed by PCR using the primers S1A and S1B (Judelson, 1996). These primers amplify a fragment of DNA of approximately 1,250 bp corresponding to locus S1, which is linked to the A1-determining allele of the mating type locus. It represents a tandemly repeated array of DNA elements that is typically present in a hemizygous state in A1 isolates, but is absent in A2 isolates (Judelson, 1996). The reaction was performed as described by Judelson. DNA from A1 and A2 mating type isolates (positive) and negative (water) controls were used.

Restriction fragment length polymorphism (RFLP). DNA hybridization analysis was performed using the probe RG57 (Goodwin et al., 1992). Three µg of DNA from each isolate were digested with *Eco* RI. Hybridization and detection were done following the protocol of the nonradioactive kit ECL[3].

Amplified fragment length polymorphism (AFLP). The AFLP assay was carried out using the protocol of J. Duncan, Scottish Crop Research Institute[4], with minor modification. The primary template was prepared in a one-step restriction-ligation reaction, with the restriction enzymes *Eco* RI and *Mse* I (Van der Lee et al., 1997). The sequence of the primers used in the preamplification step was E + A and M + A (core sequences: E = 5'-AGACTGCGTACCAATTC; M = 5'-GATGAGTCCTGAGTAA). For selective amplification, the secondary template DNA was amplified with primers containing two selective 3' nucleotides. Results were visualized by silver staining according to the manufacturer's manual (Promega). Three primer combinations were tested: E + AA and M + AC, E + AC and E + CA, and E + AA and M + CA.

3 ECL™ of Amersham, Inc.
4 SCRI, Dundee, Scotland.

Diversity and cluster analysis. Diversity estimates were calculated using the formula of Nei (1987). RFLP and AFLP fingerprints were scored visually for the presence (1) or absence (0) of polymorphic DNA fragments in binary characters. Cluster analysis was conducted using the unweighted pair group method with arithmetic mean algorithm in the software program NTSYS-pc (Rohlf, 1992). Similarity was calculated using Dice coefficient.

Results

A total of 409 isolates were collected in 1997 and 1998 from Pasco, Junin, Cusco, and Puno, contiguous departments spanning the central to southern Peruvian Andes.

A set of 287 isolates collected in 1997 and 1998 were tested for mating type by pairing with two known A1 testers of Peruvian origin. None of them formed abundant, typical oospores in these pairings. The isolates were thus tentatively considered to belong to the A1 mating type. Primers amplifying the S1 locus, which is linked to the *P. infestans* mating type locus, were used to confirm this assignment for a subset of the isolates. No amplification was detected for any of the 70 isolates tested by the PCR assay (as expected for A1 strains), although control amplifications using DNA from A2 strains showed amplification.

A total of 277 of the *P. infestans* isolates were analyzed by DNA fingerprinting using the RFLP probe RG57 (Figure 1). Ten genotypes were detected; these formed 6 groups based on cluster analysis of the RFLP band data (Figure 2). Three genotypes accounted for 95% of the collection. The calculated diversity estimates were thus rather low (H = 0.33). The collections from Pasco and Junin each had a diversity of zero (only one genotype detected); the set from Cusco had a diversity of 0.17; and the set from Puno had a diversity of 0.05. In some cases multiple pathogen lineages were detected in single fields. For example, three lineages were detected in each

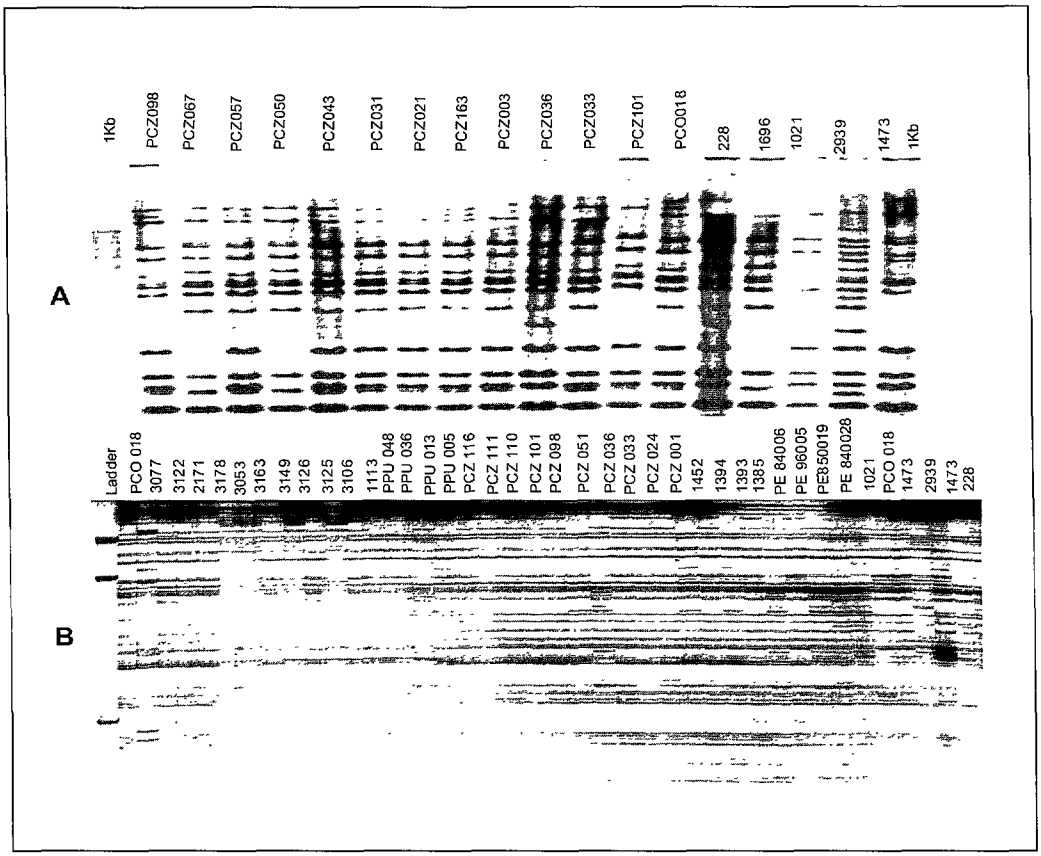

Figure 1. DNA fingerprints obtained by (A) AFLP; and by (B) RFLP analysis using the hybridization probe RG57. The molecular weight standard is a 1 kb DNA ladder.

of two fields sampled in Paucartambo, Cusco. One field had lineages EC-1, PE-3, and PE-6, whereas the other had US-1, EC-1, and PE-3.

Lineages US-1 and PE-3 were dominant in Puno. US-1 is the 'old' lineage, formerly found worldwide (Fry et al., 1993) and previously found to be predominant in Peru (Tooley et al., 1989). The 'new' lineage, EC-1, was dominant in Pasco, Junin, and Cusco. Of the 287 isolates analyzed in this study, 174 (60.6%) belonged to EC-1. Three variants of EC-1 were also detected in the Peruvian collection (Figure 2).

The alleles present in the Peruvian collection were all present in the Cornell-CIP database established by Forbes et al. (1998). Some of these alleles had been detected in isolates from Japan and the Netherlands.

Two hundred and seventy-six isolates were tested for sensitivity to the systemic fungicide metalaxyl. The majority of the isolates tested (230/276 = 82.2%) were resistant. All isolates from Pasco and Junin were fully resistant to metalaxyl. A few isolates from Cusco were moderately resistant (2/111 = 1.8%) or susceptible (5/111 = 4.5%) to the fungicide. A greater proportion of the isolates from Puno were moderately resistant (14/78 = 17.9%) or susceptible (28/78 = 35.9%). These trends correspond to the distribution of pathogen lineages in the different departments.

A set of 114 isolates was tested for virulence on a set of 11 potato lines

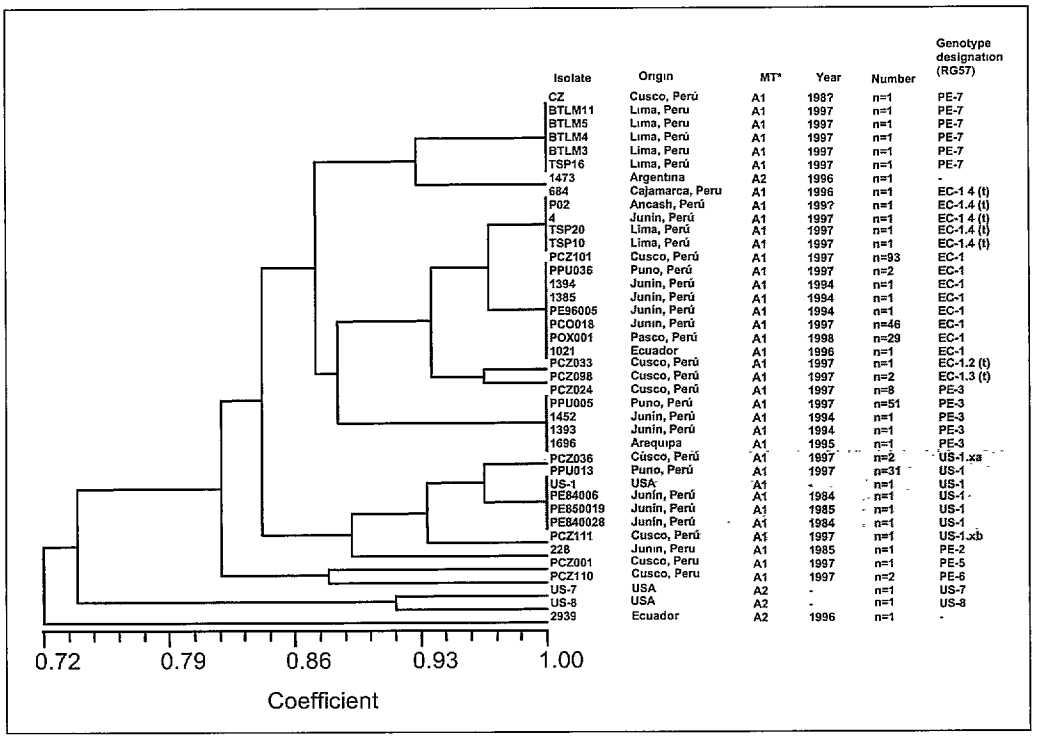

Figure 2. Annotated dendrogram derived from RFLP data obtained using the hybridization probe RG57, using the unweighted pair group method with arithmetic mean algorithm. *MT = mating type.

carrying known resistance genes (differential genotypes). Lineages EC-1, PE-3, and PE-5 showed broad-spectrum virulence (Table 1). Most, but not all, isolates of US-1 showed narrow-spectrum virulence. The isolates resistant to metalaxyl all carried virulence to between 5 and 10 R genes. Isolates moderately resistant or susceptible to metalaxyl were virulent to between two and seven R genes.

To determine whether the AFLP technique would allow greater differentiation of diversity, DNA from 43 isolates was analyzed by AFLP fingerprinting. Among these, 23 were Peruvian isolates; the others were control DNA samples. A comparison of the dendrograms yielded by RFLP and AFLP fingerprinting revealed that, as expected, the AFLP technique allowed greater differentiation (Figure 3).

Discussion

By analyzing subsets of the collection by various methods, it could be concluded that the *P. infestans* population in central and southern Peru is of the new type. Although all of the isolates tested showed the A1 mating type, the pathogen population is now relatively diverse, broadly virulent, and resistant to metalaxyl.

The *P. infestans* population has shifted dramatically since the 1980s. Twenty isolates collected in the department of Junin in 1984 and 1985 showed virulence to between 0 and 2 of the 10 R genes tested, with the greatest number (40%) showing avirulence to all of the genes (Tooley et al., 1989). In contrast, none of the 25 isolates collected from Junin in 1997 showed virulence to fewer than 4 of 11 R genes tested in this study. The majority of the

Table 1. Genotypes of *Phytophthora infestans* defined by DNA fingerprinting using the hybridization probe RG57, and their associated characteristics (virulence, reaction to metalaxyl, site of collection, and corresponding number of isolates).

Genotype	Virulence	Metalaxyl	Site	N=
EC-1	1,2,3,4,5,6,7,8,10,11	R	Comas	1
	1,2,3,4,6,7,8,10,11	R	Comas	8
	1,2,3,4,7,8,10,11	R	Cusco y Comas	13
	1,2,3,4,7	R	Comas	2
	1,3,4,7,8,10,11	R	Cusco y Comas	9
	1.3,4,7,8,11	R	Cusco	3
	1,3,4,7,11	R	Comas	1
	1,3,7,11	R	Cusco	1
EC-1.2	1,3,4,7,8,10,11	R	Cusco	1
PE-5	1,3,4,7,10,11	R	Cusco	1
PE-3	1,2,3,4,7,8,10,11	R	Puno	4
	1,2,3,4,8,10,11	MR	Puno	1
	1,2,4,7,8,10,11	R	Puno	1
	1,4,8,10,11	MR	Puno	1
	1,4,8,10,11	S	Cusco	2
	1,4,8	S	Puno	1
	2,8	S	Puno	1
	8,10,11	S	Puno	1
	8,11	S	Puno	1
US-1	1,2,3,4,7,8,10,11	R	Puno	1
	2,3,11	S	Puno	1
	2,8	S	Puno	2
	4,8	S	Puno	1
	8,11	S	Puno	2

isolates had virulence to either eight or nine R genes.

Among 212 isolates collected from potato in Ecuador between 1990 and 1993, Forbes et al. (1997) detected only three genotypes (two lineages): US-1, EC-1, and a variant of EC-1. The Peruvian collection described here was richer in pathogen diversity, with 10 genotypes detected in the 1997 collections taken from Pasco, Junin, Cusco, and Puno. The pathogen population is also apparently distinct from that present in Bolivia, which is dominated by the A2 mating type. This study was undertaken in part to determine where the Peruvian A1 population might encounter the Bolivian A2 population. Such a site was not identified in this study.

Differentiation was seen even within Peru. Collections from Puno consisted of US-1 and PE-3; those in Cusco consisted of US-1, PE-3, and EC-1; and those from Pasco and Junin consisted of EC-1. Such differentiation should be taken into account when pathogen isolates are moved for experimental or other purposes.

Isolates from Comas and Oxapampa, CIP's key screening sites for LB in Peru, belong to the new lineage EC-1, found also in Ecuador and Colombia (Forbes et al., 1998). The isolates taken from these sites show broad-spectrum virulence and resistance to metalaxyl. Thus, the pathogen population being used by CIP's LB breeding program is representative of the current

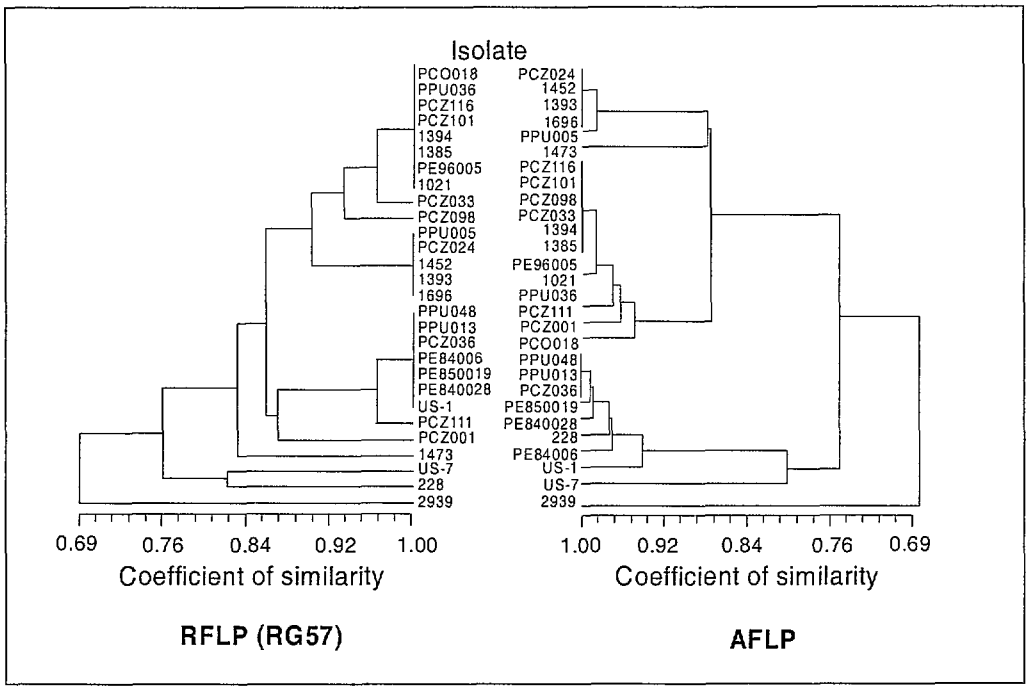

Figure 3. Comparison of dendrograms derived from RFLP analysis using the probe RG57 and from AFLP fingerprinting.

dominant population in the Andes as determined by this study.

The predominant EC-1 lineage showed resistance to the systemic fungicide metalaxyl. Farmers still use fungicides containing metalaxyl. Because the systemic fungicide is mixed with contact fungicide(s) in the products, the ineffectiveness of the more expensive systemic product is not necessarily apparent. Farmers should be made aware that metalaxyl is no longer effective.

In this study, as in others, AFLP fingerprinting revealed more diversity than did RFLP/RG57 (Kamoun et al., 1998). This technique merits further application in population genetics studies of *P. infestans* in cases where discrimination is desirable.

Acknowledgments

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Genetic Diversity among Isolates of *Phytophthora infestans* from Various Hosts in Ecuador

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The late blight (LB) pathogen (*Phytophthora infestans* Mont. de Bary) is globally distributed on potato (*Solanum tuberosum*) and tomato (*S. lycopersicon*). It is believed to have originated in Central Mexico (Goodwin et al., 1992). Elsewhere, populations contain only a subset of the genetic diversity found in Mexico and, until recently, consisted of only the A1 mating type. In the early 1980s, the A2 mating type was detected in Europe (Hohl and Iselin, 1984). New genotypes have since appeared in many countries (Drenth, 1994; Fry,1996; Goodwin, 1997). The development of molecular markers has helped to track the worldwide movements of the pathogen and two major migrations from Mexico have been documented (Goodwin, 1997). The possibility of other migrations from Mexico to South America has also been suggested (Andrivon, 1996; Tooley et al., 1989).

Much of the discussion about the origins and migrations of *P. infestans*, recently reviewed by several authors (Andrivon, 1996; Fry et al., 1993; Goodwin et al., 1997), is based primarily on what is known about isolates from potato. That is largely because LB is an economically important disease on potato in the temperate zone, where most of the research on the pathogen has been carried out, and where there appear to be few alternative hosts. *P. infestans* on tomato has also received considerable attention, but the dynamics of the pathogen population on this host are not clear. Some studies have identified genotypes of the pathogen that infect potato and tomato equally (Fry et al., 1991; Goodwin et al., 1995; Legard et al., 1995; Spielman et al., 1989) suggesting no host specialization. Other studies, however, indicate clear genetic differentiation between potato and tomato populations (Brommonschenkel, 1988; Goodwin and Fry, 1992; Koh et al., 1994; Lebreton and Andrivon, 1998; Oyarzun et al., 1998).

Uncertainty exists about relations between pathogen populations infecting potato and tomato. But even less is known about the possible role that other less important crops and wild species play in the dynamics of the pathogen population. In Central and South America, alternative hosts exist in the same geographical environment as potato and tomato. Noncultivated *Solanum* spp. from this region has been assessed for resistance to *P. infestans* (Colon et al., 1995; Glendinning, 1983), but relatively few studies have been done on pathogen populations attacking these plants in the wild. Disease severity was assessed on seven wild hosts in Mexico, but genetic analyses of the pathogen were not carried out (Rivera-Peña, 1990). Matuszak et al. (1994) included some isolates from wild species in a study on metalaxyl resistance in Mexico. They showed a similar frequency of resistance and sensitivity to isolates from cultivated species, suggesting that the isolates from wild species formed part of the same population.

Genetic characterization of the pathogen populations attacking alternative hosts of *P.*

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infestans could give new insight into biology and life history of the pathogen. For example, recent isolations from *S. brevifolium* and *S. tetrapetalum* in Ecuador have revealed the presence of the A2 mating type (Oyarzun et al., 1998) in addition to the A1 mating type populations attacking potato and tomato in that country (Forbes et al., 1997; Oyarzun et al., 1998). The A2 isolates from *S. brevifolium* and *S. tetrapetalum* differ from all *P. infestans* genotypes represented in a global marker database compiled for this pathogen (Forbes et al., 1998).

In this study, we present information from recent studies in which we have begun to characterize populations of *P. infestans* attacking Solanaceous hosts in Ecuador. Some preliminary data were presented (Erselius et al., 1998). We give here a more detailed description of these populations, and discuss their relatedness to each other and to other clonal lineages worldwide.

Materials and Methods

Hosts of *P. infestans*

All hosts of *P. infestans* are in the genus *Solanum* and include five cultivated species: tomato (*S. lycopersicon*), tomato tree (*S. betacea*), potato (*S. tuberosum*), diploid potato (*S. phureja*), and pepino dulce (*S. muricatum*); and seven wild species: *S. brevifolium, S. caripense, S. colombianum, S. ochrantum, S. tetrapetalum, S. andreanum,* and *S. tuquerrense*. The identification of the wild species is based on comparison with published descriptions (Correll, 1962), and should be considered tentative. All the wild species we studied grow in the same Andean habitat as potato.

Collection and isolation

No predetermined sampling plan was used because distribution of the hosts and disease on host colonies was patchy. Isolates were trapped with potato tuber slices (Forbes et al., 1997), or isolated on selective medium (Oyarzun et al., 1998). Some isolates, notably those from *S. ochrantum*, grew poorly and were very difficult to isolate. A smaller sample of isolates from *S. tetrapetalum* and *S. brevifolium* were described for mating type (Oyarsun et al., 1997). Some of the isolates from potato and tomato were also described (Forbes et al., 1997; Oyarzun et al., 1998). Isolates were maintained for short periods on Rye A or Rye B medium (Caten and Jinks, 1968) at 18°C in the dark, and stored for longer periods (more than 1 mo) on Rye A agar slants at 15°C with a 12-h photoperiod.

Characterization of isolates

At least 10 isolates from each host except *S. tuquerrense* and *S. andreanum* were characterized with three or more genetic and phenotypic markers (Table 1). Restriction fragment length polymorphism (RFLP) fingerprints were obtained for isolates using the moderately repetitive probe RG57 (Goodwin et al., 1992). Two µg of DNA from each isolate were digested with *Eco*RI for 24 h, then underwent electrophoresis on 0.7 or 0.8% agarose gels (56 V, 20 mA) for 24-45 h in 1X TBE. Hybridization and detection were done using the nonradioactive kit ECL™[4] according to the manufacturer's instructions.

Mitochondrial DNA haplotypes were determined by amplification of DNA of each isolate using primers designed for specific regions of the mitochondrial genome of *P. infestans* (Griffith and Shaw, 1998). Digestion of the amplified regions with *Cfo*I, *Msp*I, and *Eco*RI restriction enzymes yields band patterns by which the isolates can be classified into four haplotypes: Ia, Ib, IIa, and IIb (Carter et al., 1990; Griffith and Shaw, 1998).

The internal transcribed spacer region 2 (ITS2) of the ribosomal DNA (rDNA) of *P.*

4 Amersham, Inc.

Table 1. Host species and number of isolates of *P. infestans* assessed with neutral markers.

Host species	Mating type	Gpi[a]	Pep[a]	mtDNA[a]	Fingerprint
S. tuberosum (potato)	185	225	38	107	40
S. lycopersicon (tomato)	125	140	77	92	23
S. phureja	8	8	8	8	6
S. tuquerrense	6	6	2	6	0
S. colombianum	17	13	10	16	5
S. muricatum (pepino dulce)	15	16	11	19	1
S. caripense	28	26	15	22	7
S. betacea (tree tomato)	13	13	9	13	4
S. brevifolium	22	22	22	22	16
S. tetrapetalum	22	13	22	22	11
S. ochrantum	23	5	5	11	4
S. andreanum	11	3	3	11	4

a. Gpi = glucose-6-phosphate isomerase, Pep = peptidase, mtDNA = mitochondrial DNA.

infestans can be amplified using polymerase chain reaction (PCR) and the specific primers ITS3 and PINF2 (Tooley et al., 1997). DNA from isolates was amplified using these primers and a template of about 10 ng DNA as described previously (Tooley et al., 1997).

Isolates were tested for resistance to 5 and 100 mg/ml metalaxyl in 10% unclarified V8 medium and classified as resistant, intermediate, or sensitive. Conditions of the test and criteria for classification were described previously (Forbes et al., 1997).

Isozyme electrophoresis for the enzymes glucose-6-phosphate isomerase (Gpi) and peptidase (Pep) was done on starch gels (Spielman, 1991) and also polyacrylamide gels. Polyacrylamide gel electrophoresis (PAGE) was done using 1 mm thick 7.5% gels with 25 mM Tris-0.19 M glycine, pH 8.8 as separating gel and electrode buffer. Bands were clearer when a 1 cm stacking gel (2.5% acrylamide 0.06 M Tris-HCl, pH 6.7) was used (Davis, 1964). PAGE gels were run with a constant current of 5 mA for 1 h, then increased to 10 mA. Voltage rose continuously throughout, from about 50 to 280 V. Electrophoresis was terminated when the bromophenol blue dye reached the bottom of the gel, about 16 cm. Allozyme genotypes were scored as described by Spielman et al. (1991), which represent the relative mobilities of the enzyme alleles to an allele designated as 100. Isolates with known alleles from the collection of W. E. Fry, Cornell University, were used for comparison.

Gpi, Pep, and mating type data were combined with RFLP fingerprints as described previously (Forbes et al., 1998), to create multilocus genotypes. Multilocus genotypes of isolates from *S. brevifolium* and *S. tetrapetalum* were compared with published genotypes of *P. infestans* taken from a global marker database (Forbes et al., 1998) using cluster analysis. Data analyses and presentation of results were as described previously (Forbes et al., 1998).

Pathogenicity on potato and tomato

Two separate tests of pathogenic aggressiveness were done. In the first, one isolate from tomato was compared with three isolates from *S. muricatum* for pathogenicity on three tomato cultivars (Flora Dade, Caribe, and FMX-193) and one unknown

variety of *S. muricatum*. In the second test, one isolate from potato and six from *S. colombianum* were compared for pathogenicity on three potato cultivars (Chata Blanca, Cruza 148, and Yungay) and a single plant of *S. colombianum*. All potato and tomato cultivars used in these tests are considered free of major resistance genes (R genes for potato and Ph genes for tomato), which interact with pathogen races (Oyarzun et al., 1998). Inoculum was produced on leaves of the original hosts before inoculation. After 7 days, lesion diameter was measured and the presence of necrosis noted.

Results

All leaf lesions from which isolates were taken resembled those produced by infection with *P. infestans*, although wild species showed differing symptoms in the field. Leaves of *S. brevifolium*, for instance, which are small (less than 3 cm long) and thin, blackened rapidly and sporulation was usually visible only at the edges of lesions. *S. ochrantum* leaflets are large (up to 20 cm) and fleshy. They showed extensive chlorosis, with sporangia formation over most of the chlorotic area. All isolates reacted as *P. infestans* and closely-related species in that they all gave the 459 kb band after PCR with the ITS2 region primers (Tooley et al., 1997). Also, they grew poorly or not at all on nitrate medium (Galindo and Hohl, 1985). The morphology of sporangia from all isolates was typical of *P. infestans*—limoniform with a short pedicel (Erwin and Ribeiro, 1996). Sporangial dimensions were consistent with those published for *P. infestans* (Erwin and Ribeiro, 1996) for all isolates except some from tomato, *S. muricatum*, and *S. betacea*, which were all larger than those reported previously. Although this is not conclusive evidence that these isolates were *P. infestans*, no other described species accommodates them better.

Neutral markers

Analyses of the populations with neutral markers resulted in the identification of several multilocus genotypes, which belong to four clonal lineages (Table 2). Very limited amounts of polymorphism for RFLP fingerprints were found within the clonal lineages attacking potato, tomato, and the wild species *S. brevifolium* and *S. tetrapetalum*. The limited polymorphism with the populations attacking potato and tomato confirms previous reports (Forbes et al., 1997; Oyarzun et al., 1998).

Only two plant species were associated with more than one clonal lineage of the pathogen; in both cases the lineages were US-1 and EC-1. One plant species was *S. ochrantum*, for which there was a geographical separation of the two lineages (EC-1 is found in more northerly sites). The other was *S. andreanum*, for which both lineages were found at the same site. Each

Table 2. Clonal lineages of *Phytophthora infestans* found in Ecuador to date and host species from which they were isolated.

Clonal lineage	Gpi[a]	Pep[a]	MtDNA[a]	Hosts
US-1	86/100	92/100	IB	Tomato, *S. muricatum, S. caripense, S. ochrantum, S. andreanum*
EC-1	90/100	96/100	IIA	Potato, *S. colombianum, S. tuquerrense, S. andreanum, S. ochrantum, S. phureja S.* spp.
EC-2	100/100	76/100	New	Potato[b], *S. phureja*[b], *S. brevifolium, S. tetrapetalum*
EC-3	86/100	76/100	IA	*S. betacea*

a Gpi = glucose-6-phosphate isomerase, Pep = peptidase, mtDNA = mitochondrial DNA.
b. Only one isolate of this genotype found on this host.

of the other host plant species was attacked by only one clonal lineage of *P. infestans*.

In contrast, three of the four clonal lineages of the pathogen were associated with more than one host species. For example, isolates from potato, *S. phureja, S. tuquerrense,* and *S. colombianum* all belonged to the EC-1 clonal lineage previously described on potato in Ecuador (Forbes et al., 1997). Isolates from tomato, *S. caripense,* and *S. muricatum* belonged to the US-1 clonal lineage, previously described as the primary pathogen population attacking tomato in Ecuador (Oyarzun et al., 1998). Isolates from *S. brevifolium* and *S. tetrapetalum* formed a distinct group belonging to an unreported clonal lineage that we here name EC-2. A variant of EC-2 with three RFLP band differences has been named EC-2.1. We believe that the EC-2.1 genotype has evolved within the EC-2 clonal lineage.

Isolates from *S. betacea* were all A1 mating type and had the Gpi genotype 86/100, which is generally associated with the US-1 clonal lineage (Goodwin et al., 1994). They resembled the EC-2 lineage for some characteristics, including the unusual Pep genotype 76/100 and three novel RFLP bands (Figure 1). Before this study, these RFLP bands had been found only for EC-2 (unpubl.). The RFLP fingerprint of isolates from *S. betacea* also lacked band 1. The absence of band 1 had not been reported previously for clonal lineages of *P. infestans* (Forbes et al., 1998). The genotype of these isolates from *S. betacea* has been designated EC-3.

The patterns described here were consistent for repeated isolations. However, two exceptions occurred. We isolated the EC-2 lineage once from potato in Pichincha Province (central Ecuador) and once on *S. phureja* in Loja Province (southern Ecuador). The potato EC-2 isolate was only weakly pathogenic when reinoculated on potato. The isolate from *S. phureja* has not yet been reinoculated on that host.

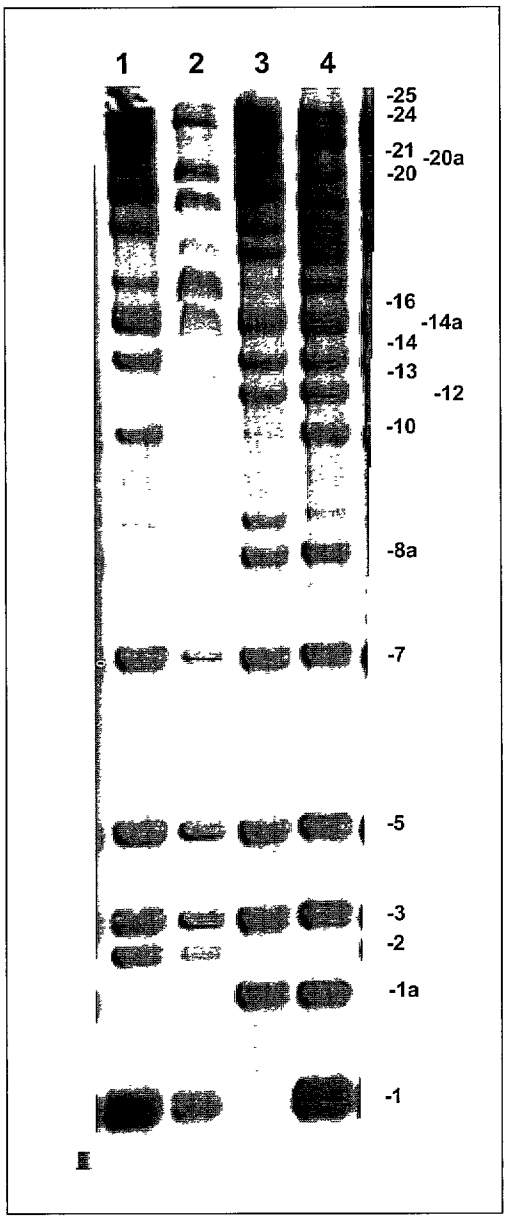

Figure 1. RFLP banding patterns from probe RG57 representing principal genotypes of three clonal lineages of *Phytophthora infestans* found in Ecuador. Lanes 1 and 2 = EC-1, lane 3 = EC-3, and lane 4 = EC-2. Bands 1a, 8a, and 20a are unique to EC-2 and EC-3.

Multilocus genotypes, consisting of RFLP, allozyme, and mating type marker data, which are found in Ecuador (US-1, EC-1,

EC-2, EC-2.1, and EC-3) and those found in a global database of *P. infestans* marker data (Forbes et al., 1998) were compared by cluster analysis (Figure 2). EC-2, EC-2.1, and EC-3 were distant to all other known genotypes reported thus far from clonal populations. EC-3 clustered with EC-2 and EC-2.1 because all contain the three unique RFLP bands and the unusual 76/100 Pep genotype. Because these alleles are unique in the database of published genotypes from clonal lineages (Forbes et al., 1998), it is not surprising that the new genotypes from Ecuador should cluster away from all others.

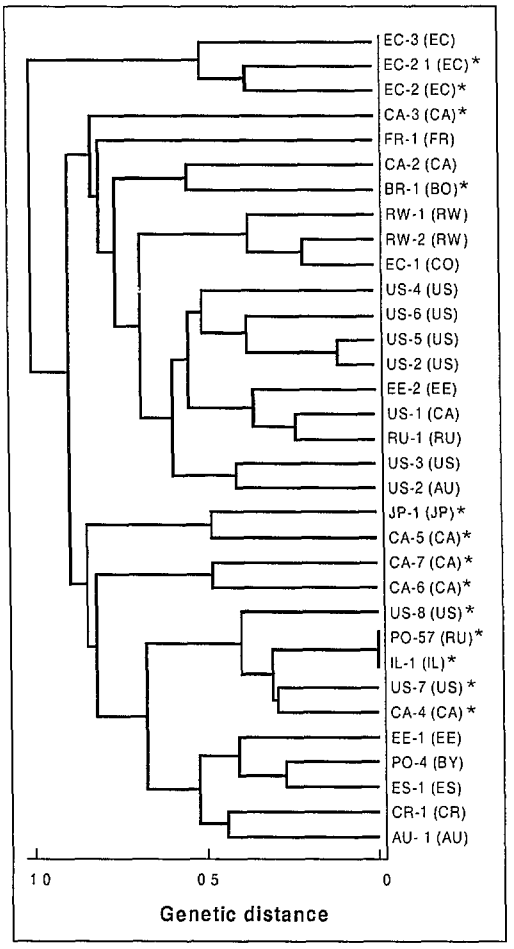

Figure 2. Cluster analysis of clonal genotypes of *Phytophthora infestans*, including isolates from wild hosts in Ecuador, based on a distance coefficient (Jaccard) for multilocus genotypes consisting of RFLP fingerprint with the RG57 probe, mating type (asterisks indicate A2 mating type), and dilocus allozyme genotype (Gpi and Pep). Genotype labels are the International Organization for Standardization (ISO) two-letter country code plus a unique number (Forbes et al., 1998).

Metalaxyl resistance

In general, the populations of *P. infestans* that we studied were sensitive to the systemic fungicide metalaxyl. Some isolates from all species had intermediate resistance, but only five isolates were resistant, and all came from potato. High frequencies of metalaxyl resistance in the EC-1 lineage have been reported previously (Forbes et al., 1997).

Pathogenicity

The primary purpose of pathogenicity tests was to detect host specificity among isolates of the same clonal lineage from different hosts. Two systems were tested in this study. The first involved one isolate from tomato and three from *S. muricatum* (*S. mur.*) (US-1). The second involved one isolate from potato and six from *S. colombianum* (*S. col.*) (EC-1). In the first test, each isolate was most aggressive (based on lesion length) on its own host. The isolates from tomato did not attack *S. muricatum*, but isolates from *S. muricatum* attacked tomato, although less aggressively than the isolate from this host (Figure 3). The interaction between isolate source and inoculated species was highly significant ($P = 0.0002$).

The second test gave different results. Isolates from potato and *S. colombianum* attacked each host with equal aggressiveness (Figure 3). The interaction between isolate source and inoculated species was not significant ($P = .7355$).

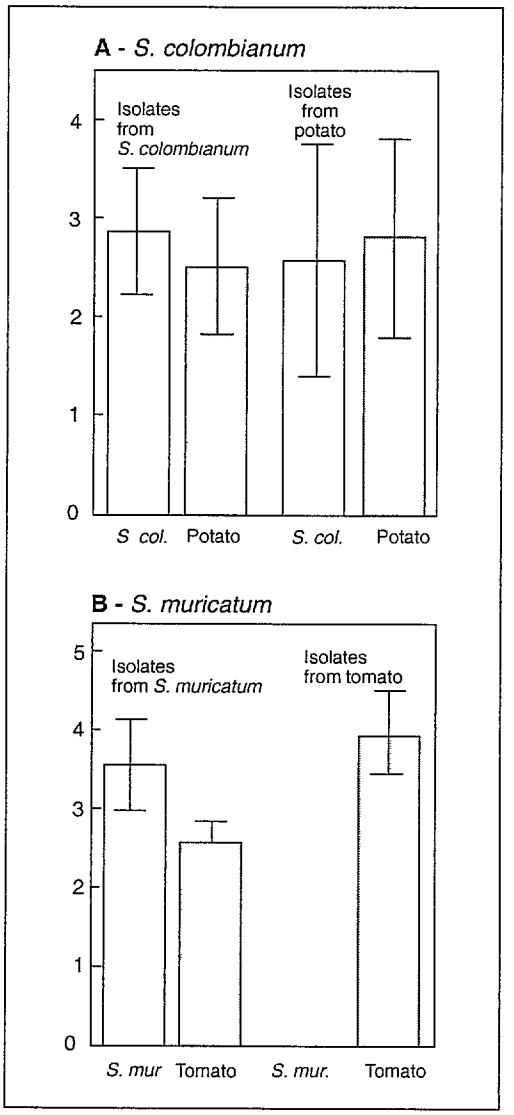

Figure 3. (A) Histogram of mean lesion length on leaflets on potato and *S. col.* plants caused by isolates collected from each host in Ecuador. (B) Histogram of mean lesion length on leaflets of tomato and *S. mur.* plants caused by isolates of *P. infestans* collected from each host in Ecuador. Error bars represent 95% confidence intervals.

Discussion

This study revealed that all isolates assessed belong to one of two lineages previously reported for Ecuador: US-1 and EC-1 (Forbes et al., 1997), and two new lineages which are reported for the first time here: EC-2 from *S. brevifolium* and *S. tetrapetalum* and EC-3 from *S. betacea*. At this time, EC-3 lineage is represented by one genotype as no polymorphism within the lineage was detected. Each lineage, except EC-3, was associated with more than one host, but rarely were hosts associated with more than one lineage.

Isolation of pathogen genotypes from a host is not an indication that they are primary pathogens of that host. There is very strong host specificity in the population of *P. infestans* in Ecuador for potato and tomato, yet on rare occasions we have found potato genotypes on tomato (Oyarzun et al., 1998).

Pathogens may at times infect alternative hosts, albeit weakly. When we collected isolates from *S. ochrantum* in Carchi (all were EC-1), lesions were difficult to find. Most of them occurred within the plant canopy, not on exposed leaves. When these isolates were reinoculated on leaves of *S. ochrantum*, they were not as aggressive as the US-1 isolates coming from the same host in the central part of the country. Therefore we assume that the US-1 population is the primary pathogen population of *S. ochrantum*, and that the EC-1 population is only weakly pathogenic on *S. ochrantum*. Disease on wild hosts is generally patchy, and the US-1 population may not have been present in Carchi when we sampled.

The EC-1 isolates from *S. ochrantum* are identical for our markers to those from potato; both hosts may be attacked by the same population. If this were true, *S. ochrantum* would have been exposed to abundant aerial inoculum because there is extensive potato production in the region. Therefore, EC-1 may be a weak pathogen of *S. ochrantum*, causing some lesions on older leaves growing in highly humid conditions within the canopy.

The EC-2 isolate from potato was also found to be weakly pathogenic when reinoculated on potato, indicating that it is

probably not a primary pathogen of that host. We are analyzing pathogenic aggressiveness with EC-1 and US-1 isolated from *S. andreanum* to determine if one lineage represents the primary pathogen population of that host.

Our analyses with neutral markers gave little insight into host specificity within clonal lineages in Ecuador. To get more information on host specificity, we did two pathogenicity trials, each in the form of a quadratic check, similar to what was done to confirm host specificity for potato and tomato in Ecuador (Oyarzun et al., 1998). One test clearly demonstrated that isolates of US-1 attacking tomato are different from isolates of US-1 attacking *S. muricatum*. The results of this test are consistent with field observations. We have seen the two plant species growing in close proximity and only one infected with *P. infestans*. We do not know if this differential reaction is due to virulence (different Ph genes) or represents differences in quantitative host specificity, as in the case of potato and tomato (Oyarzun et al., 1998).

The second aggressiveness test failed to demonstrate a difference between isolates attacking potato and those attacking *S. colombianum*. Therefore, we conclude that the same pathogen population attacks both cultivated potato and *S. colombianum*. Future research will involve more pathogenicity trials of this type to determine whether other cases of host specificity can be detected within clonal lineages in Ecuador. We also plan to use DNA fingerprinting, using the amplified fragment length polymorphism (AFLP) technique in this endeavor. For now, however, phenotypic evaluation of pathogenic aggressiveness is the tool that gives the greatest discrimination of host-specific populations occurring within the same lineage.

Conclusions

The genetic diversity of this pathogen in Ecuador is extremely wide. Four clonal lineages were found in association with different host species in the genus *Solanum*. The dissimilarity between the novel clonal lineages (EC-2 and EC-3) and other known clonal lineages leads us to the hypothesis that if the origin of EC-2 is Mexico, its introduction into South America must have involved an unreported migration. Both lineages are quite different from any described to date. It appears highly unlikely that either was introduced on potato tubers, which is considered the primary means of long distance transport of this pathogen (Fry et al., 1993). It is extremely difficult to speculate on the time when EC-2 and EC-3 were introduced into South America, or on the mechanism of introduction.

EC-2 and EC-3 are also of interest as clonal lineages because of their similarity to each other. Both share three novel RFLP bands and the unusual 76/100 Pep genotype. We have no good hypotheses to explain why EC-2 and EC-3 are genetically similar. Another interesting aspect of EC-3 is that it possesses the 86 Gpi allele. Previously, this allele had been associated with only the US-1 clonal lineage, and a few others which are very similar to it (Goodwin, 1997), although it has also been found in Mexico (Forbes et al., 1998).

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Host Specificity of *Phytophthora infestans* on Tomato and Potato in Uganda and Kenya

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Host specificity of *Phytophthora infestans*, the potato late blight (LB) pathogen, has obvious epidemiological consequences in areas where two or more potential hosts grow in close proximity. If inoculum can pass readily from one host to the other, or if more than one host is cultivated, then disease management activities must take both hosts into consideration. In addition to that practical consideration, specificity of *P. infestans* to potato (*Solanum tuberosum*) and tomato (*S. lycopersicon*) is an interesting phenomenon for study because it appears to be caused by quantitative differences in epidemic components, rather than an ability to cause disease (Oyarzun et al., 1998). Elucidation of the mechanisms that govern this type of host specificity could provide new insights into the nature of host-pathogen relations.

In spite of numerous studies on host specificity of *P. infestans* to potato and tomato, several aspects remain unclear. Many isolates attacking tomato and potato in some regions of the Netherlands (Fry et al., 1991) and in North America (Goodwin et al., 1995a; Legard et al., 1995) could not be distinguished by restriction fragment length polymorphism (RFLP) fingerprint, dilocus allozyme genotype, or mating type. That implies they might be of the same pathogen population. Furthermore, many isolates collected from tomato in North America were highly aggressive on potato in a detached leaf assay (Legard et al., 1995), again indicating that one population attacks both hosts. In contrast, the same genetic markers have shown that distinct genotypes are associated with each host in Brazil (Brommonschenkel, 1988), northwest Mexico (Goodwin et al., 1992a), the Philippines (Koh et al., 1994), one region of the Netherlands (Fry et al., 1991), France (Lebreton and Andrivon, 1998), and Ecuador (Oyarzun et al., 1998).

Studying the population of *P. infestans* in North America, Legard et al. (1995) concluded that pathogenic aggressiveness on tomato evolved from within the potato-aggressive populations. All tomato-aggressive genotypes were still aggressive on potato, so aggressiveness on tomato was not associated with any measurable loss in aggressiveness on potato. However, this model of evolution toward aggressiveness on tomato is not universally accepted. Turkensteen (1973) argued that if a genotype of *P. infestans* were able to acquire equal aggressiveness on both hosts with no loss of fitness, it would rapidly replace other genotypes that are aggressive on only one host. The presence of host-specific populations in many parts of the world supports the hypothesis that dually aggressive genotypes do not readily occur, or if they occur they are less fit than those occurring on one host are. Geographical separation of hosts could theoretically lead to separate pathogen populations. In Ecuador, however, tomatoes and potatoes growing in close proximity to one another were found to have separate pathogen populations (Oyarzun et al., 1998).

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In cases where host specificity has been corroborated with molecular markers, the pathogen genotypes were from different clonal lineages. This adds an unquantified variable, because it is not known if the highly specialized forms of the pathogen evolved sympatrically, or were introduced from separate sources. An ideal system to study host specificity would involve two host-specific populations that evolved sympatrically. Potatoes and tomatoes are grown together or in close proximity to one another on small farms in Uganda and Kenya. Our preliminary investigation (unpublished data) indicated that isolates of *P. infestans* from that region may provide such a system. The objective of the research reported here was to test the hypothesis that potato and tomato populations from Kenya and Uganda differ but belong to the same clonal lineage. We also discuss evidence supporting sympatric evolution of host-specific populations in this region.

Materials and Methods

Collection of isolates

Data reported here come from two collection events. The first took place in March 1995 in Kenya and Uganda. A sample of 14 isolates from tomato and 10 from potato were collected in Kenya; 7 isolates from tomato and 8 from potato were collected in Uganda. The specific regions within countries were recorded (data available upon request). They are not reported here because we did not find variability associated with collection site. A second collection trip was made in Kenya and Uganda in late 1997 and early 1998. Fifty-eight isolates were collected on this trip, all from potato.

P. infestans was isolated from potato leaves by trapping the isolates in potato tuber slices (Forbes et al., 1997). *P. infestans* from tomato grew poorly on tuber slices and was, therefore, isolated by placing 1 cm^2 pieces of infected tissue on a selective medium (Oyarzun et al., 1998).

Characterization of isolates

RFLP fingerprints were obtained for all isolates from both collections using the moderately repetitive probe RG57 (Goodwin et al., 1992b). Two µg of DNA from each isolate were digested with *Eco*RI for 24 h, then underwent electrophoresis on 0.7 or 0.8% agarose gels (56 V, 20 mA) for 24-45 h in TBE 1X. Hybridization and detection were done using the nonradioactive kit ECL™[5] according to the manufacturer's instructions.

Mitochondrial DNA (mtDNA) haplotypes were determined for the 1995 collection by amplification of DNA of each isolate using primers designed for specific regions of the mitochondrial genome of *P. infestans* (Griffith and Shaw, 1998). Digestion of the amplified regions with *Cfo*I, *Msp*I and *Eco*RI restriction enzymes yielded band patterns by which the isolates could be classified into four haplotypes: Ia, Ib, IIa, and IIb (Carter et al., 1990; Griffith and Shaw, 1998).

Isozyme electrophoresis for the enzymes glucose-6-phosphate isomerase (Gpi) and peptidase (Pep) was done on cellulose acetate (Goodwin et al., 1995b) for the 1997-98 collection and on polyacrylamide gels for the 1995 collection. Polyacrylamide gel electrophoresis (PAGE) was done using 1 mm thick 7.5% gels with 25 mM Tris-0.19 M glycine, pH 8.8 as separating gel and electrode buffer. Bands were clearer when a 1 cm stacking gel (2.5% acrylamide 0.06 M Tris-HCl, pH 6.7) was used (Davis, 1964). PAGE gels were run with a constant current of 5 mA for 1 h, then increased to 10 mA. Voltage rose continuously throughout, from about 50 to 280 V. Electrophoresis was terminated when the bromophenol blue dye reached the bottom of the gel, about 16 cm. Allozyme genotypes for both cellulose acetate and PAGE were scored as described in Spielman (1991), which represent the relative mobilities of the enzyme alleles to

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an allele designated as 100. Isolates with known alleles from the collection of W. E. Fry were used for comparison.

The isolates collected in 1997-98 were tested for resistance to 5 and 100 mg/ml metalaxyl in 10% unclarified V8 medium and classified as resistant, intermediate, or sensitive. Conditions of the test and criteria for classification were described previously (Forbes et al., 1997).

Two pathogenicity tests were done to compare aggressiveness of a subset of isolates from 1995 on potato and tomato. In the first, five potato and five tomato isolates were inoculated on three potato cultivars (Yungay, Cruza-148, and Chata Blanca) and three tomato cultivars (Caribe, Flora Dade, and FMX-193). The second test involved six isolates from the 1995 collection. Four were repeated from the first test (two from each host) and two (one from potato and one from tomato) were assessed for the first time. The same potato and tomato cultivars were used in the second test. Experimental design, statistical models, and evaluation procedures were as reported previously (Oyarzun et al., 1998).

Results

All isolates collected in 1995 and 1997-98 belonged to the US-1 clonal lineage, based on RFLP fingerprint (Figure 1), Pep phenotype of 92/100, and, for the 1995 collection, an mtDNA haplotype of IB (Goodwin et al., 1994; Griffith and Shaw, 1998). All isolates from potato had the US-1 Gpi phenotype 86/100 (Goodwin et al., 1994), which is typical of US-1, but all tomato isolates were 100/100 at this locus (Figure 2).

A high level of metalaxyl resistance was found among the isolates collected from potato in 1997-98 (those collected in 1995 were not assessed). The overall percentage of resistant isolates was 73%, with 86% in Kenya and 59% in Uganda. Metalaxyl resistance was found in all districts

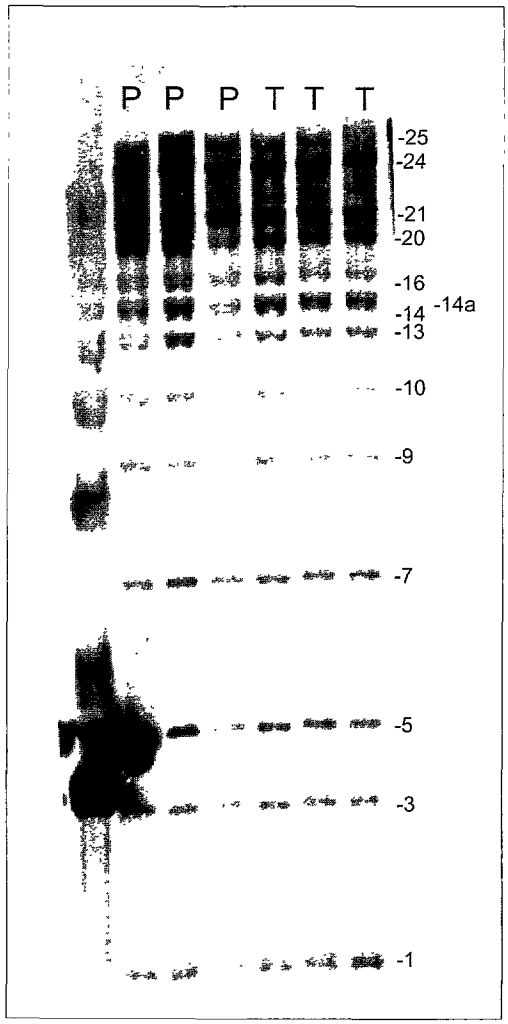

Figure 1. RFLP fingerprints of three potato (P) and three tomato (T) isolates collected in Kenya and Uganda in 1995. These are the same isolates shown in Figure 2. All represent a typical US-1 fingerprint. Numbers on the right represent conventional numbering of bands (Goodwin et al., 1992).

sampled. There were no pronounced differences between these areas. We have no quantitative information on the use of metalaxyl on potato in the two countries, but workers in the region believe that metalaxyl is seldom used on either crop (P. Ewell, CIP, Nairobi, pers. comm.).

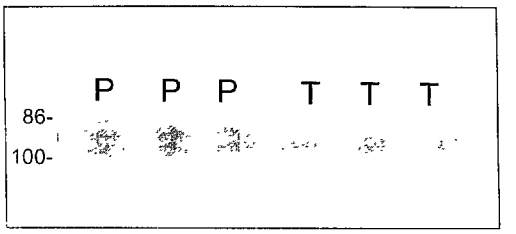

Figure 2. Glucose-6-phosphate isomerase banding pattern for three potato and three tomato isolates collected in Kenya and Uganda in 1995. These are the same isolates shown in Figure 1. The three potato isolates have an 86/100 phenotype; the tomato isolates are 100/100. Electrophoresis was done with cellulose acetate.

The 1995 sample consisted of A1 isolates only. The isolates from the 1997-98 sample were tested for mating type at Cornell University and also found to be A1. Earlier they were paired with an A1 tester in Kenya, and the number of oospores was low (1-10/plate) in 20% (13/66) of the pairings. Various oospore counts were also found in 31% (18/58) of the 1997-98 isolates of single cultures. A few isolates produced hundreds or even thousands of oospores in single culture. However, selfing and mating results were not strictly repeatable.

The interaction between the host and the source of the pathogen (potato or tomato) was evident by visual examination of plotted means of lesion length (Figure 3). This interaction was highly significant for both tests at $P < 0.0001$ (Table 1). Lesions on both hosts produced by isolates from potato were always accompanied by noticeable necrosis (Figure 3). Isolates from tomato produced no necrosis on tomato leaves during the 7 days after infection, even though abundant sporulation could be seen. On the other hand, when inoculated onto potato, these same isolates induced necrosis. We conclude that host specificity is quantitative rather than qualitative, because isolates were more aggressive on their primary hosts. This is similar to a situation recently described in Ecuador

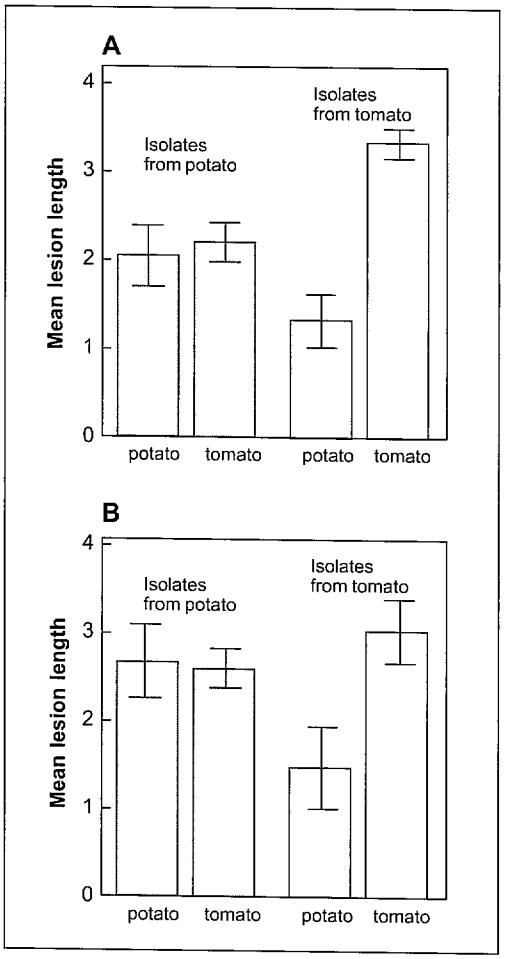

Figure 3. Histograms of mean lesion length on potato and tomato plants caused by isolates of *P. infestans* collected from potato in Kenya and Uganda in 1995. (A) Data from seven isolates each from tomato and potato. (B) For the second test, four isolates were repeated (three from each host), and two new isolates were assessed (one from each host). Error bars represent 95% confidence intervals.

(Oyarzun et al., 1998) for isolates of different clonal lineages attacking potato and tomato.

Discussion

Our data clearly show that the pathogen populations attacking potato and tomato in Kenya and Uganda are different from each

Table 1. Analyses of variance from two experiments that test effects of origin (potato or tomato) of isolates of *Phytophthora infestans* and inoculated host species (potato or tomato) on diameter of lesions (cm) in a detached-leaf inoculation assay involving isolates collected in Kenya and Uganda in 1995.

Source	Degrees of freedom	Mean square	F Value	Pr > F
First experiment				
Isolate origin (O)	1	3.71	NT[a]	
Host species (H)	1	17.23	NT	
O * H	1	21.19	58.78	0.0001
Isolate embedded in Origin (I_O)	8	3.37	9.36	0.0001
Plant embedded in host (P_H)	4	14.43	40.00	0.0001
I_O * P_H	43	0.36	NT	
Residual error[b]	60	0.25		
Second experiment				
Isolate origin (O)	1	1.52	NT	
Host species (H)	1	42.9	NT	
O * H	1	30.6	63.52	0.0001
Isolate embedded in Origin (I_O)	4	5.43	11.27	0.0001
Plant embedded in host (P_H)	4	3.27	6.79	0.0001
I_O * P_H	24	0.48	NT	
Residual error[b]	108	0.38		

[a] NT = not tested. Main effects of isolate origin and host species were not tested because of their highly significant interaction, O * H. This interaction was tested using the mean square for the interaction between individual isolates and plants, Isolate * Plant (O*H). This interaction was also used to test Isolate (O), isolate embedded in origin, and Plant (H), plant genotype embedded in plant species.

[b] Based on variance among petridishes, which are pseudo replications of the experiment.

other. Although all isolates had the US-1 RFLP fingerprint, isolates from tomato and potato could be separated based on Gpi genotype, aggressiveness on the two hosts, symptoms on tomato, and even isolation characteristics. Isolates from potato were easily trapped on potato tuber slices; isolates from tomato were most easily isolated with selective medium.

Specialization of *P. infestans* on potato and tomato has been detected at other sites (Brommonschenkel, 1998; Fry et al., 1991; Goodwin et al., 1992a; Koh et al., 1994; Oyarzun et al., 1998). In those cases the two populations belonged to different clonal lineages, or were different genotypes from areas where sexual recombination occurs. Sub-Saharan Africa seems to be the only area studied to date where two coexisting, host-specific populations belong to the same clonal lineage.

Although our research demonstrates a common origin for these populations, it does not prove that they developed sympatrically. The population attacking tomato could have been an introduced population that evolved independently of potato LB. We believe, however, that it is more likely that the tomato population in Kenya and Uganda evolved from the potato population and was not introduced. The principal reason for this is the apparent scarcity of transport mechanisms by which it would have been introduced. We are unaware that tomato plantlets or fruits are imported into this region, nor is there evidence that *P. infestans* can be transported with tomato seed.

Potato tubers are generally considered to be the primary long-distance transport mechanism for the LB pathogen (Fry et al., 1993). Reduced aggressiveness of the tomato population on potato foliage and tubers argues against this type of transport. It is more likely that *P. infestans* was introduced into the region on potato and then evolved aggressiveness on tomato. This view is consistent with that of the authors of a recent study in the USA (Legard et al., 1995), who proposed that tomato aggressiveness develops within potato populations. Our data, however, indicate that aggressiveness on tomato in Kenya and Uganda is associated with a loss of aggressiveness on potato. Our isolates from tomato were less aggressive on potato than those isolated from the potato host. Our tomato isolates also did not grow well in potato tubers, as evidenced by the difficulty in isolating them with tuber slices.

The time at which the mutation of the Gpi locus occurred remains unclear, as well as factors which may have led to the apparent universality of 100/100 Gpi phenotype within the tomato population. Mutation from 86/100 to 100/100 within the US-1 clonal lineage has been reported previously (Forbes et al., 1998; Goodwin et al., 1994). There is no evidence, nor logic we know of, that would suggest a genetic linkage between tomato aggressiveness and the Gpi genotype 100/100. In South America, the 86/100 Gpi genotype occurs in the US-1 clonal lineage attacking tomato (Brommonschenkel, 1988; Oyarzun et al., 1998).

Our data also demonstrate that the populations of *P. infestans* in this region are not substructured geographically. In none of the characters we assessed was there any detectable polymorphism that could be associated with a geographical region. The area that was sampled in Uganda is in the southwestern part of the country, the principal potato-growing region. It is contiguous with the potato-growing region of Rwanda, so our results can probably be extrapolated to Rwanda.

The high level of resistance to metalaxyl is noteworthy because it demonstrates the degree to which this characteristic can develop within the US-1 lineage. Metalaxyl resistance has frequently been associated with other lineages or sexual populations that have occurred as a result of recent migrations of the pathogen (Fry et al., 1993; Goodwin, 1997).

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Genotype by Environment Reaction of Potato to the Late Blight Pathogen

G.A. Forbes[1]

Quantitative or horizontal resistance of potato (*Solanum tuberosum*) to the oomycete *Phytophthora infestans* (Mont.) de Bary, the causal agent of late blight (LB), does not confer absolute protection. It is generally considered effective, however, against all known races of the pathogen (Forbes and Jarvis, 1994). In contrast, qualitative or vertical resistance to the pathogen is highly race-specific and is rapidly rendered ineffective because of changes in the pathogen population (Goodwin et al., 1995; Wastie, 1991). The effectiveness of quantitative resistance against different populations of the pathogen was demonstrated recently both in Europe (Turkensteen, 1993) and North America (Inglis et al., 1996). In both cases, the authors demonstrated that resistance rankings of very old cultivars have remained constant over time, although pathogen populations have changed (Fry and Goodwin, 1997).

One aspect of quantitative resistance that is still unclear is the degree to which a cultivar selected as resistant at one site will also be resistant at another. Haynes et al. (1998) recently demonstrated that resistance was stable at eight sites in the USA. Another experiment showed that cv. Alpha was more resistant in New York, USA, than in Toluca, Mexico, relative to three other cultivars that behaved similarly in both states (Parker et al., 1992). It appears, however, that no studies of this type have been done for a broader geographic range.

In response to the lack of information on the stability of quantitative resistance to LB, CIP and a group of collaborators developed a genotype by environment (GXE) project to study resistance to *P. infestans* in a standard set of cultivars at several sites worldwide. These cultivars differ in their levels of resistance. Their resistance has not broken down over time and is therefore considered to be quantitative, although that has not been confirmed by genetic studies. The cultivars possess few or no R genes that confer qualitative resistance.

Materials and Methods

Participants

Eleven sites were included in the study, but not all were used in each of the 3 yr of the experiment (Table 1). Fourteen potato cultivars were used in the study: Alpha, Bintje, Robijn, Eigenheimer, Record and Pimpernel from Netherlands; Stirling, Teena, and Torridon from Scotland; Chata Blanca and Yungay from Peru; Monserrate from Colombia; Seseni from Democratic Republic of the Congo, and Cruza 148, bred in Mexico and now grown extensively in sub-Saharan Africa. The Scottish Crop Research Institute (SCRI), National Agricultural Research Institute (INRA) in France, and CIP provided tubers or in vitro material. Investigators in the northern latitudes found it was difficult to get some of the short-daylength materials to produce tubers. In those cases plant cuttings were used instead of tubers.

A similar experimental design was used at each site, but there were some site-specific modifications. Cultivars were sown in plots of four or more plants in a

1 CIP, Quito, Ecuador

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Table 1. Sites and trial (years) of participation in the assessment of phenotypic stability of resistance in potato to *Phytophthora infestans.*

Participating institution[a]	Country	Latitude	Longitude	Altitude (m)	Cultivar set used in each trial[b] Trial 1	Trial 2	Trial 3
INTA, Balcarce	Argentina				1,2	1,2	1,2
Agriculture Canada	Canada	46° 00′ N	63° 00′ W	15	1,2	1,2	-
Landbrugets Kartoffelfond	Denmark	55° 42′ N	09° 12′ E	79	-	1,2	1,2
International Potato Center	Ecuador	00° 22′ S	78° 33′ W	3,058	1	1,2	-
INRA, Ploudaniel	France	48° 00′ N	04° 00′ W	36	1	1,2	1,2
INRA, LeRheu	France	48° 01′ N	01° 43′ W	100	-	1,2	1,2
PICTIPAPA	Mexico	19° 12′ N	99° 35′ W	2,640	-	-	1,2
SCRI	Scotland	55° 23′ N	4° 32′ W	110	1,2	1,2	1,2
CPRO, Wageningen	Netherlands				1,2	-	-
Cornell University	USA				1	1,2	1,2
Washington State University	USA				-	1,2	-

a. INTA = Instituto Nacional de Technología Agropecuaria, Argentina; INRA = Institut National de la Reserche Agronomique, France; PICTIPAPA = Programa International Cooperation del Tizon Tordío de la Papa, Mexico; SCRI = Scottish Crop Research Institute; CPRO = Centre for Plant Breeding and Reproduction Research, Netherlands

b. Cultivar set 1 = Bintje, Chata Blanca, Cruza 148, Monserrate, Sesini, Alpha, and Yungay; cultivar set 2 = Stirling, Teena, Torridon , Record, Robijn, Pimpernel, and Eigenheimer.

randomized complete block design with 3 or 4 replications. In some cases spreader rows planted between the plots were inoculated. In other cases the plants being studied were inoculated. In a few cases plants were left to natural infection.

In the 1st yr, distribution to some sites was incomplete. Therefore not all cultivars were assessed at all sites. During the 1st yr seven cultivars (set 1), Bintje, Chata Blanca, Cruza 148, Monserrate, Sesini, Robijn, and Yungay were assessed at seven sites (Argentina, Canada, Ecuador, France [Ploudaniel]), Netherlands, Scotland, and USA (Trial 1, Table 1); and the remaining seven cultivars (set 2) were tested only in Argentina, Canada, Netherlands, and Scotland. In year 2, all 14 cultivars were assessed at nine sites (Trial 2, Table 1) and in year 3 all 14 cultivars were assessed at seven sites (Trial 3, Table 1). Only data from the 1st seven sites are presented here.

At all sites in all years, percentage infection at the plot level was estimated visually every 4-8 d. Values were converted to the relative area under the disease progress curve (AUDPC) as described previously (Fry, 1978; Shaner and Finney, 1977).

Statistical analyses

Variances for each site-by-year combination were calculated for cultivar, block, and error effects (Table 2), and examined for homogeneity between sites. Nonparametric analyses were conducted separately for each year. This test does not require homogeneity of variances and was developed for determining stability of cultivars in multilocation studies (Huehn, 1990a). This nonparametric approach was used recently in a similar study done in the USA (Haynes et al., 1998).

In several cases in this study, values were missing for certain cultivars at certain sites. Although use of stability parameters

Table 2. Mean square errors (type III) for cultivar, block, and error effects of stability experiments carried out at sites in nine countries over 3 yr in the genotype x environment (GXE) study.

Source	Argentina	Canada	Denmark	Ecuador	France	Mexico	France	Netherlands	Scotland	USA	USA
	INTA, Balcarce	Agriculture Canada	Landbrugets Kartoffelfond	CIP	INRA, LeRheu	PICTIPAPA	INRA, Ploudaniel	(CPRO)	(SCRI)	(Cornell)	(WSU)
Trial											
Year 1											
Cultivar	0.065	0.127		0.357			0.032	0.114	0.086	0.164	
Block	0.007	<0.001		0.001			0.001	0.008	0.003	0.005	
Error	0.003	0.002		0.004			0.001	0.041	0.001	0.003	
Year 2											
Cultivar	0.020	0.152	0.004	0.273	0.048		0.050		0.180	0.116	0.023
Block	0.017	0.005	<0.001	0.007	0.011		<0.001		0.023	0.002	0.006
Error	0.004	0.006	0.001	0.010	0.001		0.001		0.008	0.001	0.001
Year 3											
Cultivar	0.003		0.034		0.008	0.018	0.042		0.002	0.031	
Block	<0.001		0.001		<0.001	0.001	0.001		0.006	0.004	
Error	<0.001		0.003		<0.001	0.001	0.001		0.049	0.001	

is theoretically robust for missing data (Huehn, 1990a), the computer code used to calculate these parameters (Lu, 1995) did not work well with missing data. For this reason, missing data were replaced with the average rank of the cultivar for the year in question. For the 1st yr, average ranks were used for Chata Blanca and Robijn in Argentina and for Bintje, Chata Blanca, and Robijn in Ecuador. For the 2nd yr, average ranks were used for Bintje, Teena, Record, and Pimpernel in the USA (Washington State University); Robijn and Chata Blanca in Argentina; Stirling in Ecuador; and Torridon in France (LeRheu). For the 3rd yr, average ranks were used for Chata Blanca, Cruza 148, and Pimpernel in Mexico; Robijn and Record in Argentina; and Stirling in the USA (Cornell University). The original disease severity data are also being analyzed in an effort to confirm the accuracy of data collection and compilation, and to possibly reduce the number of cases where averaged ranks must be used.

Cultivar stability was also examined graphically by plotting relative AUDPC (vertical axis) for each cultivar at each site (horizontal axis). For graphing purposes, relative AUDPC was standardized by dividing it by the site mean. That was done because some sites had very small relative AUDPC values while others had very large values.

Results

Mean square errors in ANOVA varied by site for cultivar, block, and error terms (Table 2). For that reason, nonparametric analyses were used. The two nonparametric parameters used in the study are denoted S1 and S2. S1 is the average rank deviation of a cultivar and for that reason has rather clear biological interpretation. S2 is the variance of the ranks and is highly correlated with S1. Both S parameters are based on corrected AUDPCs. The correction factor eliminates the overall effect of resistance (Huehn, 1990a) and results in new AUDPC values, which may not be completely correlated with the original values. Therefore, S1 and S2 are parameters of stability after correcting for resistance. Both parameters have been evaluated theoretically (Huehn, 1990a) and in practical applications (Huehn, 1990b).

The S1 and S2 parameters were quite low in all almost all cases (Tables 3, 4, 5). None of the individual Z statistics were close to the values for significance at P = 0.05. Neither were total Z statistics (a measure of overall cultivar stability)

Table 3. Mean AUDPC, rank of mean AUDPC, mean of absolute rank differences of a clone (S1), approximate test of significance of S1 (Z1), common variance of ranks (S2), and approximate test of significance of S2 (Z2); analysis of seven cultivars at seven sites in the 1st yr of the GXE project.

Cultivar	Mean AUDPC	Rank	S1	Z1[a]	S2	Z2[a]
Cruza 148	0.08	1	2.48	0.14	4.67	0.18
Monserrate	0.11	2	2.29	0.00	3.67	0.04
Seseni	0.20	3	2.38	0.04	3.95	0.00
Yungay	0.22	4	1.24	4.32	1.14	3.30
Robijn	0.30	5	2.19	0.04	3.81	0.01
Chata Blanca	0.43	6	2.10	0.14	3.14	0.30
Bintje	0.53	7	2.76	0.89	5.29	0 67
Total				**5.57**		**4.50**

a. Z statistics are measures of stability. The tests for the significance of the sum of Z1 or Z2 are compared to a X^2 value of 14.07 Individual Z1 or Z2 values are compared to a X^2 value of 7.24.

Table 4. Mean AUDPC, rank of mean AUDPC, mean of absolute rank differences of a clone (S1), approximate test of significance of S1 (Z1), common variance of ranks (S2), and approximate test of significance of S2 (Z2); analysis of 14 cultivars at 9 sites in the 2nd yr of the GXE project.

Variety	Mean AUDPC	Rank	S1	Z1[a]	S2	Z2[a]
Stirling	0.04	1	3.67	1.32	10.00	1.28
Torridon	0.05	2	4.39	0.09	14.53	0.10
Cruza 148	0.09	3	3.94	0.68	10.75	0.99
Monserrate	0.15	4	3.94	0.68	12.28	0.52
Teena	0.17	5	4.56	0.01	15.44	0.02
Robijn	0.17	6	3.78	1.04	10.94	0.92
Seseni	0.21	7	4.50	0.03	14.94	0.06
Yungay	0.22	8	4.67	0.00	14.94	0 06
Record	0.30	9	3.67	1.32	10 19	1.20
Eigenheimer	0.35	10	4.33	0.13	13.19	0.31
Chata Blanca	0.36	11	6.50	4.79	30.36	6.54
Pimpernel	0.36	12	5.06	0.24	21.44	0.89
Alpha	0.38	13	4.33	0.13	13.44	0.26
Bintje	0 44	14	3.94	0.68	11.75	0.67
Total				**11.14**		**13.81**

[a] Z statistics are measures of stability. The tests for the significance of the sum of Z1 or Z2 are compared to a X^2 value of 23 68. Individual Z1 or Z2 values are compared to a X^2 value of 8 49.

significant. But this statistic was much higher in the 3rd yr than in the 1st and 2nd yr, indicating that cultivar ranks were more variable the 3rd yr. Overall, the nonparametric tests did not provide evidence for instability of the resistance reactions of the cultivars.

Visual examination generally corroborated the nonparametric statistics. Highly resistant and highly susceptible cultivars were generally consistent at all sites. The cultivars appeared to vary more in their reactions in the 3rd yr than in the 1st and 2nd yr (compare Figures 1 - 5), as indicated by the nonparametric analysis.

There were some unusual results for particular site-by-cultivar combinations, but most of these were not repeated. For example, Chata Blanca was relatively resistant at Cornell University (USA) in the 2nd yr (Figure 2), but was susceptible in the 3rd yr (Figure 5). Chata Blanca was also more resistant than normal at Washington State University (USA) in the 2nd yr (Figure 2). Data from the 3rd yr at that site are not yet available for comparison.

The most surprising result that occurred more than once was that Stirling was more susceptible in Argentina than at other sites (see Figures 2 and 5). Otherwise, Stirling was one of the most resistant cultivars at all sites.

Discussion

This research indicated that horizontal resistance to LB is relatively stable. Tropically-adapted resistant materials (e.g., Cruza 148) were resistant in the temperate areas of this study, and Torridon and Stirling from Scotland were resistant in Quito, Ecuador. The primary cases of instability appear to be isolated events, except for the repeated increase in susceptibility of Stirling in Argentina.

Table 5. Mean AUDPC, rank of mean AUDPC, mean of absolute rank differences of a clone (S1), approximate test of significance of S1 (Z1), common variance of ranks (S2), and approximate test of significance of S2 (Z2); analysis of 14 cultivars at 7 sites in the 3rd yr of the GXE project.

Variety	Mean AUDPC	Rank	S1	Z1[a]	S2	Z2[a]
Torridon	0.03	1	6.00	1.79	26.57	2.52
Stirling	0.03	2	5.52	0.75	21.81	0.73
Teena	0.09	3	4.95	0.09	16.81	0.01
Cruza 148	0.09	4	2.86	3.09	5.57	2.70
Seseni	0.10	5	2.38	4.96	3.95	3.58
Monserrate	0.12	6	4.10	0.29	11 24	0.59
Robijn	0.13	7	2.76	3.43	5.29	2.84
Yungay	0.14	8	6.38	2.93	28.33	3.45
Record	0.17	9	3.62	1.02	9.33	1.13
Pimpernel	0.18	10	4.10	0.29	14.81	0.05
Eigenheimer	0.20	11	4.76	0.01	16.29	0.00
Alpha	0 21	12	4.67	0.00	15.24	0.02
Chata Blanca	0.24	13	5.90	1.54	23.81	1.35
Bintje	0.28	14	4.95	0.09	17.14	0.02
Total				**20.28**		**18.99**

a Z statistics are measures of stability. The tests for the significance of the sum of Z1 or Z2 are compared to a X^2 value of 23.68. Individual Z1 or Z2 values are compared to a X^2 value of 8.49.

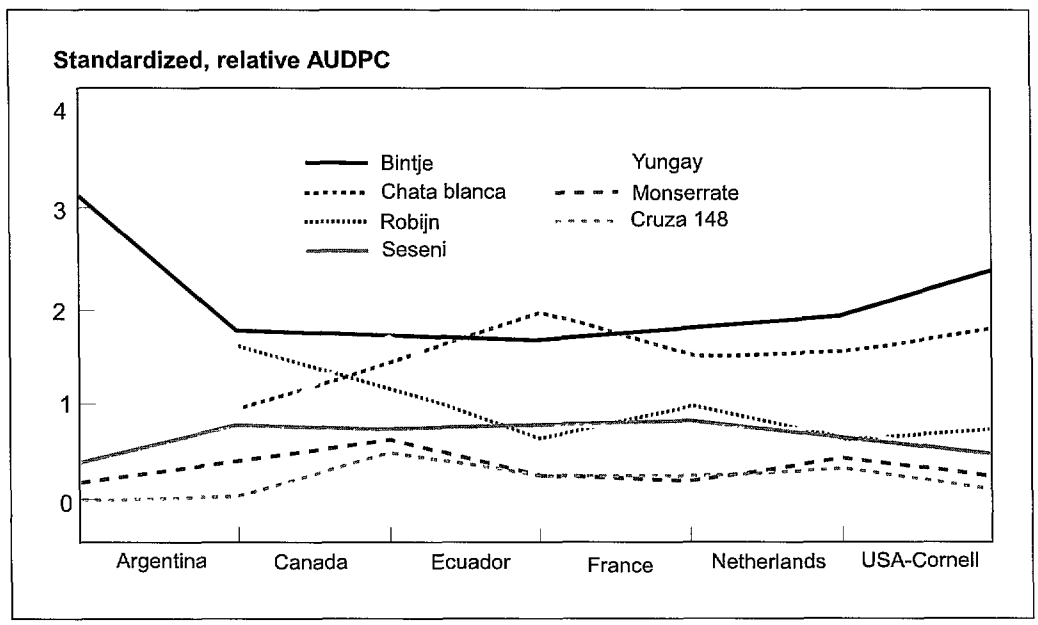

Figure 1. Seven cultivars tested at seven sites in the 1st yr of the international genotype x environment (GXE) experiment.

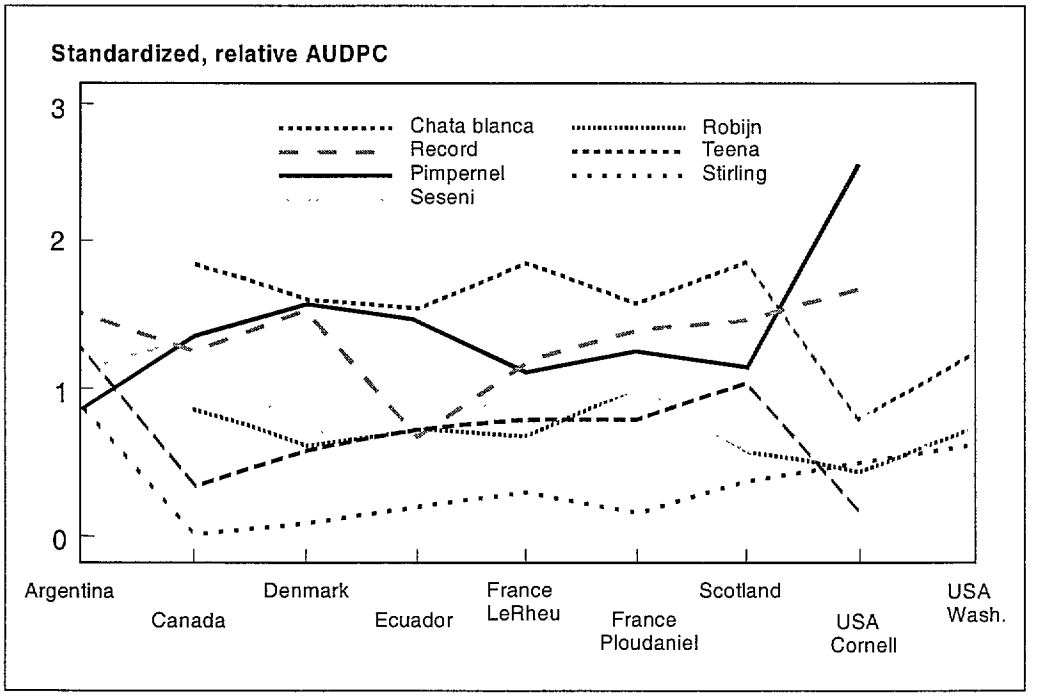

Figure 2. Seven cultivars tested at nine sites in the 2nd yr of the international GXE experiment.

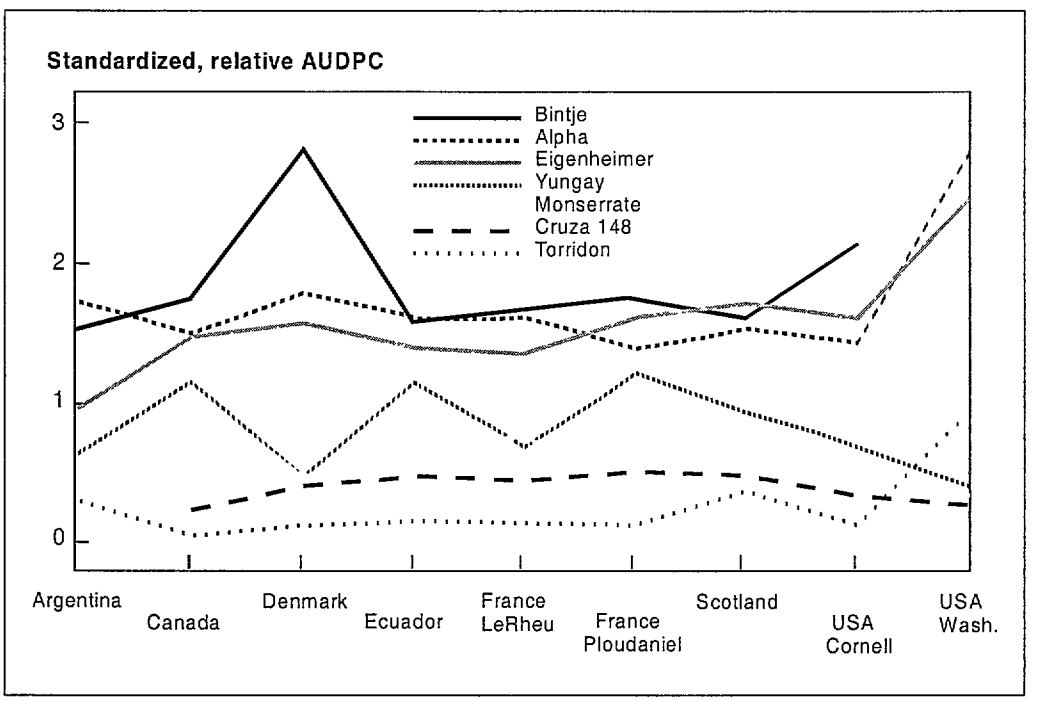

Figure 3. Seven additional cultivars tested at nine sites in the 2nd yr of the international GXE experiment.

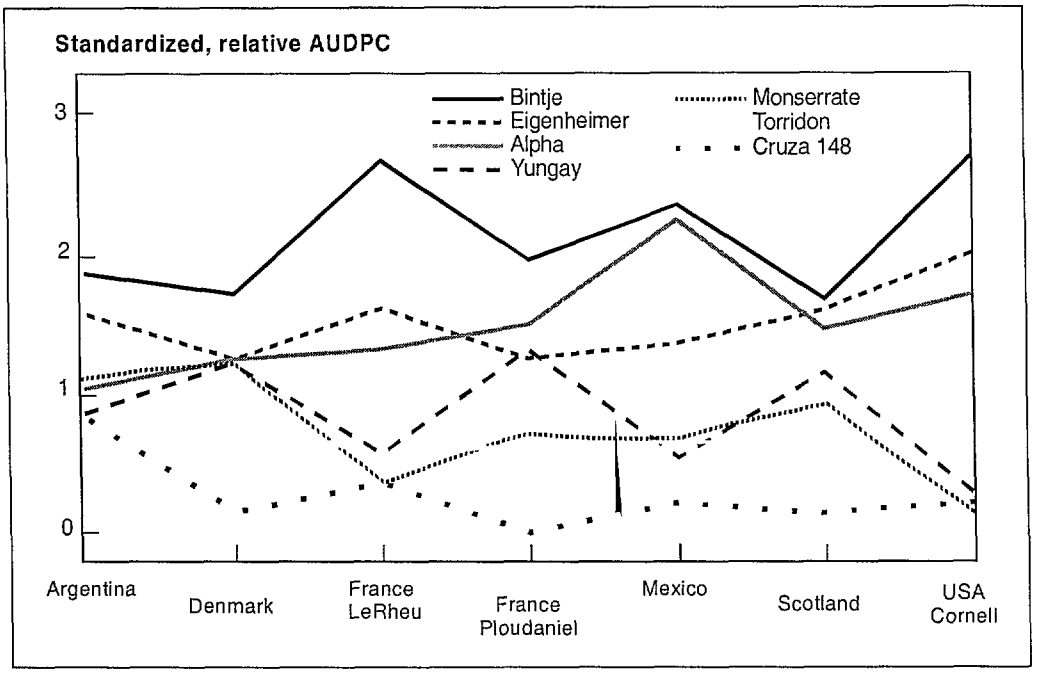

Figure 4. Seven cultivars tested at seven sites in the 3rd yr of the international GXE experiment.

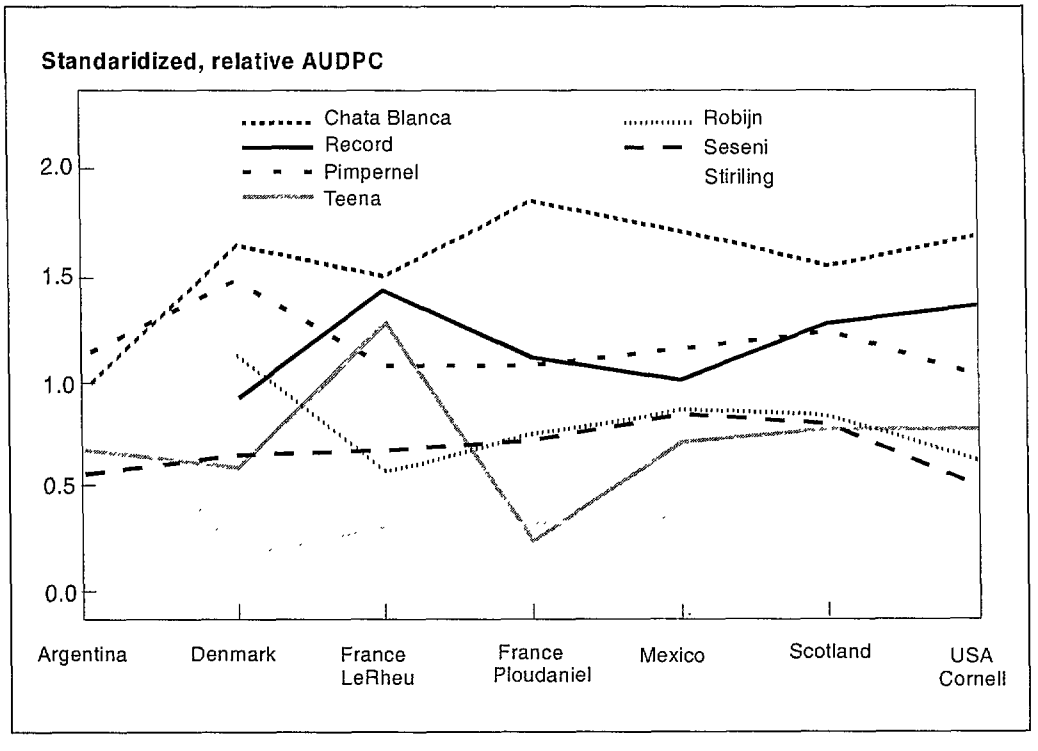

Figure 5. Seven additional cultivars tested at seven sites in the 3rd yr of the international GXE experiment.

The high level of resistance of Stirling in Ecuador and Scotland would appear to argue against a relation between daylength sensitivity and resistance. This relation could have been tested with greater certainty had more short-daylength sites participated in the study. Nonetheless, other factors may explain the differential reaction of Stirling in Argentina. Argentina is known to have an unusual population of the pathogen comprising both A1 and A2 mating types (Forbes et al., 1998). It appears important to reevaluate Stirling in Argentina to determine whether it is truly susceptible there. Subsequently, research could be designed to determine whether the putative effect is related to environmental factors or pathogen genotype.

In general, this study corroborates a recent and similar study in the USA (Haynes et al., 1998). S parameters in the USA study were also insignificant, although somewhat higher than those reported here. Thus, two independent studies have arrived at the same general conclusion: there is little evidence for phenotypic instability of quantitative resistance to potato LB.

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Identification of QTLs for Late Blight Resistance in a Cross Between *S. phureja* and a Dihaploid *S. tuberosum* and Association with a Plant Defense Gene

M. Ghislain, B. Trognitz, R. Nelson, Ma. del R. Herrera, L. Portal, M. Orillo, and F. Trognitz[1]

Race nonspecific resistance to late blight (LB) disease in potato, caused by *Phytophthora infestans*, is thought to be quantitatively inherited and has been characterized in several cultivated South American potato species (Colon et al., 1995; Trognitz et al., 1997). A cross between a LB resistant accession of the diploid cultivated potato, *Solanum phureja* (*phu*), and a susceptible dihaploid clone from *S. tuberosum* (dih-*tbr*) produced a segregating (PD) population of 246 progenies. The resulting hybrids were assayed at two field sites under natural infection by *P. infestans*. Evaluations of field resistance revealed large variation—from high partial resistance to susceptibility (Trognitz et al., 1997). Randomly amplified polymorphic DNA (RAPD) and amplified fragment length polymorphic (AFLP) markers were used to genotype 94 hybrids selected randomly from the PD population (Ghislain et al., 1997). To better understand the inheritance of horizontal resistance to LB, we developed genetic maps and quantitative trait loci (QTL) analysis using the field evaluation data. Association between QTL and known genes was also tested by searching for linkage disequilibrium in selective genotypes of the phenotypic extremes.

Materials and Methods

The PD population is the progeny of the cross of *S. phureja* (*phu*) clone CHS-625 by dihaploid *S. tuberosum* (dih-*tbr*) clone PS-3 (Trognitz et al., 1997). Field evaluations with naturally occurring *P. infestans* populations were done in both Quito, Ecuador, and Huancayo, Peru. Horizontal resistance was quantified by the average of the diseased foliage area (ADFA) taken six times at weekly intervals and area under the disease progress curve (AUDPC).

Molecular techniques used in the study have been described elsewhere (Ghislain et al., 1999). Template DNA of five parents of reference potato mapping populations was provided by H. van Eck and J. R. van der Voort, Wageningen University, Netherlands. Sixty-eight simple sequence repeats (SSR) or microsatellite primer pairs corresponding to loci on the potato genetic map were provided by R. Waugh, Scottish Crop Research Institute, Dundee, Scotland. Two restriction fragment length polymorphism (RFLP) markers per chromosome were selected from the database of potato-tomato RFLP probes. They were used to anchor the *phu* and dih-*tbr* linkage groups to the potato genetic map by linkage analysis. RFLP probes were provided by C. Gebhardt, Max Planck Institut, Germany, and S. Tanksley, Cornell University, USA.

Single-marker analysis was used to detect associations between marker (genotypic) classes (presence or absence of the band) and their respective phenotypic values. Significance of association was determined with a two-sample Student's t-test. Interval mapping method using LOD score (Lander and Botstein, 1989) was applied through the use of MAPMAKER/QTL v1.1b software.

1 CIP, Lima, Peru.

Results

Phenotypic data of the PD population

Field evaluations of the 94 hybrids used to develop the genetic maps were compared between the two environments. Good correlation, r = 0.75 and 0.77, were observed between data sets using ADFA and AUDPC, respectively. Such correlation for data collected in two distinct field environments under natural infestation, is very high and may indicate that some QTL of resistance to LB are common in both environments.

Genetic linkage maps

DNA markers for the two parents are expected to have a 1:1 segregation ratio (presence of the band-absence of the band) in the F_1 cross between heterozygous parents under a pseudo-test cross model. Several markers displayed a skewed segregation tested by a χ^2 test at $P<0.01$. The number of markers with skewed segregation observed from the *phu* parent is similar to that reported for other genetic analyses in plants. In contrast, 24% of markers from the dih-*tbr* parent have a skewed segregation at a $P<0.01$, which is unusually high. Both female- and male-derived genetic maps have been constructed using the linkage analysis program MAPMAKER/EXP v3.0b™[2]. The *phu* linkage map consists of 13 linkage groups totaling 993.6 cM, of which 11 have been anchored to known potato chromosomes (Figure 1A[3]). The dih-*tbr* linkage map consists of 12 linkage groups totaling 889.9 cM, each with markers anchored to the potato genetic map (Figure 1B).

The anchoring was performed with informative RFLP, SSR, and AFLP markers with known positions on the potato genetic map (Figure 1).

- AFLP anchors: Eight out of 12 primer combinations with known mapped AFLP markers (Rouppe van der Voort et al., 1998) turned out to be informative with PD material and were used to identify the AFLP markers with known map positions.
- SSR anchors: 26 out of 68 primer combinations proved to be informative for the PD maps (polymorphic and heterozygous loci) and amplified loci with known locations in the potato genetic map.
- RFLP anchors: 13 RFLP markers were informative for the PD genetic maps.

Genetic analysis of field resistance

Notably, markers associated with field resistance were primarily from the dih-*tbr*, susceptible parent, and in particular on chromosomes III and XII (Table 1).

Several QTL were detected using interval-mapping analyses (Figure 1A and 1B). The QTL analysis (significance of QTL detection with a LOD score ≥ 2) revealed only minor QTL positioned on chromosomes VII, XI, and XII of the *phu* map, and 3 QTL located on the dih-*tbr* map: 2 minor on chromosomes III and V, and one large (explaining up to 36% of the trait variation) on chromosome XII, using the field data.

Selective genotyping of the phenotypic extremes

A series of anonymous RFLP markers, R gene primers amplifying R gene-like sequences (Rls), and candidate genes were tested for linkage disequilibrium with the most resistant and susceptible extremes of the PD population to test the hypothesis of association between known QTL for LB resistance, defense genes in other material or plant-pathogen systems and the PD trait variation.

A set of 21 RFLP markers, previously found to be associated with effects on quantitative resistance to LB (Leonards-Schippers et al., 1994), was used to probe DNA extracted from the most resistant and susceptible plants of the PD population (17-20 plants for each group). Among these,

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2 Whitehead Institute, *web:* http://www-genome.wi.mit.edu/genome_software; *ftp:* <ftp://ftp-genome.wi.mit.edu/distribution/software/mapmaker3>

3 Figures follow references cited section.

Table 1. Number of markers associated with LB resistance (t-test at $P<0.05$) and chromosome assignment of *S. phureja* CHS-625 and the dihaploid *S. tuberosum* PS3.

			Potato chromosomes											
			I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
phu	Markers	ADFA-QUI	0	0	4	0	0	0	0	0	1	0	2	5
	associated with	AUDPC-QUI	0	0	4	0	0	0	0	0	1	0	2	2
CHS-625	LB resistance	ADFA-HYO	0	0	0	5	0	0	1	0	0	0	2	6
		AUDPC-HYO	0	0	0	2	0	0	1	0	0	0	2	6
	Total analyzed	**168**	**30**	**11**	**29**	**15**	**9**	**19**	**9**	**10**	**9**	**8**	**11**	**8**
dih-*tbr*	Markers	ADFA-QUI	0	0	41	1	18	1	1	1	2	8	0	29
	associated with	AUDPC-QUI	0	0	39	0	22	0	0	1	1	12	0	29
PS-3	LB resistance	ADFA-HYO	0	1	36	5	0	0	0	3	4	0	0	29
		AUDPC-HYO	0	0	38	5	0	0	0	2	4	0	0	29
	Total analyzed	**279**	**48**	**10**	**46**	**18**	**56**	**5**	**6**	**19**	**11**	**11**	**20**	**29**

ADFA = average of the diseased foliage area, QUI = Quito,
AUDPC = area under the disease progress curve, HYO = Huancayo.

four markers (CP116, GP313, CI21, and GP186) showed bands associated with resistance in the PD population (Table 2). One of these mapped at a QTL position on chromosome III.

Of 47 segregating bands detected using 5 primer pairs corresponding to conserved R gene domains, one has been found to be associated with the quantitative resistance observed in the field with the PD population (see RIs in Table 2).

Several candidate genes were selected to be tested for association with LB resistance based on their role in plant defense. The intron of the *PR10a* gene (formerly *STH-2*) amplified and digested with *Taq*I (cleaved amplified polymorphic sequence, CAPS) displayed weak association with resistance (Table 2). Three genes of the phenylpropanoid pathway were tested by DNA hybridization analysis: phenylalanine ammonium lyase (*PAL*), 4-coumarate-CoA ligase (4*CL*), and chalcone flavanone isomerase (*CHI*). Bands hybridizing with all three of these genes showed significant associations with resistance. Several *PAL* bands segregating from both parents mapped on chromosome III to a QTL position for the dih-*tbr* parent. This result might be of functional significance for this QTL. The osmotin clone pA13, cloned from *S. commersonii*, hybridized with several bands of which two from the dih-*tbr* parent showed significant association with resistance. These bands cosegregated with the resistance-associated band hybridizing with GP313 (tentatively on chromosome V). Other candidate genes, probes encoding lipoxygenase, glucanase, solanidine glucosyl transferase (SGT), catalase, and genes involved in the *Pseudomonas*-tomato incompatible reaction *Pto, Pti-4, Pti-5,* and *Pti-6,* were tested but no clear association with resistance was found.

Conclusion

The QTL analysis reported here for the PD population revealed an important QTL on chromosome XII that seems to be the most interesting. It was identified with both parental maps and with a large effect on the variation of field resistance to LB in Huancayo and Quito. Other QTL were

Table 2. Candidate genes and markers associated with one of the contrasting phenotypic classes tested by χ^2 statistics, the PD population, and chromosome assignment to the *phu* and the dih-*tbr* maps (- not mapped).

Marker type	Band/kb	Total tested[a]		Observed		χ^2	P[a]	Chromosome[a]
		r	s	r	s			
RFLP probe	CI21/*Eco*R V/6.5	30	31	18	5	7.78	**	(D) -
	GP186/*Eco*R I/8	25	21	3	11	6.11	*	(D) -
	GP313/*Xba*I /6.5	29	29	9	20	4.17	*	(D) V
	CP116/*Dra*I /3	25	23	19	1	14.8	***	(D) -
RIs[a]	AS1-S2/0.23	17	16	12	3	4.87	*	(P) -
CAPS[a]	*STH/Taq*I/4	33	31	5	16	6.48	*	(D) IX
Candidate genes	*PAL/Eco*RI/3	34	33	31	10	10.1	**	(P) III
	*PAL/Eco*RI/2.8	34	33	25	5	12.7	***	(D) III
	*PAL/Eco*RI/2	34	33	10	23	5.52	*	(D) -
	*PAL/Eco*RI/1.9	34	33	12	24	4.37	*	(P) III
	*PAL/Nde*I/6.9	34	33	26	5	13.6	***	(D) III
	*PAL/Nde*I/6	34	33	26	1	22.4	***	(D) -
	*PAL/Nde*I/5.9	34	33	22	6	8.67	**	(P) III
	*PAL/Nde*I/4.4	34	33	9	27	9.55	**	(D) III
	*PAL/Nde*I/4	34	33	9	26	8.77	**	(D) III
	*PAL/Nde*I/3.6	34	33	26	8	9	**	(D) III
	*PAL/Hind*III/5.5	34	27	8	21	9.32	**	(D) III
	*PAL/Hind*III/5	34	27	15	4	4.15	*	(P) -
	*PAL/Hind*III/2.8	34	27	9	22	8.96	**	(D) III
	*PAL/Hind*III/2.7	34	27	9	22	8.96	**	(D) III
	4*CL/Eco*RI/9	33	32	24	11	4.19	*	(D) -
	4*CL/Hind*III/8	34	33	25	12	4.19	*	(D) III
	4*CL/Nde*I/4.5	34	33	9	22	5.85	*	(D) III
	osmotin/*Eco*RV/13	33	33	10	23	5.12	*	(D) -
	osmotin/*Xba*I/12	33	33	24	10	5.76	*	(D) -
	osmotin/*Xba*I/6.8	33	33	9	24	6.82	**	(D) -

a. r = resistant, s = susceptible, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$, - = not mapped, RIs = R gene-like sequence, CAPS = cleaved amplified polymorphic sequence

detected in both parental genetic maps, but with lower contributions to the phenotypic variation. Some of the QTL detected in the PD genetic maps locate at different map positions homologous to those found by Leonards-Schippers et al. (1994). Hence, the genetic base of LB field resistance in our PD population seems to differ from the published map locations. Therefore, breeding for LB resistance can broaden the genetic complex of field resistance. Future developments will be on the application of QTL-associated markers to selection of genotypes with field resistance to LB.

Acknowledgments

The authors are grateful to the dedicated students who contributed to this work: J. Solis, G. Casallo, C. Vásques, O. Hurtado, D. Niño, P. Manosalva, and R. Castillo.

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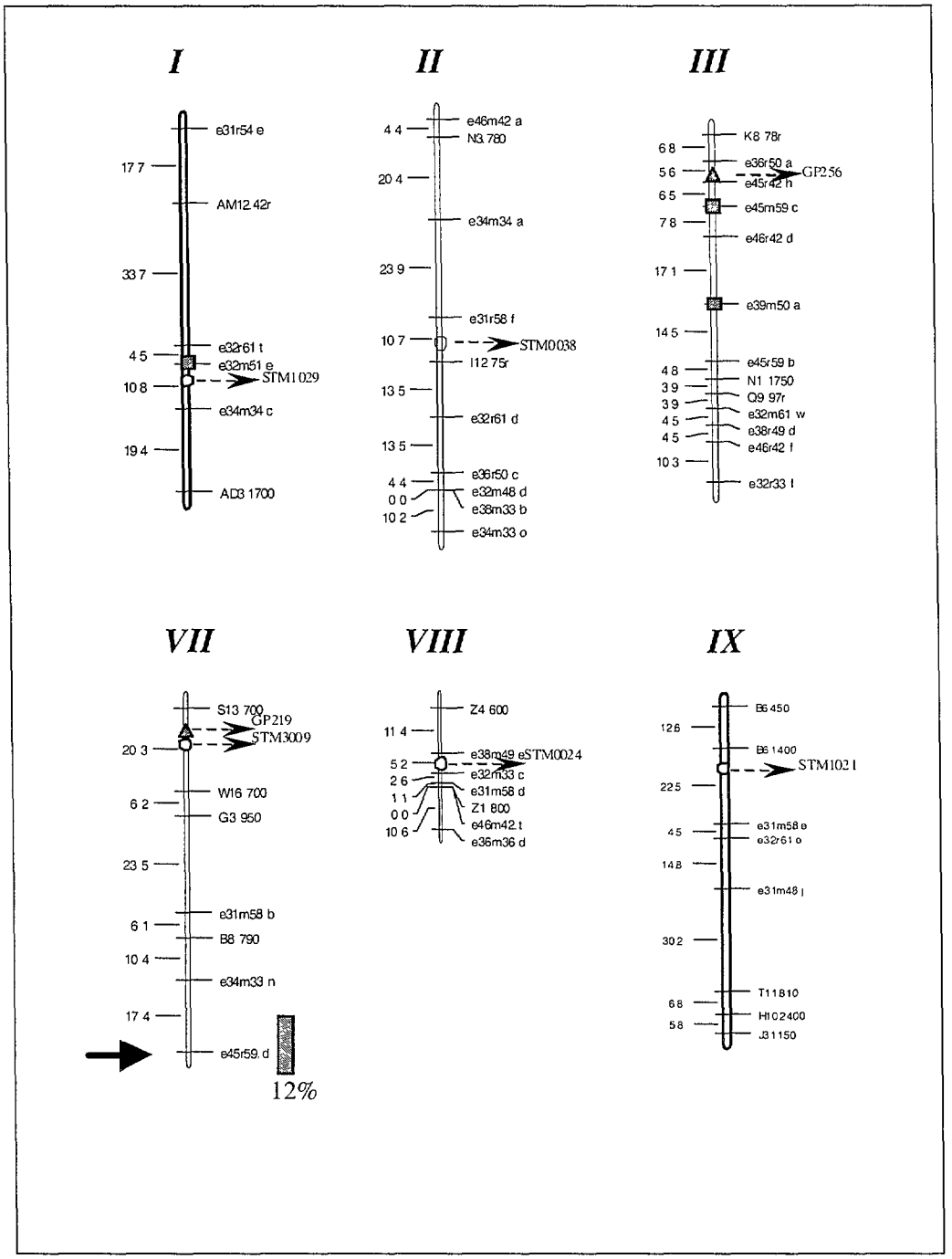
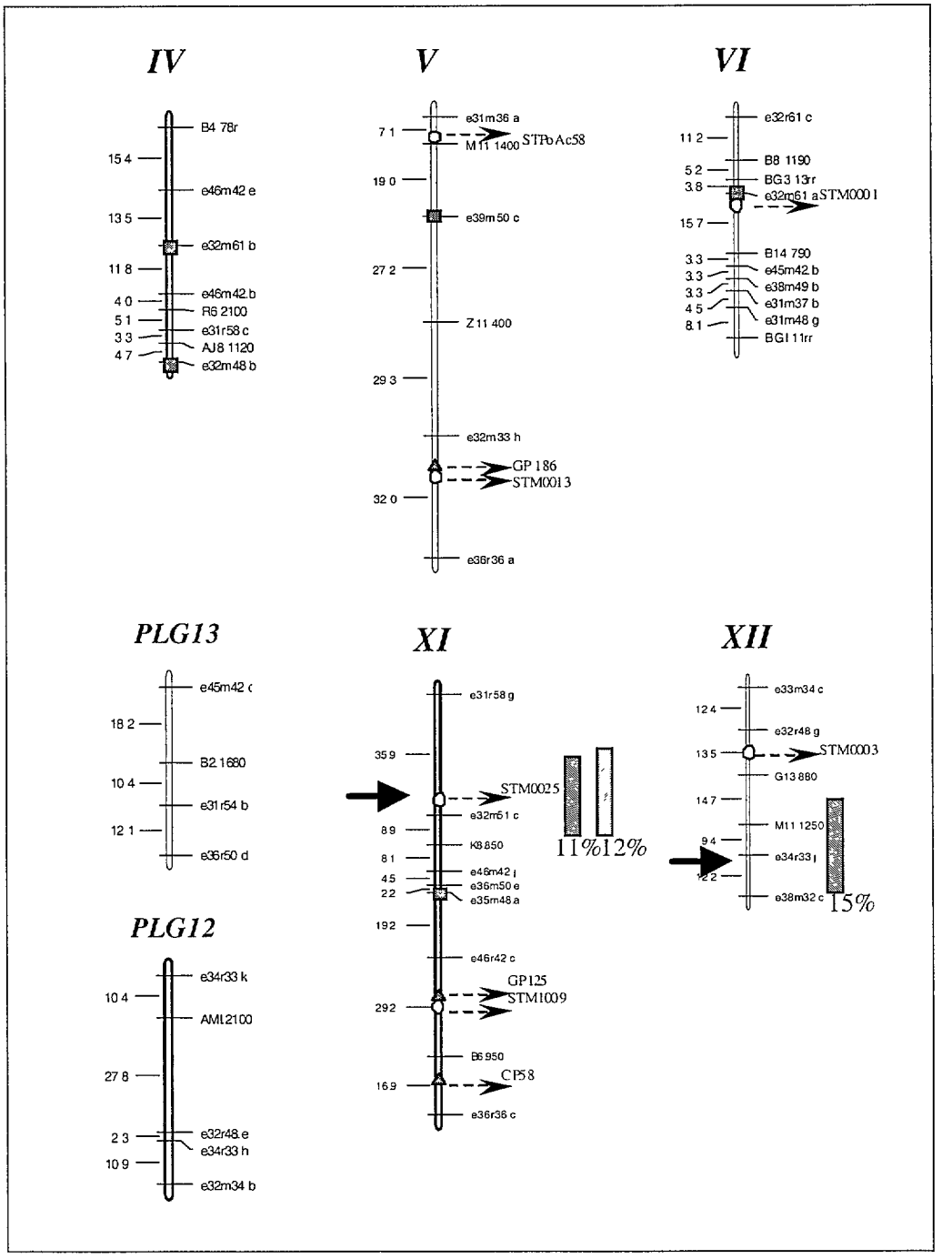


Figure 1A. Genetic linkage map of the *phu* parent including markers anchored to the potato genetic map: ● = SSR, ■ = AFLP, ▲ = RFLP. Genetic distance in cM are indicated left; markers at right. Location of QTL associated with field resistance to LB , position (→), and the respective percentage of phenotypic variation explained (bottom of bars). Field data are ADFA in Huancayo (▒) and in Quito (▨).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11 8
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R6 2100
5 1
e31r58 c
3 3
AJ8 1120
4 7
e32m48 b
V
e31m36 a
7 1
M11 1400
STPbAc58
19 0
e39m50 c
27 2
Z11 400
29 3
e32m33 h
GP 186
STM0013
32 0
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VI
e32r61 c
11 2
B8 1190
5 2
BG3 13rr
3.8
e32m61 aSTM0001
15 7
B14 790
3.3
e45m42.b
3.3
e38m49 b
3.3
e31m37 b
4 5
e31m48 g
8.1
BGI 11rr
PLG13
e45m42 c
18 2
B2 1680
10 4
e31r54 b
12 1
e36r50 d
PLG12
e34r33 k
10 4
AMI2100
27 8
2 3
e32r48.e
e34r33 h
10 9
e32m34 b
XI
e31r58 g
35 9
STM0025
e32m61 c
8 9
K8.850
8 1
e46m42 j
4 5
e36m50 e
2 2
e35m48 a
11%12%
19 2
e46r42 c
GP125
29 2
STM1009
B6 950
16 9
CP58
e36r36 c
XII
e33m34 c
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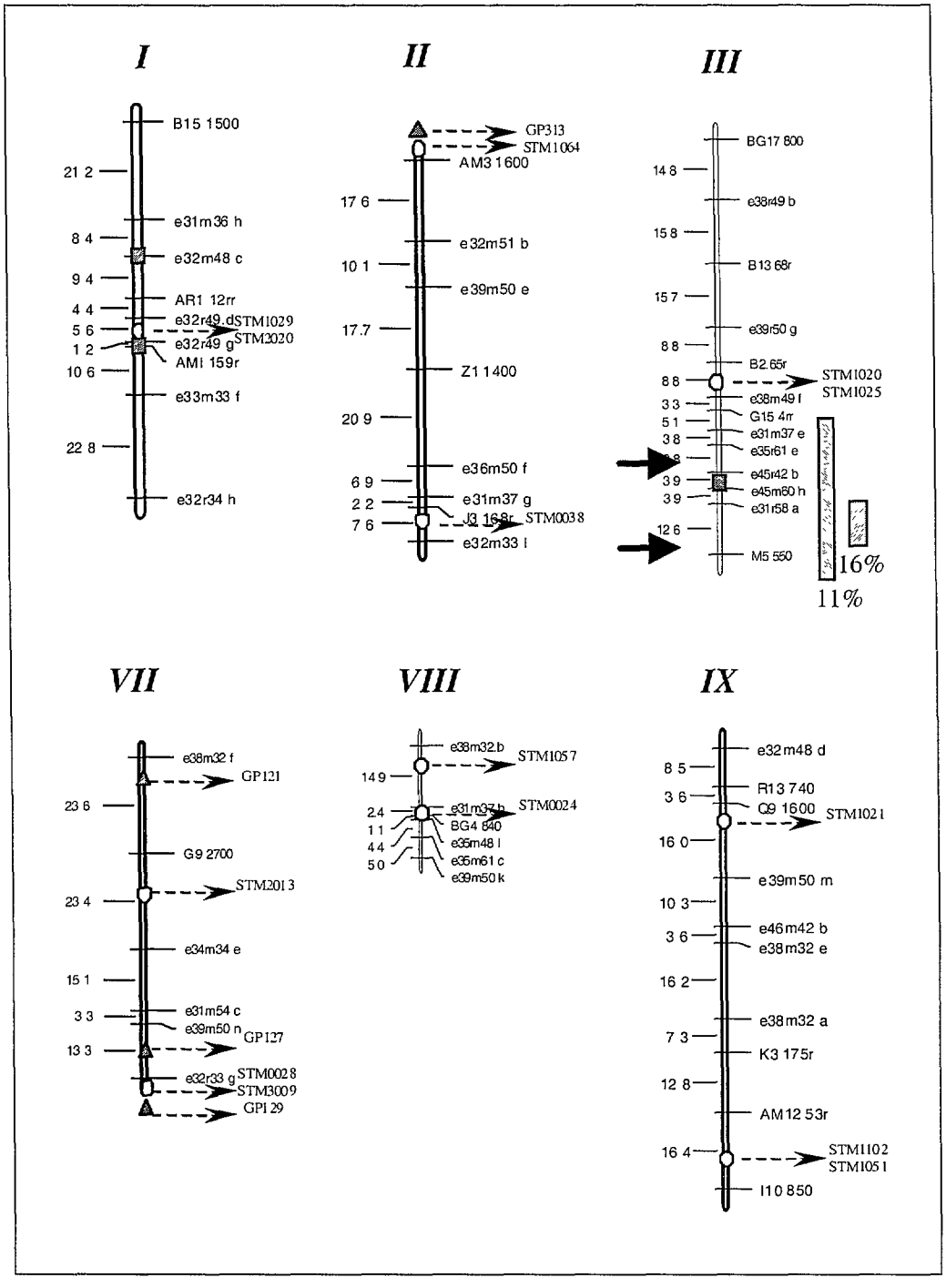
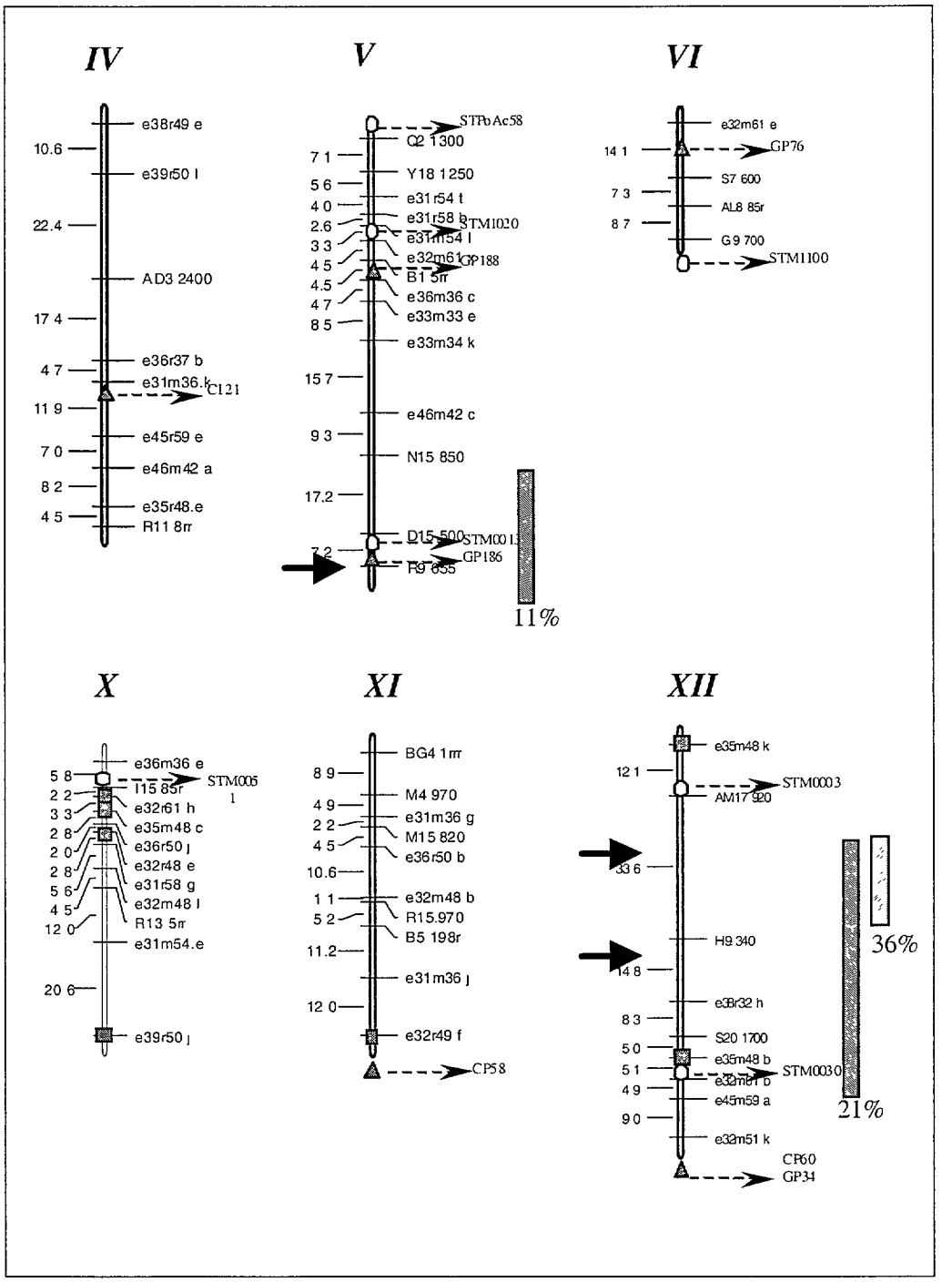


Figure 1B. Genetic linkage map of the dih-*tbr* parent including markers anchored to the potato genetic map: ● = SSR, ■ = AFLP, ▲ = RFLP. Genetic distance in cM are indicated left; markers at right. Location of QTL associated with field resistance to LB, position (→), and the respective percentage of phenotypic variation explained (bottom of bars). Field data are ADFA in Huancayo (▩) and in Quito (▨).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e45r59 e
7 0
e46m42 a
8 2
e35r48.e
4 5
R11 8rr
V
STPoAc58
Q2 1300
7 1
Y18 1250
5 6
e31r54 t
4 0
e31r58 b
STM1020
2.6
e31m54 l
3 3
e32m61
GP188
4 5
B1 5rr
4.5
e36m36 c
4 7
e33m33 e
8 5
e33m34 k
15 7
e46m42 c
9 3
N15 850
17.2
D15 500
STM001
GP186
R9 855
11%
VI
e32m61 e
14 1
GP76
S7 600
7 3
AL8 85r
8 7
G9 700
STM1100
X
e36m36 e
5 8
STM005
1
I15 85r
2 2
e32r61 h
3 3
e35m48 c
2 8
e36r50 j
2 0
e32r48 e
2 8
e31r58 g
5 6
e32m48 l
4 5
R13 5rr
12 0
e31m54.e
20 6
e39r50 j
XI
BG4 1rr
8 9
M4 970
4 9
e31m36 g
2 2
M15 820
4 5
e36r50 b
10.6
e32m48 b
1 1
R15.970
5 2
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11.2
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CP58
XII
e35m48 k
12 1
STM0003
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33 6
H9 340
14 8
e38r32 h
8 3
S20 1700
5 0
e35m48 b
5 1
STM0030
e32m51 b
4 9
e45m59 a
9 0
e32m51 k
CP60
GP34
36%
21%

Parasitic Fitness and Temperature Response of New Lineages of *Phytophthora infestans* from Peru

J.L. Andrade Piedra[1], G.A. Forbes[2], W.E. Fry[3], and R. Nelson[1]

The main methods for controlling late blight (LB) caused by *Phytophthora infestans* include the use of fungicides and resistant cultivars (Umaerus et al., 1983; Schwinn, 1983). Computer simulation techniques are being used to improve the efficiency with which these components can be used (Bruhn and Fry, 1981). The epidemiology of the disease is complex, and mathematical models using simplifying equations help in its analysis. Simulators are used to generate hypotheses, identify topics for research, and develop forecasts (Fry, 1982). Simulation should also be useful for adapting LB management strategies to a range of agroecosystems, for ex ante impact assessment, and for evaluating risk across time and space.

This study is part of the development, calibration, and validation of the simulator SIMPOL (Hijman, Forbes, Grunwald, and Andrade, personal communication), which is based on the simulator LATEBLIGHT (Bruhn and Fry, 1981). The components of resistance on which the simulator is based were quantified in American cultivars infected by isolates of the"old" *P. infestans* lineage US-1, which was once dominant in many potato production areas of the world, but which is now relatively rare. The equations that define the effect of temperature on pathogen development were calculated based on data of Crosier (1934), who very probably worked with US-1. This clonal lineage was previously predominant in Peru (Tooley et al., 1989; Goodwin et al., 1994) and probably in Ecuador (Forbes et al., 1997), but recent studies show that it has been replaced by "new" populations (Forbes et al., 1997) dominated by lineage EC-1. The greater aggressiveness of some new clonal lineages has been documented (Kato et al., 1997; Day and Shattock, 1997; Mizubuti and Fry, 1998; Miller et al., 1998), but the components of parasitic fitness of the Andean lineages have not been studied.

Mizubuti and Fry (1998), studying the effect of temperature on the development of lineages US-1, US-7, and US-8, found that the interaction of temperature by lineage was significant for sporangial germination, but not for components of parasitic fitness. The Andean agroecosystem, in contrast to the potato production areas of the USA, is characterized by its extreme environmental heterogeneity. Temperature adaptation of Andean isolates of the same clonal lineage coming from different altitudes is possible. Such adaptation would have important implications for simulation.

The objectives of this study were to (1) determine the aggressiveness of new populations of *P. infestans* of Peru, (2) study the effect of temperature on the development of the predominant lineage of Peru, (3) determine if adaptation occurs in isolates of the same clonal lineage collected from different altitudes, and (4) obtain data to validate the simulator SIMPOL under highland tropical conditions.

Materials and Methods

Two experiments were carried out. Experiment 1 was done in September and October of 1998 at CIP-Lima. Experiment 2 was conducted in November and December of 1998 at Cornell University, Ithaca, NY, USA.

1 CIP, Lima, Peru.
2 CIP, Quito, Ecuador.
3 Cornell University, Ithaca, New York, USA.

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For experiment 1, we used 11 isolates representing the clonal lineages US-1 (n = 3), EC-1 (n = 4), and PE-3 (n = 4). For experiment 2, we used eight EC-1 isolates collected in Comas (2,400 masl) (n = 4) and Oxapampa (1,800 m) (n = 4). Both sites are in the highlands of Peru. All isolates collected were maintained on Rye A agar. Before the experiments, isolates were transferred to tuber slices and then to Rye B agar. Inoculum for studies was collected from leaves of cv. Tomasa Tito Condemayta (experiment 1) and Superior (experiment 2). Peruvian isolates were carried from Peru under a permit from the Instituto Nacional de Recursos Naturales and into the United States under a permit from the Animal and Plant Health Inspection Service of the United States Department of Agriculture. At Cornell, Peruvian isolates were transferred in a laminar-flow biosafety cabinet (class II, type A) in a level P2 laboratory. At the end of the experiment, all materials were autoclaved before disposal.

The potato cultivars Tomasa Tito Condemayta (very susceptible), Yungay (moderately susceptible), and Amarilis-INIA (resistant) were used in experiment 1. The plants were grown in a greenhouse at temperatures between 14° and 24°C. In experiment 2, Superior (a susceptible cultivar) was used. In this case, plants were grown in a greenhouse with temperatures between 18° and 25°C and a 14-h day photoperiod.

Inoculation basically followed the method described in Mizubuti and Fry (1998). For experiment 1, inoculum concentration was 5 x 10^3 sporangia/ml. Leaflets were incubated at 18°C with a 14-h day of weak light (0.5 $mEm^{-2}s^{-1}$). Incubation period (IP) and latent period (LP) were evaluated at 36, 42, 48, 54, 60, 66, 72, 78, 84, 90, 96, 102, 114, 120, 126, and 138 hours after inoculation (h.a.i.) using a dissecting microscope. For experiment 2, inoculum concentration was 15 x 10^3 sporangia/ml and leaflets were incubated at 8, 13, 18, 23, and 28°C with a 14-h day of intense light (150 $mEm^{-2}s^{-1}$). IP and LP were evaluated at 24, 30, 36, 42, 48, 54, 60, 66, 72, 78, 84, 90, 96, 102, 114, 120, 126, 138, 144, 150, 162, 168, 174, 186, 192, 198, and 210 h.a.i. In both experiments, lesion area (LA) and sporulation capacity (SC) were measured as described by Mizubuti and Fry (1998). IP was defined as the time necrotic spots appeared; LP was defined as the time when sporangia appeared.

Analysis of variance was done using a model that made it possible to compare clonal lineages in experiment 1 or sites in experiment 2. In both cases, the error term was based on the variability between isolates within clonal lineages or within sites. We used contrasts to compare treatments or groups of treatments. All analyses were done using SAS software v6.11[4].

Results

Experiment 1

The interaction lineage by cultivar was not significant for IP (P = 0.1596), LP (P = 0.0975), and LA (P = 0.2839), which means that the effects of lineage and cultivar could be studied separately. Amarilis had an IP significantly shorter than Yungay (P = 0.0001) and Tomasa (P = 0.0012), while Yungay and Tomasa had similar values (P = 0.4560).

In contrast, Amarilis had a significantly longer LP than Yungay or Tomasa (P < 0.01) and, again, differences between these last two cultivars were not detected (P = 0.0753). The LA on Tomasa was significantly larger than on Amarilis or Yungay (P < 0.01), which were statistically equal (P = 0.9087) for that component. We did not find differences between clonal lineages for IP (P = 0.0682), LP (P = 0.4678), or LA (P = 0.3484).

4 SAS Institute, Inc., Cary, NC, USA.

For SC, the interaction between lineage and cultivar was highly significant (P = 0.0009). Through a simple effects analysis, we found highly significant differences (P <0.01) for all the clonal lineages within every cultivar and vice versa (Figure 1). The lowest SC values occurred with Amarilis and the highest with Tomasa. Nonorthogonal comparisons showed that the new population of *P. infestans* (EC-1 and PE-3) sporulated significantly less than the old population (US-1) on all the cultivars (P <0.01). The SC for lineage EC-1 was significantly less than that of PE-3 in the three cultivars (P <0.01).

The interaction cultivar by isolate within every clonal lineage was not significant for any component: IP (P = 0.5248), LP (P = 0.9796), LA (P = 0.4406), and SC (P = 0.9689). However, differences between isolates within clonal lineages were found for IP (P = 0.0120), LP (P = 0.0001), and SC (P = 0.0001), but not for LA (P = 0.3650).

Experiment 2

The interaction between site and temperature was not significant for IP (P = 0.8608), LP (P = 0.2275), LA (P = 0.7171), or SC (P = 0.7946). The isolates collected in Comas were similar to those collected in Oxapampa for IP (P = 0.1321), and SC (P = 0.7371). Differences were significant for LP (P = 0.051): isolates from Comas sporulated at 99.8 h.a.i. and those from Oxapampa at 93.5 h.a.i. Isolates from Oxapampa caused lesions that were 0.72 cm^2 larger than those caused by isolates from Comas (P = 0.0139).

The effects of temperature were highly significant for all the components (P = 0.0001) (Figure 2). The models that explained the variability of each component as a function of temperature were highly significant (P = 0.0001). The determination coefficients (R^2) were 0.7318 for IP, 0.9173 for LP, 0.7377 for LA, and 0.5019 for SC. The equations for IP and LP had a quadratic shape with the minimum value at 27.28°C for IP and 22.99°C for LP.

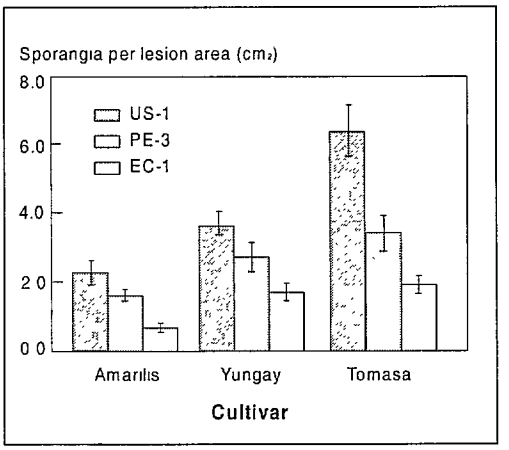

Figure 1. Sporulation capacity of three clonal lineages of *Phytophthora infestans* on three potato cultivars. Each data point represents the average of three or four isolates inoculated on each cultivar. Vertical bars indicate the standard error of the mean.

Models for LA and SC also had a quadratic shape with the maximum at 22.22°C for LA and 17.15°C for SC.

Discussion

The displacement of US-1 by a new population (EC-1, PE-3) in Peru could not be explained by the components of parasitic fitness studied. The three clonal lineages had similar values for IP, LP, and LA. Unexpectedly, the SC of the old population was significantly greater than that of the new population.

Previous reports (Mizubuti and Fry, 1998; Miller et al., 1998; Kato et al., 1997; Chycosky and Punja, 1996) attributed the displacement of US-1 to a greater aggressiveness of new populations, partly due to lower values of IP and LP, and higher values of LA. Day and Shattock (1997) found that the new populations presented a greater fitness index (infection frequency by number of sporangia/lesion).

We speculate that the greater aggressiveness of the new Andean populations of *P.*

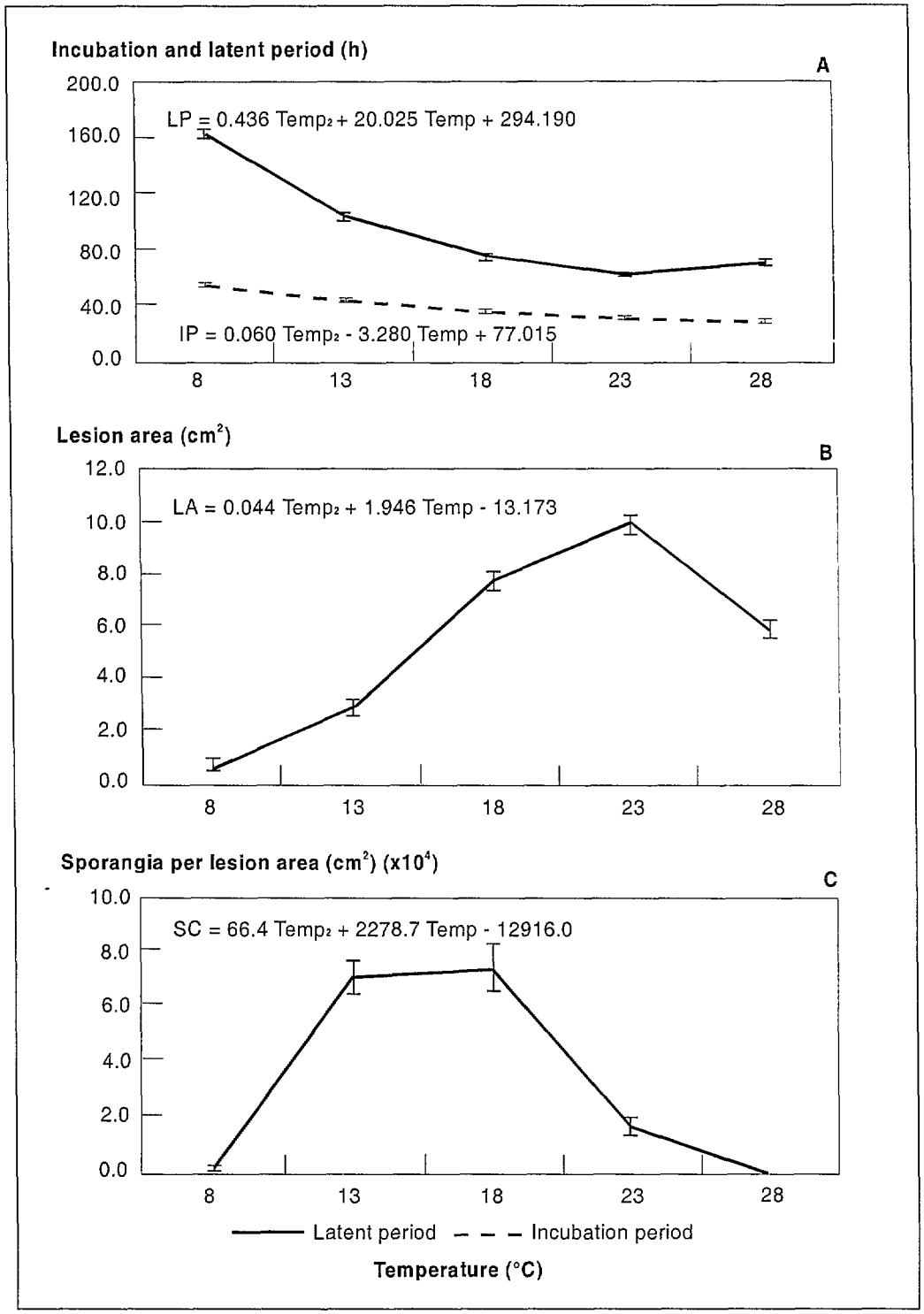

Figure 2. Effect of temperature on (A) incubation and latent period, (B) lesion area, and (C) sporulation capacity in the EC-1 clonal lineage of *Phytophthora infestans*. Each data point represents the average of eight isolates at each temperature. Vertical bars indicate the standard error of the mean.

infestans could be due to other components of parasitic fitness such as infection frequency, infectious period, or improved adaptation to environmental factors like temperature, humidity, or solar radiation. Further data would need to be gathered to test these hypotheses.

The low SC of the new population was also observed in experiment 2. Under similar conditions, Mizubuti and Fry (1998) found SC values of between 3.2 and 5.3 x 10^4 sporangia/cm^2 of lesion for lineages US-7 and US-8. In our experiment we did not find values higher than 0.8 x 10^4 sporangia/cm^2. A lower parasitic fitness has been reported for metalaxyl-insensitive isolates (Dowley and O'Sullivan, 1985; Davidse et al., 1989). Dowley (1987) found that this reduction was due to a lower sporulation. The majority of EC-1 isolates from Peru are insensitive to metalaxyl (Raymundo, 1998); the lower SC could thus be associated with resistance to the fungicide.

In contrast to observations on the pathogen, differences between cultivars were easily detected. The previously reported reaction (Franco, 1994) of cultivars in the field was confirmed in this study. Resistance was associated with lower values of IP, LA, and SC, and higher values of LP. The seemingly illogical negative correlation between IP and LP in our study occurred because the resistant cultivar had a rapid visible response to inoculation. Necrosis occurred earlier in the resistant cultivar Amarilis-INIA than in the other cultivars.

The response to temperature of EC-1 isolates was similar to that previously reported by Mizubuti and Fry (1998). They found similar values for IP, LA, and SC in both old and new populations. We found that the interaction of site by temperature was not significant for the components that were evaluated. This suggests isolates of the same clonal lineage collected from different altitudes have not adapted to temperature in relation to IP, LP, LA, or SC. The movement of the pathogen through infected seed could prevent the isolation necessary for the adaptation of *P. infestans* to temperature. Seed movement between potato production areas is common in the Peruvian Andes.

The data obtained will make it possible to continue with the validation of the SIMPOL simulation model. The regional impact of new disease management technologies will be estimated by linking this simulation model with geographic information systems.

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Estimating the Global Severity of Potato Late Blight with a GIS-Linked Disease Forecaster

R.J. Hijmans[1], G.A. Forbes[2] and T.S. Walker[1]

Late blight (LB), caused by *Phytophthora infestans*, is the most important disease of potato worldwide (Hardy et al., 1995). In many parts of the world, potato production depends on the control of LB with the routine use of fungicides. Poor farmers in developing countries, however, often cannot control the disease, losses can be heavy, and crop abandonment may occur (Ortiz et al., 1999). Although the extent of these losses is difficult to estimate, LB is generally considered the primary biotic constraint to potato production in developing countries (Forbes and Jarvis, 1994; Haverkort, 1990).

CIP has a research program on integrated management of LB that provides resistant varieties and disease management principles to farmers in developing countries. The extent of LB poses a problem for allocating the limited resources available for this work. Ideally, allocations should be made to activities that contribute most to poverty alleviation, food security, and environmental quality. Thus, decisions about resource allocation should be supported by systematic estimates of the loss due to LB in different parts of the world. Unfortunately, that kind of information currently available is incomplete and highly uncertain.

As an alternative, agroecological zoning has been used to guide resource allocation for agricultural research and development (Greyseels et al., 1992). However, generic agroecological zones may not be very useful to deal with specific production constraints such as potato LB. Instead, an agroecological zoning approach that is specific for an agricultural technology or production constraint can be used (Wood and Pardey, 1998; Corbett, 1998).

The strong technological progress in computer hardware and geographical information systems (GIS) software has made the manipulation of large georeferenced databases relatively straightforward. The use of these databases for crop or constraint-specific zoning requires the development or identification of zoning criteria. Criteria that link climatic data with crop growth and production constraints are encapsulated in simulation and forecasting models. Crop growth simulators have been linked to GIS to examine potential crop growth (Han et al., 1995; Van Keulen and Stol, 1995), effects of abiotic constraints such as drought (Van Keulen and Stol, 1995), and effects of biotic constraints (Seem, 1995). Effects of global climate change on plant disease severity were evaluated for rice leaf blast caused by *Pyricularia oryzae* using disease simulation models linked to GIS (Luo et al., 1998).

In this paper we describe the use of a GIS-linked LB forecaster to estimate global disease severity. Running a potato LB forecaster for a complete growing season allows estimating the number of fungicide sprays needed for effective disease management. By linking the forecaster to interpolated climate data on a grid, the number of sprays needed to manage the disease can be calculated for the whole world. The number of sprays needed is an adequate and easy-to-understand proxy for disease severity. Differences in fungicide use have

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2 CIP, Quito, Ecuador.

clear impacts on farmer safety, crop productivity, environmental contamination, and the potential for successful disease management.

Materials and Methods

The LB forecaster used in this study was developed at Cornell University, USA (Fry et al., 1983). It uses daily rainfall, average temperature, and hours of leaf-wetness (estimated to occur when relative humidity ≥90%), to predict the need for protectant fungicide sprays on a susceptible, moderately susceptible, or moderately resistant cultivar.

The necessity for the first spray is forecast on the day that accumulated blight units (BU) reach a threshold. Either a BU or accumulated fungicide unit (FU) threshold, whichever is reached first, predicts subsequent sprays. BU accumulation is based on daily average temperature, hours of leaf wetness, and level of host resistance. FU accumulates with time (unit = day) and rainfall, and represent fungicide obsolescence. BU accumulation and thresholds are dependent on cultivar resistance, but FU accumulation and thresholds are not. There is a minimum interval of 5 days between sprays.

The calculation of BU, FU, and the threshold values were established by iterations of a well-validated LB simulator, also developed at Cornell (Bruhn and Fry, 1981a,b). In the development of the forecaster, cv. Hudson was used as the susceptible, Rosa as moderately susceptible, and Sebago as moderately resistant (Fry et al., 1983).

Climate data were taken from GCLIM10, a database with global monthly climate data on a 10-minute grid (Hijmans, 1999). Minimum and average temperatures, precipitation, number of days with precipitation, and minimum and maximum relative humidity were used in this study. Daily temperature data were derived by linear interpolation between monthly averages. Daily leaf wetness and precipitation were estimated with stochastic weather generators (See Supit et al., 1994, for precipitation).

In temperate regions there may be one clearly distinguishable season in which potato is grown. However, in Mediterranean and (sub)tropical areas, potato may be grown at different times of the year, or even year-round (Forbes et al., 1998; Haverkort, 1990). There is no comprehensive database on planting dates and growing seasons of potato worldwide. Therefore, we determined the most likely growing season(s) for each 10-minute grid cell following rules adapted from previous studies (Stol et al., 1991; Van Keulen and Stol, 1995). In each grid cell there can be between 0 and 12 growing seasons a year, with emergence on the 15th of each month. Potato can be grown in a month where minimum temperature is above 3°C and average temperature is below 22°C. At temperatures below 3°C, frost risk is very high; at temperatures above 22°C, tuberization is strongly reduced (Stol et al., 1991). A growing season can start in any month that permits an accumulation of at least 1,000 degree days (°Cd) in consecutive months without reaching either of the temperature limits. Degree days were calculated as the sum of daily average temperatures minus a base temperature of 2°C. The growing season ends when 1,500 °Cd are accumulated, at 140 days after planting, or when either of the temperature limits is reached.

These rules reflect the fact that growing seasons are generally longer in cooler climates due to slower crop development. Because potato is an irrigated crop in many areas, precipitation is not taken into account to determine length of growing seasons, and irrigation is assumed to be available where needed.

The LB model was run for each grid cell and for each growing season, from emergence until 1 week before the end of the growing season. The number of sprays needed to fully protect a potato crop from

yield loss due to LB was recorded for susceptible and resistant cultivars. Because of the stochastic character of the leaf wetness and rainfall generators, each run was repeated 30 times, and the number of sprays/run was averaged. For grid cells with more than one growing season, the model was run 30 times for each season and the average of all runs was used.

Country averages were calculated using a georeferenced database of world potato production that delineates the potato production zones in each country and indicates the area planted with potato in each zone (Huaccho and Hijmans, 1999). For each potato production zone, the fraction of the national potato area was multiplied by the average number of sprays/ha and then aggregated by country. The results were compared with earlier estimates of actual fungicide use in developing countries. Those estimates were made independently of this study for CIP research priority setting (Walker and Collion, 1997).

Results

The estimated number of fungicide applications required for complete control of LB in a susceptible potato variety is shown in Figure 1. There are striking differences in LB severity between potato production zones. The optimum number of sprays is especially high in the tropical highlands of Latin America, Africa, and Asia; in western Europe, the east coast of Canada, and the northern USA; southeast Brazil, central-south China, and in many coastal areas. Major potato producing areas with low LB pressure include northern China; the plains in India and Bangladesh, where irrigated potato is produced in the cool dry season; and northwestern USA.

By comparing Figures 1 and 2, one can qualitatively appreciate the benefits of a shift from a susceptible to a resistant cultivar. When compared on a country-by-country basis, there is an average reduction of 15% in the optimum number of sprays if susceptible varieties are replaced by resistant varieties (Figure 3). In most countries where LB is a significant problem, the actual number of sprays is below optimum (Figure 4). Large differences between the optimum and actual number of sprays indicate the potential for increasing productivity through improved management of LB.

Discussion

The GIS-linked forecaster appears to be a valid tool for distinguishing areas with different LB severity on a global scale. The tool is probably most useful for comparisons of relative effects, e.g., the relative benefits of host resistance in two countries.

On the whole the predicted optimum number of sprays seems to be low. For a number of countries the estimated current fungicide use is even higher than what is predicted to be optimal (Figure 4). This could be due to errors in the climate and potato distribution data, in the delimitation of the growing seasons, in the forecaster, and in the estimates of current fungicide use. Errors in fungicide use estimates may be due to a bias toward those areas where LB is a problem when the estimates are made. Nonetheless, our results seem reasonable. The actual number of sprays approaches or surpasses the optimum number of sprays in countries with a known high level of control, such as Costa Rica, and is below optimum in countries with a known fungicide use deficit, such as Rwanda (Figure 4).

The accuracy of our predictions in absolute terms is dependent on the quality of the climate and potato distribution data, but especially on the decision criteria. These criteria are encapsulated in a forecasting system that has been validated previously at the field level in the USA (Fry et al., 1983), and the Toluca Valley of Mexico (N. Grunwald, Cornell University, pers. comm., 1999). This forecaster was developed from iterations of a well-validated LB simulator (Bruhn and Fry, 1981a,b), which is driven by weather

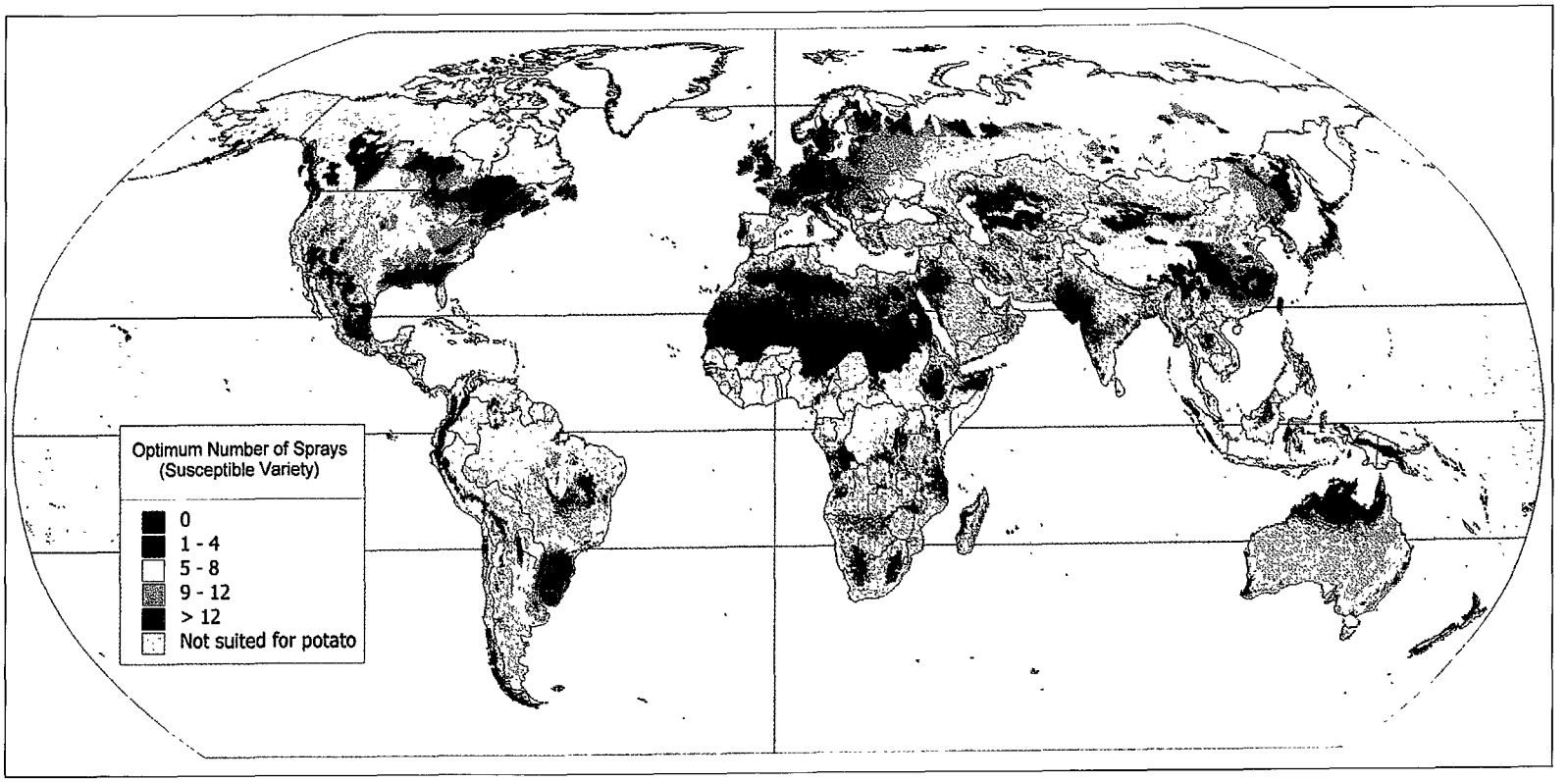

Figure 1. Optimum number of sprays to control late blight in a susceptible potato cultivar.

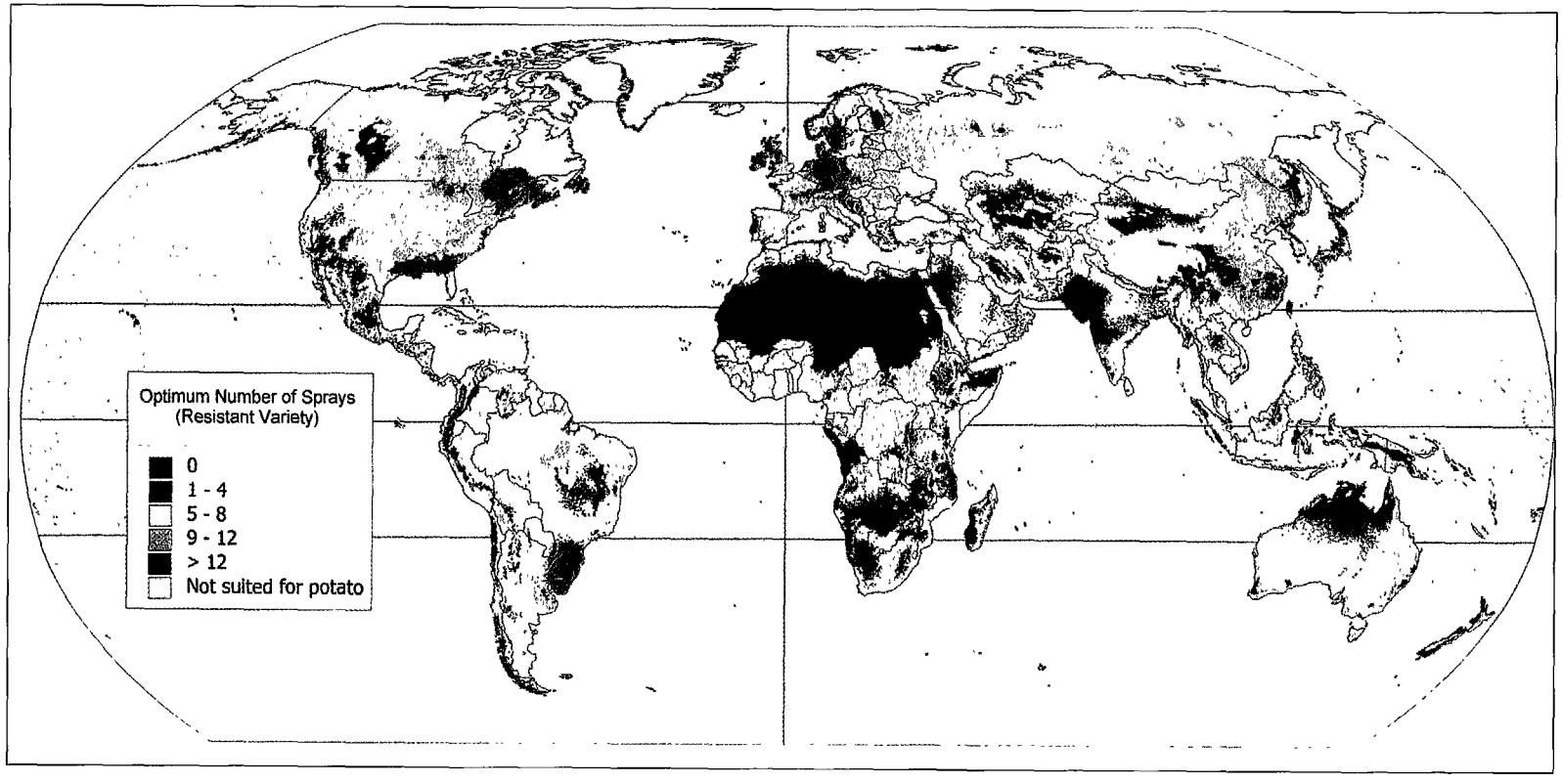

Figure 2. Optimum number of sprays to control late blight in a resistant potato cultivar.

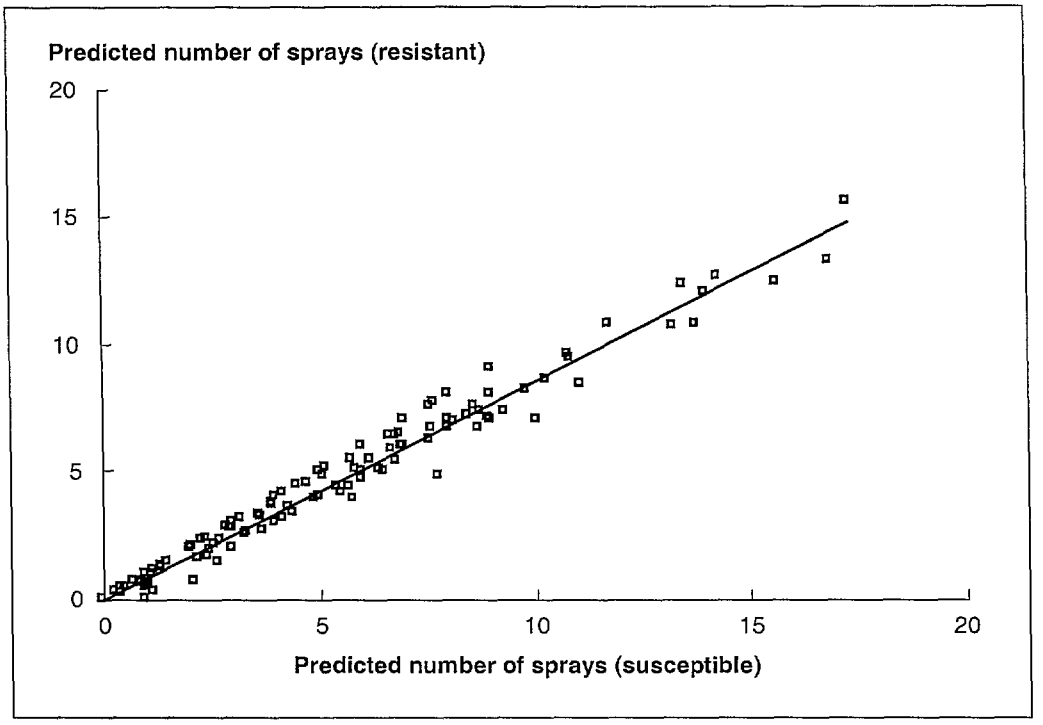

Figure 3. Optimum number of sprays for a susceptible cultivar versus a resistant cultivar. Aggregate values for all potato producing countries. Line: $y = 0.85x$; $R^2 = 0.97$.

variables. A forecaster developed by empirical experimentation would be limited to the conditions in which it was developed.

Fewer actual than optimal sprays in many developing countries, especially in sub-Saharan Africa, were to be expected. In the African highlands, fungicides are generally considered to be underused, one of the reasons behind the widespread cultivation of Cruza-148, a highly resistant cultivar (Forbes and Jarvis, 1994). The opposite case is Indonesia. There the current number of sprays is above optimum and the dominant susceptible cultivar, Granola, is hard to replace because of market preference. In those cases there may be a potential gain in profitability through optimizing fungicide use.

The potential impact of the introduction of LB resistance is huge, especially considering the level of resistance that was used in the forecaster is lower than that used in current breeding programs. Although host resistance is widely used in Sub-Saharan Africa, our results illustrate the potential benefit of a further increase in the deployment of resistance. In addition, increasing access to fungicides and ensuring their safe and effective use could make a great direct impact in this region. A different strategy might be employed for countries such as Mexico. Here fungicide usage is close to that predicted (Figure 4), so that the introduction of host resistance and optimizing fungicide use (Thiele et al., 1998) may have a relatively greater impact. Countries near the origin in Figure 4 should be assigned a low priority in the allocation of funds for global LB research.

Our zoning is based on a number of assumptions. We think they are transparent and simple, and helped us to present a

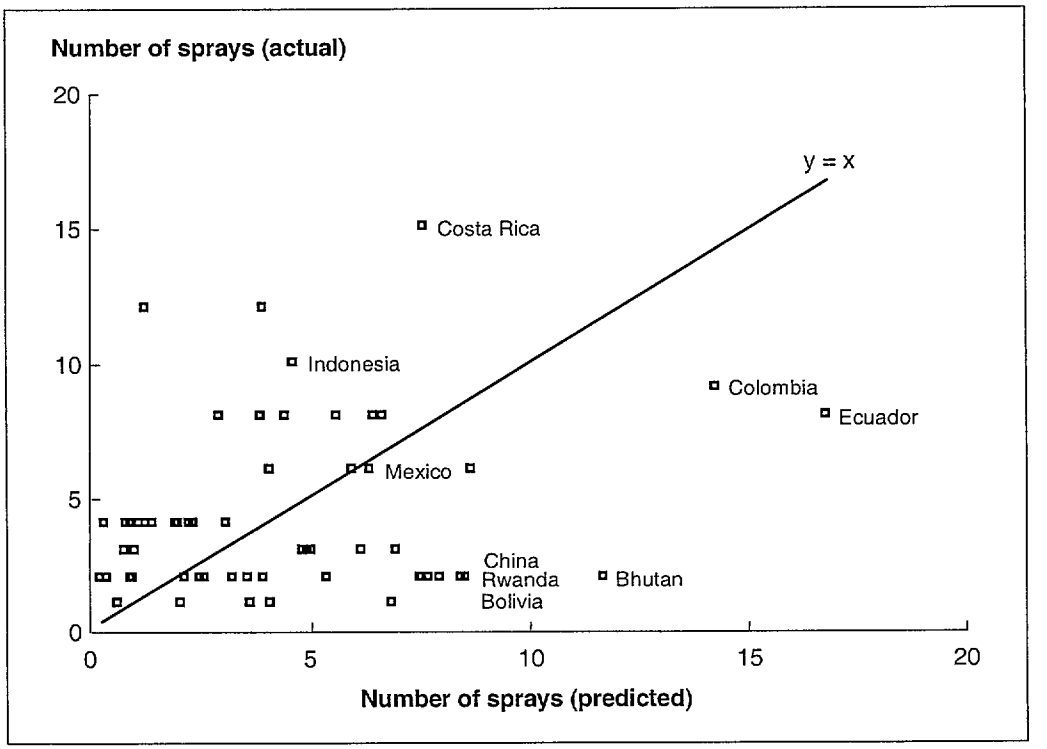

Figure 4. Optimum number of sprays for a susceptible cultivar versus the actual number of fungicide sprays to control late blight. Aggregate values for developing countries.

close approximation to reality. They are, however, subject to discussion and improvement. For example, our method of estimating planting dates should be more formally tested. How farmers adapt to LB pressure would also be of interest. In the African highlands, for example, farmers tend to plant early or late to avoid the wettest season, that most conducive to LB, thereby accepting the increased risk of drought stress (Devaux and Haverkort, 1987). In these areas, the introduction of resistance may actually lead to higher fungicide use if the higher levels of resistance allow planting in the rainy season.

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Implementing IPM for Late Blight in the Andes

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To manage late blight (LB) Andean farmers use resistant potato cultivars and fungicides, as well as other control techniques. Since the spores of the LB pathogen (*Phytophthora infestans*) are too small to see, farmers have neither a clear understanding of the disease or of methods for controlling it. As a result they suffer heavy losses (Ortiz et al., 1999). CIP has been developing potato genotypes with strong levels of partial resistance which slow rather than prevent the epidemic, resulting in less disease and higher yields with fewer fungicide sprays. To get the most out of these new genotypes, however, farmers need to understand the disease better and integrate resistant cultivars with improved fungicide use and other practices.

The farmer field school (FFS) approach is a relatively new extension method based on hands-on learning that has been implemented widely in Asia (van de Fliert et al., 1995). It has been used extensively for managing insect pests in rice, but has also been applied for disease management. The FFS approach should have a number of advantages for implementing integrated management of LB. The season-long training and research format creates an opportunity for farmers, extensionists, and researchers to exchange information and experiences. For example, by learning farmers' reactions to new genotypes, researchers have a better understanding of which characteristics to include in advanced breeding materials. The FFS also gives farmers an opportunity to enhance their knowledge of diseases and disease management through experiments and other hands-on learning activities, as well as through discussions and games. The field experiments provide farmers with earlier access to new partially resistant cultivars and give them an opportunity to systematically evaluate this material. Follow-up experiments allow farmers and scientists to develop integrated management practices appropriate to local conditions and needs. In 1997-98, pilot testing of the FFS approach for managing LB was carried out in Peru and Bolivia. This paper provides a critical assessment of early progress.

Methods

We selected seven pilot sites to test the new approach on the grounds that potatoes grown by small farmers were the main crop, LB was the principal production constraint they faced, and local institutions were interested in collaborating. In Cajamarca, Peru, the non-governmental organization (NGO) CARE was responsible for four, whereas INIA (Instituto Nacional de Investigación Agraria) led a fifth. In Morochata, Bolivia, the National Potato Research Program (PROINPA), led two FFS, and began to involve an NGO, ASAR (Asociación de Servicios Artesanales y Rurales). Fixed groups of farmers interested in learning more about LB and its control participated at each pilot site.

We developed and refined field guides for use by FFS facilitators. These contained different training sessions sequenced to fit a whole growing season and to progressively facilitate farmers' acquisition of knowledge and skills in managing LB. In Bolivia, a strategy for controlling LB in susceptible cultivars had already been extensively field-tested, and this formed the focal point for the FFS (Thiele et al., 1998). The strategy

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2 CARE, Peru.
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includes early preventive application of a systemic fungicide, alternating the use of systemic and contact fungicides, and climate dependent intervals between sprays (Navia et al., 1995). In Peru, the FFS curriculum was broader including aspects such as research principles, biological aspects of LB, and fungicide action (Table 1). At the core of the FFS in Peru was a trial managed by the farmers to evaluate new LB resistant cultivars and understand the interaction between resistance and fungicide use. In both Peru and Bolivia emphasis was placed on learning underlying biological principles, although teaching styles differed between the two sites (Table 2).

Table 1. Activities carried out during the FFS (Peru).

Session no.	Topic	Type of activity
1	• Introduction to FFS • Review of activities planned • Evaluation of farmer knowledge and practices	• Group discussion
2	• Experimental design: concepts of experimentation and randomization • Field experiments: varieties vs. strategies for chemical control	• Field exercise • Hands-on learning activity
3	• Seed quality • Tuber blight • Supplementary small experiments	• Group discussion • Hands-on learning activity
4	• Sources of inoculum • Diagnosis and disease culture experiment	• Hands-on learning activity
5	• Life cycle of *P. infestans* • Results of disease culture experiment • Evaluation of tuber blight	• Group discussion and hands-on learning activity
6	• Disease and environment • Results of life cycle experiment	• Group discussion • Hands-on learning activity
7	• What is integrated disease management? • Chemical control • Exercise with fungicides	• Group discussion • Hands-on learning activity
8	• Fungicide application Nozzle selection Backpack calibration Good spraying practice • Results of fungicide exercise	• Field exercise • Hands-on learning activity
9	• Simulation of disease spread • Genetic resistance	• Hands-on learning activity
10	• Precautions in the use and proper storage of pesticides • Chemical control strategies	• Group discussion and practice
11	• Positive selection	• Group discussion and field exercise
12	• Harvest and economic analysis • Discussion and future plans	• Group discussion

Table 2. Training methods compared.

	Bolivia	Peru
Pilot areas	Morochata	San Miguel
Collaborating institutions	Research Center, some NGO	NGO, some Research Center
Number of field schools	2	5
Participants in each FFS	10 to 20	7 to 25
Sessions in FFS	10	12
Potato varieties used	One moderately susceptible	12 with different levels of resistance
Emphasis	Technology adaptation and training in fungicide use	Knowledge acquisition by farmers and access to new materials with LB resistance
Focus of technological development	Validating existing strategy for chemical control	Selecting resistant varieties and developing strategy for combining resistance with levels of fungicide use
Experimental design	Each farmer had single plot where strategy was tested and compared to farmers without training	Experiments were conducted at the schools and consisted of 12 varieties and three intensities of fungicide use
Principal learning activities	Games, observation, hands on learning	Group dynamics, hands on learning, observation
Impact indicators	Farmer knowledge, practices, AUDPC, yield, and economic benefits	Farmers opinions about benefits (impact evaluation will begin in 1999)

Integrated pest management (IPM) technology was tested at both sites. In Bolivia, this principally involved farmers validating the existing strategy for managing LB based on improved fungicide use with the moderately susceptible cultivar Waych'a (grown by nearly all farmers in the pilot region). There was no experimental design as each farmer tried out what he had learned on a whole plot. Farmers purchased all their own inputs. Facilitators collected data on the fungicides applied, doses and dates of application, and measured LB damage periodically on the plots of 20 of the participating farmers. Yields were measured by taking two 10 m crop cuts on each plot. The LB damage data were used to calculate the area under the disease progress curve (AUDPC). The same data were collected from a control group of 15 farmers who did not participate in the training. Farmers in the FFS evaluated all of the plots at flowering and harvest to appreciate the contribution of different control regimes.

In Peru, no fungicide spray strategy existed. The overall aim was to work with farmers to develop efficient site specific management strategies integrating fungicide use with different levels of partial resistance. Trials of cultivars and breeding lines were intended to allow farmers to evaluate new materials with partial resistance at different levels of fungicide use. An experimental design was used with 12 cultivars showing different types of resistance and three levels of fungicide use: low (2 sprays), medium (4 sprays), and high (6 sprays). Each treatment was identified with a

colored plastic flag and a group of farmers was in charge of spraying and evaluating. Farmers helped collect data on LB damage and yields, and drew conclusions through their observations and discussions over the course of the season. The CARE facilitators and CIP staff recorded and analyzed the data and calculated AUDPCs. Apart from the formal evaluations of disease damage, farmers evaluated the different cultivars and treatments informally as the crop was growing, by studying foliage and checking yields.

Results

In Bolivia, participation in the FFS led to an increase in farmer knowledge (Table 3). Farmers who received training began spraying on average five days before farmers without training and continued for five days longer. They applied fungicides more frequently, with doses closer to recommended levels and better coverage of foliage. This was translated into lower levels of AUDPC among the FFS farmers even when different numbers of applications of fungicide are controlled for (Figure 1).

Costs were slightly higher for farmers who participated in training as they made more fungicide applications. But the plots of farmers with training yielded over 8 tons more on average (an increase of 86%), giving an additional net benefit to FFS farmers of more than US$2,000 (Torrez et al., 1999).

The 1997-98 cropping season in Peru was unusually humid because of El Niño, and LB pressure was particularly high. The effects of this can be seen in the AUDPCs for the different treatments, with six genotype cultivars having high AUDPCs even with high levels of fungicide use (Figure 2). Since it was such an exceptional year farmers focused their attention more on varietal response to the disease and less on evaluating strategies for fungicide use. Only seven cultivars had a yield of at least 1 kg per plot (40-plant plots from which tubers from surviving plants in the two center rows were harvested [a maximum of 20 plants]). Farmers eliminated two of the seven cultivars from their final selection because of poor culinary quality (Figure 3). They selected three cultivars and one clone

Disease culture experiment: An example of hands-on learning

In the fourth session of the farmer field school in Peru, farmers prepared a sporangial suspension by washing infected foliage. Using a mini-microscope and hand lenses, the farmers observed the sporangia in the wash-water and on the lesions that were the sources of the inoculum. They enhanced their observations by sketching the specimens.

Healthy potato leaves were dipped in the sporangial suspension and then placed in plastic boxes (disposable containers obtained at a local supermarket) which served as humid growth chambers. Farmers also dipped healthy leaves in clean water and placed them in plastic boxes. Farmers observed changes in the leaves over the subsequent week, and analyzed the results in the FFS session a week later.

By asking questions about what happened and why, farmers discovered for themselves mechanisms of infection. This exercise provided farmers the opportunity to know where late blight comes from and to understand that this disease is caused by a living entity and not by humid climatic conditions that only contribute to its development. In this way, scientific information helps farmers build new understanding.

Table 3. Knowledge of LB and control measures in Morochata, Bolivia.

	Farmers responding correctly (%)	
Learning component (question)	FFS group (20 persons)	Control group (15 persons)
Sporulation on the back of the leaf is symptom of LB	65	27
Concentric rings or yellowing is symptom of *Alternaria*	65	13
A systemic fungicide moves within the plant	90	33
A contact fungicide only protects where it reaches	80	26
A fungicide is for plant diseases	45	27
An insecticide is for insects	60	27
Name two or more contact fungicides	65	40
Name two or more systemic fungicides	70	26

Source: Veizaga, 1999.

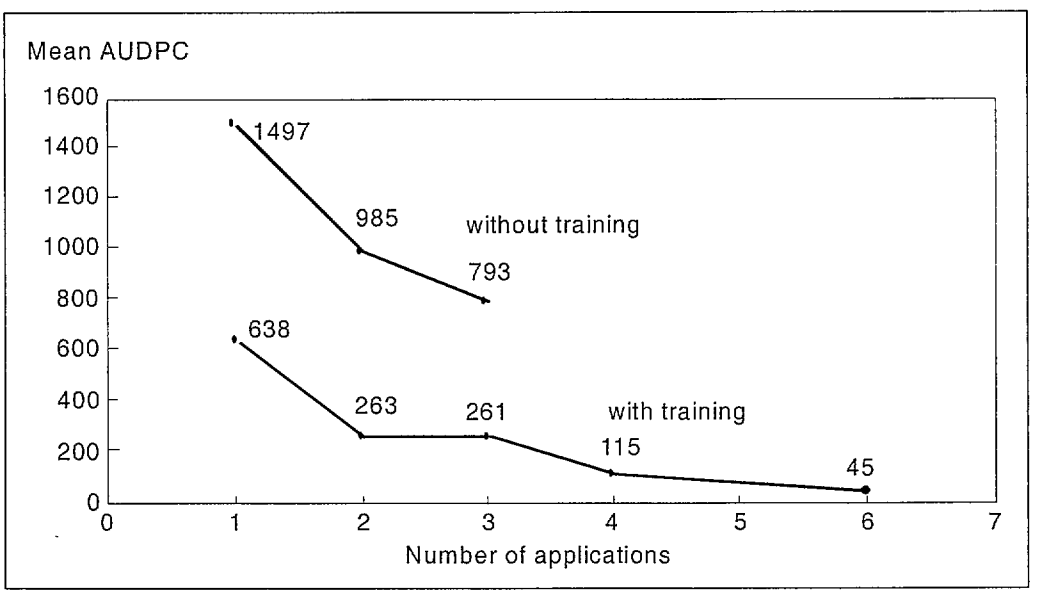

Figure 1. AUDPC and number of applications of fungicide, Morochata, Bolivia.

(Amarilis, Chagllina, Atahualpa, and 377740.1) for further evaluation and use because these were perceived to have good market acceptability (similar to local traditional cultivars) and because they yielded well even with low levels of fungicide. Farmers identified access to new cultivars that are not yet available on the local market as an important benefit of participating in the FFS (Groeneweg and Schouten, 1999), and they have begun multiplying seed of the materials they selected on their own.

A baseline study of LB management in Peru showed some differences in farmers' knowledge about the biology of LB amongst FFS farmers (Table 4). So far, evaluation of impact on farmers' production systems has been largely qualitative. Two focus groups were conducted to identify farmers' opinions about the benefits of the FFS. Farmers

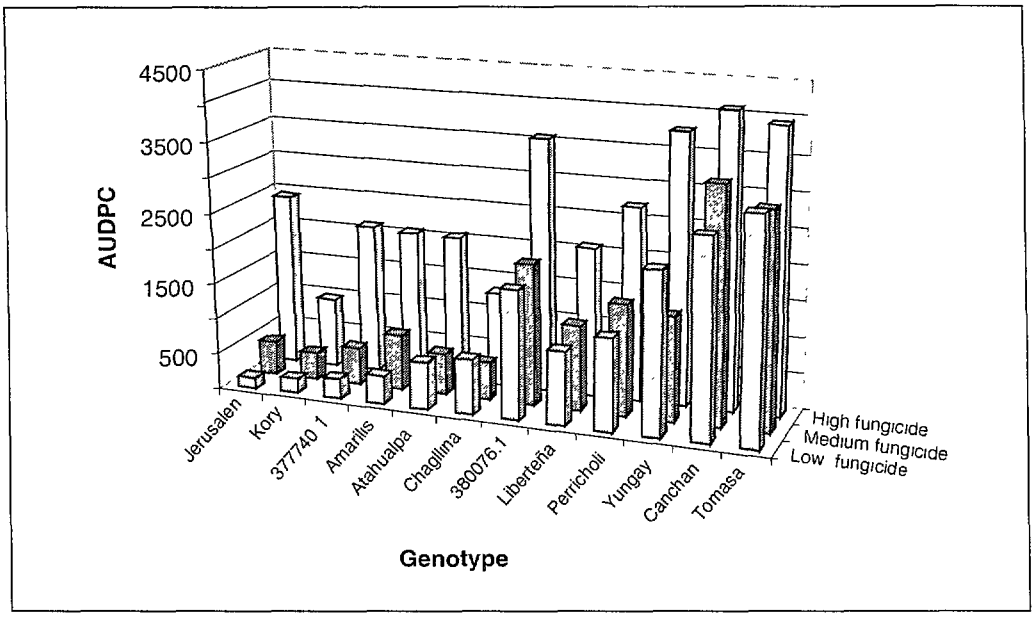

Figure 2. AUDPC and levels of fungicide use, Cajamarca, Peru.

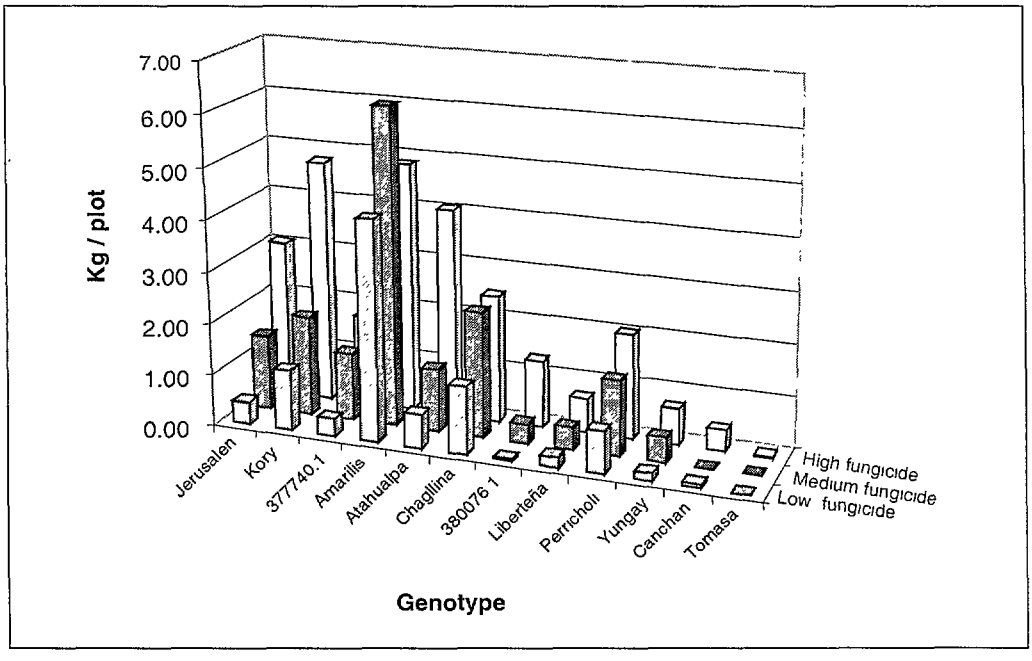

Figure 3. Yield and levels of fungicide use, Cajamarca, Peru.

Table 4. Knowledge of LB and control measures in Cajamarca, Peru.

	Farmers responding correctly (%)	
Learning component (question)	FFS (10 persons)	Non-FFS (30 persons)
LB is caused by rain, fog, or lightening (false)	70	4
LB is caused by a fungus (true)	70	4
Any dark spot is LB (false)	70	0
Sporulation as symptom of LB (true)	70	0

Source: Ortiz and Winters, 1998. Part of a baseline study of LB conducted in Cajamarca, Peru, in 1998. Unpublished

indicated that the most important benefit was improved understanding of the principles involved in disease progression and management. This helped them understand that LB was not something "magical" but something that could be controlled. Knowing this also enhanced their confidence and self-esteem. A three-year impact evaluation project will begin in 1999 to assess the extent to which new knowledge helps farmers to reduce losses and increase profits.

Some Difficulties to Overcome

This was very much a learning experience for those developing the FFS approach for integrated pest management of late blight, and not everything went perfectly. In both Peru and Bolivia, FFS facilitators received little training in the method and as a consequence there was a tendency to use traditional extension methods and not fully exploit hands-on learning. Intensive FFS facilitator training is being planned to overcome this critical difficulty. These pilot FFS efforts focused on LB control but farmers and facilitators noted that other pests were also important. New versions of the FFS curriculum under development should help address this weakness.

In Peru, the FFS attempted to develop understanding of more complex concepts, including experimentation, randomization, and genetic resistance. Examples were taken from the farmers' own context but the link between the example and reality was not always clear to the farmers. In the cultivar by fungicide trial, some farmers failed to see that the objective of the experiment was to identify best fungicide treatments for each cultivar. One group declined to continue the studies for a second season because they did not like to see potato plants dying (Groeneweg and Schouten, 1999). This suggests that more time and effort needs to be taken to develop farmers' understanding of the role of experimentation in learning. Finally, the FFS presents a new approach to which farmers are not yet accustomed. The FFS is designed basically to provide information and knowledge but farmers have come to expect material inputs (seed, fertilizer, pesticides), as they have received these materials from other organizations in the past. Care needs to be taken in clarifying the new philosophy with farmers at the outset.

In Bolivia, one weakness of implementation was the almost exclusive concentration on chemical control methods. The curriculum is being expanded to give more importance to genetic resistance and FFS farmers will also evaluate new resistant materials. There were also problems with the sequencing of some of the sessions. A key session on the life cycle of the pathogen took place after a session on the strategy of chemical control. As a result, farmers were less able to understand the principles underlying the control strategy. As the curriculum is reworked more care is being taken with appropriate sequencing. Finally, women took no part in the FFS.

Even though men typically make most decisions relating to pesticide use, more attention needs to be paid to understanding how women can be appropriately involved.

Despite these difficulties, in both Peru and Bolivia the FFS participatory approach was clearly a success as judged by the enormous enthusiasm on the part of the farmers in learning more about LB.

Conclusions

While there were some elements in common between the experiences at the two sites, there were also substantial differences. To a certain extent the experiences were complementary. In Bolivia, the focus was on adaptation of an existing technology as farmers tested a strategy for chemical control with a susceptible cultivar. In Peru the emphasis was on learning to work with resistance, and on improving farmers knowledge about LB and its management without promoting a specific strategy. This complementarity means that much can be learned by sharing information between countries and partners.

A careful study of the longer-term impacts of the approaches taken in Peru and Bolivia should help us design FFS better. Impact studies are planned for Peru to determine whether in the case of LB, enhancing knowledge about biological principles and increasing availability of cultivars with resistance results in increased yields and profits. It is also important to determine how information imparted through FFS spreads, as it may be that complex knowledge about biophysical principles does not spread easily from farmer to farmer. A careful comparison of the longer term costs and benefits of the technology adaptation approach taken in Bolivia compared with the knowledge enhancing approach taken in Peru should help us to understand the appropriate weight to be given to each in the FFS.

It is clear from the first year's experience that an FFS requires considerable time and resources. Nevertheless, as the data from Bolivia show, the returns that can be achieved by helping farmers to control LB are very high, indeed much greater than those reported for insect pests in rice, (studies in Java indicated yield gains of 12 to 24%) where FFS has been widely used (van de Fliert et al., 1995) . And although FFS are intensive and relatively costly, the financial investment in FFS for LB is highly attractive. A project supported by the International Fund for Agricultural Development has recently been initiated to scale up the initiative reported here, involving China, Bangladesh, Uganda, and Ethiopia, as well as Peru and Bolivia. In each country, partners from national agricultural research centers and NGOs work together with farmers. Critical elements to success are ensuring that partner institutions understand and are committed to FFS and that those facilitating FFS are themselves properly trained.

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Understanding Farmers' Responses to Late Blight: Evidence from Peru, Bolivia, Ecuador, and Uganda

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It is ultimately a farmer's decision whether or not to adopt a technological solution to a problem. In developing countries, however, information for farmers' decision-making is scarce, and the infrastructure for generating and maintaining decision-support systems to assist farmers is deficient. Therefore, in order to identify potential points for intervention in disease management, it is necessary to understand how farmers respond to diseases such as late blight in potatoes. As a first step toward this understanding, a baseline study was conducted in Peru, Bolivia, Ecuador, and Uganda between November 1997 and August 1998. The results of this study will help the participatory development of integrated late blight (LB) management. Specific objectives of the study were (1) to estimate losses in yield and income due to this disease; (2) to document farmers' knowledge and practices (particularly of fungicide use) in relation to LB control; and (3) to document potato-related activities of extension organizations at the pilot sites.

Methods

For each of the four countries, a semi-structured questionnaire was the main data collection tool. Additionally, informal interviews, focus groups, non-participant observation, and field evaluations were used to enhance the validity of the research. The research was carried out in collaboration with personnel from the corresponding national programs.

Pilot sites were selected where potato is an important crop, and where LB is endemic. In Peru, the work was focused in the Department of Cajamarca with the participation of 131 farmers. In Bolivia, data were collected from 45 farmers in Ayopaya Province. Two hundred and seven farmers in the Ecuadorian provinces of El Carchi, Cotopaxi, Chimborazo, and Bolivar were included, and in Uganda, Kabale, Kisoro, and Mbarara districts were included in the research with data collected from 118 respondents. This paper summarizes the main findings of this study in the four countries. Information is based on the data collected by teams working in each of the countries and the reports written by those teams.

Results and Discussion

Farmers and the potato systems

The potato crop was important for income and food security at each pilot site, although it was one of several crops managed by farmers. Most informants in the study were small farmers with less than 5 ha of land. The majority owned their land. In Uganda and Ecuador, a sizable minority (28% and 14%, respectively) were tenants.

Most of the participating households derived the bulk of their income from agriculture and livestock management. Some farmers (less than 30% of informants in Peru and Uganda) also depended on off-farm activities to generate supplementary income, such as small businesses, temporary labor, and artisanal activities.

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5 NARO, Uganda.

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On average, Bolivian and Peruvian farmers planted less than 1 ha of potato, which is typical for subsistence farmers in the Andean Region. In the Ecuadorian case, the figure was higher (1.8 ha) because the sample included commercial areas such as El Carchi Province. In Uganda, however, farmers grow about a fifth of a hectare (0.18 ha) in potato because they have less land available for cultivation. Yields varied across countries. In Bolivia 12.7 t/ha, and in Ecuador 12.6 t/ha were reported. These numbers represent relatively good yields compared with Peruvian farmers who harvested an average of 4.9 t/ha. In Peru, yield was greatly influenced by the adverse weather conditions caused by "El Niño" during early 1998. In Bolivia, Ecuador, and Peru, yields were evaluated by sampling fields; in Uganda, yields were estimated from information provided by farmers where an average of 7.0 t/ha was reported.

Importance of late blight for farmers

From the farmers' point of view, LB is considered either as the primary or secondary potato pest in the pilot sites in the four countries. Figure 1 presents the indexes obtained from the farmers' ranking of pest problems in Peru and Uganda. The Peruvian case also applies to Ecuador and Bolivia. In all countries, however, LB was not the only problem. There were other pests that caused concern and were perceived as reducing potato yields and quality. In Uganda, for example, bacterial wilt was ranked as more important than LB. In Ecuador, Bolivia, and Peru, the Andean potato weevil ranked just below LB as a key pest (Ortiz et al., 1996). Hence, in designing programs for the improved management of potato pests, it is important to recognize that farmers face multiple problems.

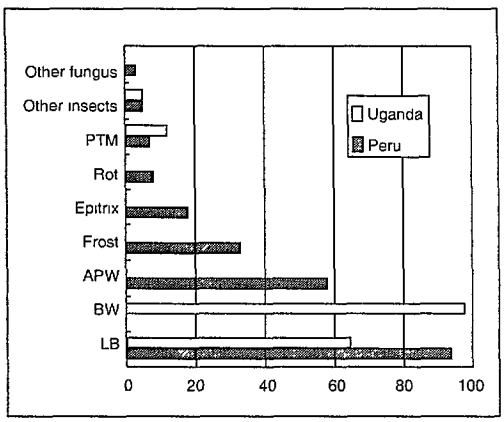

Figure 1. Index of pest problems perceived by farmers in Peru (n=131) and Uganda (n=118). Note that farmers in Peru consider frost a pest. Key: LB: Late blight, BW: Bacterial wilt, APW: Andean potato weevil, PTM: Potato tuber moth.

Late blight damage was evident during field evaluations in the Andean countries, but damage varied according to a number of factors (Table 1). The disease increased during the potato season, and those fields that were planted late (coinciding with the rainy period) tended to have more damage. Late blight damage was inversely correlated to fungicide applications. Plot location and the cultivar of potato that farmers used also influenced disease damage.

Potato fields were evaluated during the growing season and also at harvest time in Peru, Ecuador, and Bolivia. In Uganda, this part of the study will be repeated in 1999. Considering potato yield as a dependent variable, and disease damage as an independent variable and controlling for other factors, it was clear in Peru, Bolivia, and Ecuador that LB reduces potato yields. Figure 2 illustrates the negative relationship between LB damage and yield in four Bolivian communities, where an R^2 of 0.8 was obtained. In addition, data from Peru and Ecuador also provided evidence of the devastating effects of this disease at the field level.

A conservative 20% difference in severity between appropriate and inappropriate LB control can be used as the lower bound to estimate losses. According to estimates, each 20% increase in LB severity reduces yield from between 1 t/ha (in Peru) to 4 t/ha (in Ecuador). This conservative

Table 1. Regression of late blight severity in the Peruvian sample.

Variable	t-statistic[a]	Coefficient
Days after planting	0.31	2.06 **
Days after planting squared	0.002	3.10 ***
Planting date	0.55	10.18 ***
Fungicide applications	- 1.21	- 2.88 ***
Potato varieties:		
Amarilis	- 14.40	- 3.74 ***
Canchan	15.20	4.10 ***
Chaucha	- 9.45	- 1.84 *
Liberteña	- 8.86	- 2.70 ***
Perricholi	1.01	0.18
Yungay	4.35	1.18
Places		
Contumaza	10.08	2.45 **
San Miguel	8.58	2.59 ***
Constant	- 7568.41	- 10.18
Number of observations		355
R^2	0.54	

[a] t-statistic reference location is Cajamarca and varieties are those that are either native or not used by a substantial number of farmers. *, **, and *** indicate significance with 99%, 95%, and 90% confidence, respectively.

estimate is lower than the figures reported by Baylon (1987) who indicated losses of about 6 t/ha in Peru, and those reported by Thiele et al. (1998) who indicate that an average of 6.5 t/ha could be lost to LB in Bolivia.

With 1998 prices, US$140/t, a reduction in potato yield would mean a loss of between US$140/ha to US$560/ha in Peru, and between US$250/ha and US$1,000/ha in Bolivia where potatoes are valued at US$250/t. For small farmers, yield reduction caused by LB causes a significant loss of income from their land, and reduces food availability for the household.

It is difficult to extrapolate the results of a pilot study to the situation in an entire country, but the extent of the losses can be estimated. In Peru, farmers grow an average of 250,000 ha of potatoes per year. Using conservative estimates, 20% of the total area planted to potatoes could be severely affected by LB each year. This would mean a total monetary loss of between US$7 million and US$25 million per year. In Bolivia, Thiele et al. (1998) report that LB affects 20,000 ha. Using 1998 potato prices, this represents a loss of between US$5 million and US$20 million per year. It is clear that this range of losses justifies investment in developing control strategies. And any strategy that can contribute to the reduction of LB damage will have a direct effect on increasing yields, and in turn, farmers' income and food security (Torrez et al., 1999).

Farmers' knowledge of late blight and practices to control the disease

Unlike insects, diseases are difficult to see; farmers do not usually know the causal agent of plant diseases (Bentley, 1990, 1991). This was confirmed by the findings of this study that showed that farmers lack

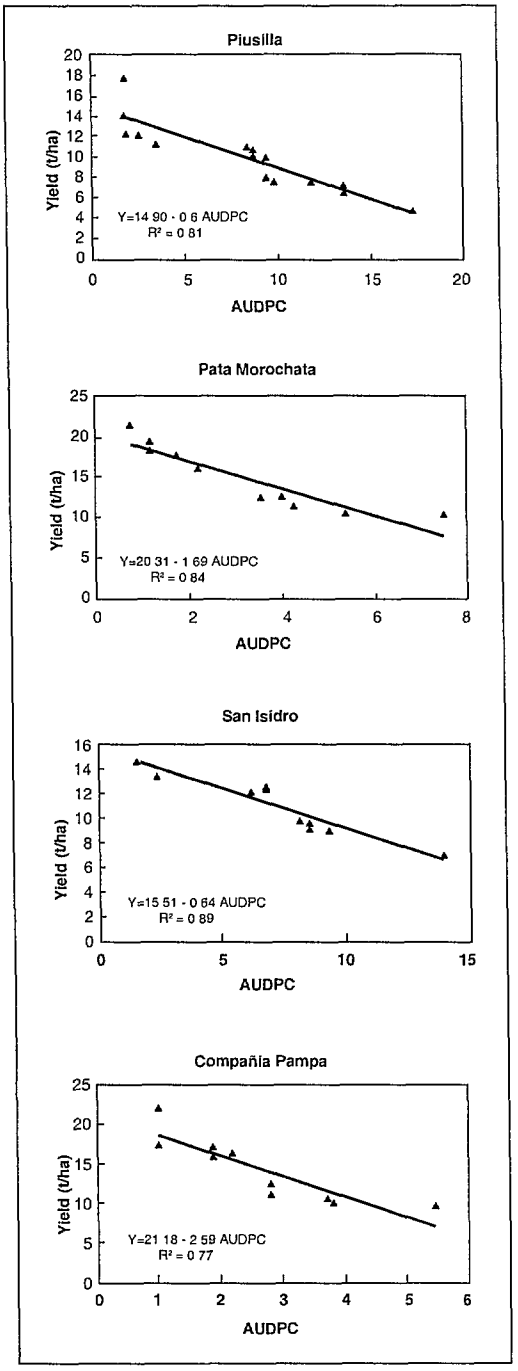

Figure 2. Relationship between late blight damage and yields in four Bolivian communities during 1997-1998 cropping season. Key: AUDPCr (area under the curve - an index for disease progression).

knowledge of late blight biology. Most of them did not know that the real cause of late blight is a microorganism. They associated the disease with the weather conditions that favor its occurrence such as heavy rainfall, fog, cold weather, and even lightning. Additionally, farmers were unable to correctly diagnose the disease. More than 88% of informants confused the symptoms of late blight with other fungal diseases or with "leaf burning" caused by excess pesticide use.

When asked about different control practices, farmers in all the participating countries were most familiar with fungicide use, and LB control is largely based on this chemical control method. In Uganda about 69% of farmers used fungicidal products compared to more than 95% in the Andean Countries. Yet it was clear that most farmers did not know how to differentiate contact fungicides from systemic fungicides, and they tended to spray any available product according to their experience.

During the study period, farmers sprayed an average of 3 times per cropping season in Uganda and Bolivia, 5 times in Ecuador and 7 times in Peru (3 to 4 sprays are common in Peru in a normal year). The number of sprays was influenced by local weather conditions. According to a multi-variable regression analysis run in Peru, fungicide use was influenced by a number of factors (Table 2). Younger, educated, and wealthier farmers tended to spray more. The planting season also influenced fungicide use; those farmers who planted in the rainy season sprayed more often because this period is most conducive to the disease. Plot location also influenced the pattern of fungicide use, so farmers spray more frequently in those places that have higher relative humidity (San Miguel and Contumaza shown in Table 2). It is important to note that there is no evidence that the use of resistant cultivars influences fungicide use in Peru. The reason may be that most farmers plant resistant and susceptible cultivars together (in strips) and

Table 2. Regression on fungicide use in the Peruvian sample.

Variable	Coefficient	t-statistic[a]
Age	-0.04	- 1.95*
Education level	0.26	2.33**
Family labor	0.01	0.06
Land owned	0.53	2.16**
Potato varieties:		
Amarilis	-3.66	-0.66
Canchan	0.47	0.84
Chaucha	1.38	1.63
Liberteña	-0.35	-0.62
Perricholi	0.93	1.22
Yungay	-0.18	-0.37
Planting date	0.21	3.27***
Places		
Contumaza	3.34	4.24***
San Miguel	3.38	4.29***
Constant	- 286.03	- 3.22***
Number of observations		131
R^2		0.56

[a] t-statistic reference location is Cajamarca and varieties are those that are either native or not used by a substantial number of farmers; *, **, *** indicate significance with 99%, 95%, and 90% confidence, respectively.

tend to spray both at the same time. Evidence from the countries included in this study shows that each farmer may have his own control strategy, as opposed to the uniform control strategies used in temperate countries (Mackenzie, 1981).

The Peruvian and Bolivian data indicated that the number of sprays was inversely and significantly associated with the extent of LB damage. Potato fields in which farmers sprayed more tended to have less damage.

Farmers used a number of commercial products with a range of active ingredients (Table 3). In Uganda just two active ingredients were found on the market. Between six and eighteen were present in the Andean countries. Mancozeb was by far the most commonly used active ingredient in Uganda because it was relatively inexpensive. At the Bolivian pilot site, farmers used up to six active ingredients; propanocarb was the most common. The Peruvian pilot area presented more variability of active ingredients. A total of 13 different ingredients was found in the sample, and metalaxyl was the most commonly used. The Ecuadorian case had an even higher variability of chemical products to control LB (up to 18), and the most common active ingredient, mancozeb, was used in a total of 47% of applications. This variability of chemical products used to control LB, mixed frequently with insecticides, represents a threat to other living organisms (Pilling and Jepson, 1993; Schuster and Schoreder, 1990). The higher variability of active ingredients in Latin America also reflects the growing market for pesticides in the region, in comparison to the less developed market for these products in Africa (Repetto and Baliga, 1996).

Table 3. Main active ingredients used as fungicides by farmers in the pilot sites.

Country	Active ingredients	Most common active ingredients[a]	Proportion of sprays (%)
Uganda	2	mancozeb	90
		metalaxyl	9
Bolivia	6	propanocarb	44
		ofurace + mancozeb[b]	25
		chlorothalonil	19
Ecuador	18	mancozeb	25
		cymoxanil + mancozeb	16
		cymoxnil + propineb	9
		sulfur	6
Peru	13	metalaxyl + mancozeb	42
		mancozeb	24
		propanocarb	19
		metiram	7

[a] Only the most common active ingredients are included in this column.
[b] (+) Means both active ingredients were combined in the same commercial product.

There was also a great deal of variability of fungicide doses used by farmers to control LB. In Peru, for example, farmers tended to use less than the recommended dose. In commercial potato growing areas in Ecuador, however, farmers tended to use a higher dose than that recommended, generally by mixing different chemical products (Crissman et al. 1998). In Uganda, 30% of farmers also used more than the recommended dose. But, according to farmers and extension officers, the reason is the existence of adulterated products. Farmers increased the dose in order to make sure that they could control the disease.

The cost of fungicides was difficult to elicit from farmers because in most cases they did not keep records of the products they use. However, costs in Peru and Ecuador average US$140/ha and US$150/ha, ranging from zero to US$500/ha. These estimates are equivalent to 10-15% of total production costs. This is consistent with data reported by Baylon and Otazu (1987) in Peru, and Crissman et al. (1998) in Ecuador. An important issue is that pesticide use represents an out-of-pocket cost. The challenge is to develop less expensive methods of pest control using either nonchemical or more appropriate chemical methods, so that farmers can reduce the amount of fungicide they use.

Cultivar use and LB damage

Between 50% and 100% of farmers in the four countries were aware of the differences in LB resistance of potato cultivars. However, farmers preferred particular cultivars for more reasons than just LB resistance. Farmers in Uganda preferred cultivars that matured early. They wanted to harvest potatoes in approximately four months in order to have the land free for another crop. In Peru, earliness was less important because most farmers have only one growing season per year. Among the Peruvian farmers, 85% preferred cultivars with resistance to LB, whereas in Uganda only 12% of farmers felt that

resistance was an important attribute. LB was not their main source of concern.

Evidence from Peru suggests that LB severity is statistically correlated with cultivar use (see Table 1). There were cultivars (Amarilis, Chaucha, and Liberteña) that showed resistance at the field level. There were also susceptible cultivars such as Canchán. This suggests that genetic resistance can play a key role in reducing LB damage at the field level, and that resistant cultivars can be a crucial component of an integrated management strategy against this disease. The continuous deployment of resistant cultivars would mitigate the risk associated with resistant cultivars currently in the field becoming susceptible to LB.

Extension activities and LB control

In Peru, Bolivia, and Ecuador, nearly all institutions working with agriculture in the pilot areas focused to some degree on potato production. In Uganda, however, this was not the case because potatoes are not as important a crop there as they are in the Andes. Government extension services in all four countries were inappropriate in terms of number of extension personnel, coverage and facilities. However, non-government organizations (NGOs) have been increasingly participating in providing these kinds of services to farmers (Bebbington and Thiele, 1993).

The main potato-related activity carried out by extension organizations is the provision of technical assistance, particularly related to the use of agro-chemicals, and the provision of credit though revolving funds for seed, fertilizer, and pesticide. The participation of NGOs as pesticide providers to farmers has increased in recent years. However, evidence suggests that extension institutions are also important sources of new potato seed for farmers, so that new cultivars could be distributed through this channel.

Farmer training on LB biology and how to control this disease is limited. Most organizations still use a top-down technology transfer approach based on providing recommendations. This could have negative implications when trying to promote integrated pest management. This technology requires horizontal and participatory methods of exchanging information and knowledge as suggested by Röling and Van de Fliert (1994), and Torrez et al. (1999).

Conclusion

According to farmers' perceptions, LB ranks as the most important pest problem in the Andean countries included in the study, and as the second most important pest in Uganda. Farmers' concern with LB is understandable considering that, as this study shows, this disease indeed reduces potato yields, and is a real threat to potato production, food security, and farmers' profits. This suggests that investment in developing and disseminating control strategies in developing countries would be profitable. However, LB is also part of a complex pest system that depends on location, type of farmer, and management strategies. Development of control strategies must be flexible enough to integrate other local pests of economic importance. In addition, pest control is only one of several endeavors for farmers, therefore any control strategy should be adaptable to existing production activities and goals.

Farmers' lack of knowledge about biophysical principles related to pest control was a common feature in the participating countries. Any effort to improve pest control at the field level should start by providing farmers with missing information, so that they can acquire new knowledge. However, to what extent new knowledge about biophysical principles would be reflected in better decision-making about the control of LB is a question that remains unanswered.

In spite of the negative effects of fungicide use on peoples' health and the environment, these products are still the

primary control measure at the field level. Fungicide use does reduce LB damage and increases potato yields. Evidence suggests that there is room for including fungicide use in LB control strategies, at least until other control options are available. Farmers in the developing countries studied, however, lack knowledge about the appropriate use of fungicides.

The study demonstrated a clear relationship between potato cultivars and LB damage at the field level. Hence, genetic resistance can play an important role as part of an integrated management strategy against this disease, and may be a way to reduce fungicide use per hectare. However, so far there is no evidence that fungicide use has been reduced.

Inter-institutional cooperation becomes a key issue in overcoming difficulties encountered by extension services and to facilitate farmers' access to new information, knowledge, and resistant cultivars. Participation of all persons involved, particularly farmers, is required to develop and disseminate control alternatives in order to reduce the devastating effects of LB in developing countries.

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Sensitive Detection of *Ralstonia solanacearum* in Latently Infected Potato Tubers and Soil by Postenrichment ELISA

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Ralstonia solanacearum is the causal agent of the disease known as bacterial wilt (BW) or brown rot, the second major constraint to potato (*Solanum tuberosum*) production in tropical and subtropical regions worldwide (Hayward, 1991). Brown rot has recently become a serious threat to potato seed production in cool, temperate countries of Northern Europe (Janse, 1996). Since the pathogen is mainly transmitted through tuber seed, the use of healthy planting material is the most effective means to control the disease (Hayward, 1991). Under cool conditions, the plant can be infected without exhibiting visible symptoms, resulting in latent infection in vascular tissues of progeny tubers (Ciampi et al., 1980; Hayward, 1991). Efficient detection techniques for routine use in quarantine procedures and seed certification schemes are crucial.

In the European Union, standard methods to monitor the occurrence of *R. solanacearum* in potato seed tubers involve the use of indirect immunofluorescence antibody staining (IFAS) and isolation on a selective medium (OEPP/EPPO, 1990). The most commonly used techniques to confirm positive samples in IFAS are the bioassay on tomato plants and the detection of *R. solanacearum*-specific DNA sequences by polymerase chain reaction (PCR) from pure bacterial cultures that have been isolated on a selective medium (OEPP/EPPO, 1990). Other techniques have become available and have been reviewed by Seal and Elphinstone (1994). There is still no method to detect latent infection in tubers that combines the advantages of high sensitivity and specificity, low cost, and suitability for routine use in developing countries where laboratory facilities and skilled personnel are often limited (Black and Elphinstone, 1998).

Another major component of BW management is the planting of potato in *R. solanacearum*-free soils. The pathogen can survive in plant debris and in the rhizosphere of potato, many weeds, and other crops (Hayward, 1991). Studies on the ecology, epidemiology, and control of *R. solanacearum* have been limited by the inability to detect the pathogen in low populations in soil. The most widely used methods to detect *R. solanacearum* in soil consist of streaking soil solution onto a specific medium (Granada and Sequeira, 1983; Englebrecht, 1994). The plating technique requires skilled personnel to distinguish colonies of the pathogen from other bacterial saprophytes, limiting its extensive use. Sensitivity of the method also varies by soil sample because soil antagonistic microflora can impair the growth of *R. solanacearum*. The use of indicator plants such as tomato has been reported (Graham and Lloyd, 1978), but the sensitivity of the bioassay is low (10^4-10^5 cells/g soil). Indirect enzyme-linked immunosorbent assay (ELISA) has also been developed (Robinson-Smith et al., 1995), but it lacks sensitivity (10^4 cells/g soil) and specificity.

Detection sensitivity can be increased by enrichment, i.e., incubating the extracts in a selective broth to multiply the bacteria. In a preliminary study (Gorris et al., 1997), the existing methods of enrichment of the

1 CIP, Lima, Peru.

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bacteria in tuber extracts were compared and refined to increase the sensitivity of serological techniques. Maximum growth rate of *R. solanacearum* during enrichment was obtained using citrate buffer for sample extraction from tubers and the modified selective broth (M-SMSA) developed by Elphinstone et al. (1996). This paper reports the improvement of the immunoassay on nitrocellulose membrane (NCM-ELISA) and of the antiserum specificity. For the detection of *R. solanacearum* in soil, double antibody sandwich immunoassay (DAS-ELISA) in microtitration plates has been set up using the same antiserum used for detection in potato. The detection effectiveness of postenrichment ELISA is compared with microbiological techniques and a nucleic acid spot hybridization procedure (NASH).

Materials and Methods

Tuber extracts

Preparation of tuber extracts and enrichment. Tubers were washed and disinfected. A thin slice of the tuber was removed from around the stolon end with a scalpel, and 3 x 3 mm strips along the vascular ring were removed. The tuber fragments were put into a plastic bag on ice and weighed. Two ml of sterile 0.1 M citrate buffer (pH 5.6) per g of tuber tissue were added, and tuber fragments were squashed with a rubber mallet. The enriched tuber extracts were prepared by mixing 500 µL of the supernatant tuber extract with 500 µL of M-SMSA in a 1.5 ml Eppendorf tube, and incubating for 48 h at 30°C with constant agitation (170 rpm) or manual agitation twice a day.

Preparation of inoculated tuber extracts. A healthy tuber extract (HTE) was prepared with *R. solanacearum*-free tubers (cv. Revolución) produced by CIP Seed Unit. A suspension of *R. solanacearum* in citrate buffer was prepared by culturing strain CIP 204 (biovar 2A) for 48 h at 30°C on modified Kelman's medium (MKM; French et al., 1995), but without tetrazolium chloride. The HTE was mixed with the suspension of *R. solanacearum* to obtain a final bacterial concentration of 2 x 10^8 cells/ml. Nine, tenfold dilution series in HTE were prepared to reach the theoretical concentration of 0.2 cells/ml. Each dilution was enriched in M-SMSA. The HTE and the M-SMSA broth were incubated for 48 h at 30°C as controls. The population of *R. solanacearum* in the initial inoculated tuber extract was assessed by spreading 50 µL of a 10^{-5} dilution in sterile, distilled water on MKM (3 plates per dilution) and by counting colonies of the pathogen after 48 h incubation at 30°C. The experiment was repeated three times.

Preparation of naturally infected tuber extracts. Eight single-tuber extracts were prepared from infected tubers (cv. Yungay) harvested in a race 3-infested field (Carhuaz, Peru). Ten, tenfold dilution series of the 8 infected extracts in HTE were prepared, and each dilution was enriched in M-SMSA. Populations of *R. solanacearum* in the original infected extracts were assessed by spreading 50 µL of each of the dilutions on MKM (3 plates each).

A total of 255 extracts were prepared from tubers of 122 different potato clones and cultivars: Revolución, Yungay, and, Canchán (all susceptible), Molinera (tolerant), and Cruza 148 (resistant), which were harvested from symptomless plants in the same germplasm evaluation trial. The tuber extracts were prepared by mixing the tuber fragments removed from 20 tubers/genotype taken at random from the harvest of 5 plants. Isolations of *R. solanacearum* were performed on MKM from the nonenriched extracts.

Soil extracts

Preparation of inoculated soil extracts. A nonsterile *R. solanacearum*-free soil from Huancayo, Peru, was inoculated by mixing 10 ml of a water suspension of *R. solanacearum* strain 204 (biovar 2A) with 90 g of soil to obtain final concentrations of 10^7, 10^4, 10^2, 20, 2, and 0.2 cells/g soil. Three replications of each concentration of

soil inoculum were prepared. Inoculated soils were kept at room temperature for 24 h before use. Soil suspensions were prepared by mixing 10 g of soil with 90 ml of PBS buffer. The soil suspension was agitated for 30 min and allowed to settle for 40 sec. The supernatant was either used directly for detection or enriched. The enriched soil extracts were prepared by mixing in an erlenmeyer flask 2 ml of soil solution with 38 ml of M-SMSA supplemented with potato broth (1:1), and incubating the mixture for 48 h at 30°C with constant agitation (170 rpm). Fifty µL of each soil solution were plated on M-SMSA medium. Three plates per concentration were incubated for 48 h at 30°C and colonies of *R. solanacearum* were counted to estimate the original soil population.

Preparation of naturally infested soil extracts. Ten soil samples were taken from a race-1 infested field (San Ramon, Peru) and 15 from a race-3 infested field (Carhuaz, Peru) in the rhizosphere of infected and symptomless potato plants (at approximately 20-30 cm depth). Soil extracts were prepared 1 or 2 d after sampling as previously described for inoculated soils, and 8, tenfold serial dilutions were done in sterile, distilled water. Nondiluted and diluted soil solutions were enriched in M-SMSA-potato broth and plated in M-SMSA medium to estimate the original soil population of *R. solanacearum*.

Polyclonal antisera production

Antigen preparation. Strains of CIP 204 (biovar 2A) and CIP 104 (biovar 2A) of *R. solanacearum* were used for the rabbit immunizations. They were cultured on MKM without tetrazolium chloride for 48 h at 30°C. The cells were harvested in 0.01 M phosphate-buffered saline, pH 7.4 (0.5X PBS), centrifuged for 10 min at 10,000 x *g* and washed 3 times in 0.5X PBS. They were resuspended in 0.5X PBS, and their number was estimated by absorbance at 600 nm and the concentration adjusted to 2 x 10^9 cells/ml. The cells were then fixed with 2% glutaraldehyde following the method of Allan and Kelman (1977).

Rabbit immunization. Female Rex x New Zealander rabbits were immunized by intradermic injection of 2 x 10^9 glutaraldehyde-fixed whole cells of an equal mixture of strains CIP 204 and CIP 104 in 1 mL of 0.5X PBS, which was emulsified in an equal volume of Freund's incomplete adjuvant (Difco). The rabbits were immunized intramuscularly 32 d later in each hindleg with a total of 10^8 glutaraldehyde-fixed whole cells (same strain mixture) in 1 mL of 0.5X PBS, which again was emulsified in an equal volume of Freund's incomplete adjuvant. This last injection was repeated once a week for 9 wk. Blood was collected from the lateral ear vein 52 d after the first immunization, and then weekly. The blood was allowed to clot at 4°C, separated by centrifugation (15 min at 10,000 *g*) and the serum fraction collected. Antibody levels in the serum were determined by NCM-ELISA.

Antiserum adsorption. One ml of each antiserum was mixed with 9 ml of a bacterial suspension in 0.5X PBS containing a total of 1.5 x 10^{10} cells of an equal mixture of 5 species: *Erwinia carotovora* subsp. *atroseptica* (CIP 421), *E. carotovora* subsp. *carotovora* (CIP 400), *E. chrysanthemi* (CIP 367), *Pseudomonas syzygii* (CNPPB 3792), and *R. pickettii* (NCPPB 3899). This mixture was incubated 1 h at 32°C with constant agitation (50 rpm) and centrifuged for 10 min at 10,000 *g*. Supernatant was collected and the antibody level determined by NCM-ELISA.

NCM-ELISA. Dot-blotting and NCM-ELISA were performed as described in a CIP training manual (CIP, 1997) with the following modifications. The blocking and antibody solutions were composed of 2% nonfat powdered milk in TBS buffer; *R. solanacearum*-specific antiserum and the goat-antirabbit antibodies conjugated to alkaline phosphatase (Biorad) were diluted 1:1,000 and 1:4,000, respectively. The concentrations of NBT and BCIP solutions in N-dimethylformamide used to prepare the substrate solution were doubled (40 mg/ml and 20 mg/ml, respectively).

DAS-ELISA. DAS-ELISA was performed as described by Clark and Adams (1977) using the immunoglobulins (IgG, diluted 1:1,500) purified from the polyclonal rabbit antiserum used for NCM-ELISA. The IgG were conjugated to alkaline phosphatase and diluted 1:1,500 for detection. Bioreba microtitre plates were coated with the IgG for 4 h at 37°C, incubated with the samples overnight at 4°C, and then for an additional 4 h with the conjugated IgG at 37°C. Absorbance at 405 nm was determined using a Biorad Model 2550 plate reader following 1 h incubation at room temperature. ELISA readings were considered positive when they exceeded two times the mean of the negative controls.

NASH. NASH was used to check the specificity of NCM-ELISA. For dot-blotting of the samples, NCM was immersed for 15 min in 5X SSC. Bacterial DNA from tuber extracts on the NCM was released with alkali, neutralized, and fixed by UV crosslinking. A 2 Kb DNA fragment specific for *R. solanacearum* race-3, developed by Cook and Sequeira (1991), was used for hybridization of *R. solanacearum* in tuber extracts. Probe labeling and hybridization at 55°C were performed as described in a CIP training manual (CIP, 1997). Only the first three washing steps were applied. Genomic DNAs of *R. solanacearum* (strains CIP 204 and CIP 311, biovar 2A) and *E. carotovora.* subsp. *carotovora* (CIP 400) were used as positive and negative controls and were prepared according to Cook and Sequeira (1991).

Bacterial isolates and cross-reaction tests

A total of 259 potato isolates of *R. solanacearum* from CIP's international collection including different biovars (170 isolates of biovar 2A, 20 of biovar 2T, 48 of biovar 1, 15 of biovar 3, and 6 of biovar 4) originating from several countries, were used to check the antiserum. Other bacteria were also used and are listed in Table 1. All bacterial strains were cultured for 48 h at 30°C on MKM without tetrazolium chloride, and the cells were harvested in citrate buffer. The suspensions were adjusted to 2 x 10^9 cells/ml for NASH, and 2 x 10^8 cells/ml for NCM-ELISA. Suspensions of the 11 identified non-*R. solanacearum* bacterial strains listed in Table 1, and of 11 unknown saprophytes isolated from enriched tuber extracts, were also diluted in HTE to a final concentration of 2 x 10^6 cells/ml and enriched to check the cross-reactivity of NCM-ELISA after enrichment. Since the tuber extracts were prepared from the tuber vascular ring, very few saprophytic bacteria could be isolated from enriched extracts (unlike with soil extracts). Those 11 isolates were a representative sample of the variability of colonies isolated on MKM plates. To verify the specificity of DAS-ELISA after enrichment, 66 unknown saprophytes were isolated from soil extracts of 3 different soils (Huancayo, Carhuaz, and San Ramon, Peru). These isolates were diluted in soil extract to a final concentration of 2 x 10^6 cells/ml soil solution and enriched.

Results

Improvement of antiserum specificity

Several antisera had previously been obtained by immunizing rabbits following various protocols. The immunization schedule reported in this paper produced more specific antibodies and a higher titre. When immunization was done only with strain CIP 204, the antiserum reacted with all *R. solanacearum* potato strains of biovars 1, 2T, 3, and 4 tested. The antiserum did not, however, recognize a group of strains of biovar 2A (data not shown). Therefore, two strains, CIP 204 and CIP 104 (biovar 2A), the latter belonging to the nonrecognized group, were used for immunization. From the two antisera produced, antiserum P-359 was chosen because it recognized all strains of *R. solanacearum* tested at 10^8 cells/ml of citrate buffer. After adsorption of the antiserum, all 259 *R. solanacearum* strains tested were still recognized by the adsorbed antiserum. The cross-reactions of saprophytes were significantly reduced (Table 1). After enrichment, none of the 11 saprophytic bacteria isolated from enriched

potato extracts cross-reacted in NCM-ELISA. Only *Pseudomonas celebensis*, the banana blood disease bacterium genetically closely related to *R. solanacearum*, still reacted strongly in NCM-ELISA, but this pathogen is unlikely to occur in tubers.

In NCM-ELISA, many cross-reactions were obtained after enrichment of soil extracts inoculated with saprophytes (Table 1). Since no cross-reaction was observed in DAS-ELISA with the 66 saprophytes isolated from soil extracts, DAS-ELISA was chosen for the detection of soil populations of *R. solanacearum*. *P. celebensis* was slightly detected in DAS-ELISA but not *P. syzygii*, the agent of the Sumatra disease of clove, also present in Asian soils.

All *R. solanacearum* biovar 2A strains tested were hybridized by the probe used, but none of the non-*R. solanacearum* bacterial strains tested. NASH thus provided a tool to evaluate the specificity of the serological methods in assessing the risk of

Table 1. Cross-reactions obtained with non-*Ralstonia solanacearum* bacterial strains in NCM-ELISA using the crude or the adsorbed antibodies (Ab), and in DAS-ELISA using purified immunoglobulins (IgG), when in pure culture in citrate buffer at 2 x 10^8 cells/ml without enrichment (- E) and after 48 h enrichment (+ E) from an original concentration of 2 x 10^6 cells/ml tuber extract or 2 x 10^6 cells/ml soil solution, CIP, 1998.

		NCM-ELISA[a]				DAS-ELISA[a]	
		Nonadsorbed Ab		Adsorbed Ab		Purified IgG	
Bacteria	Strain (no.)	- E	+ E	- E	+ E	- E	+ E
Erwinia carotovora subsp. *carotovora*	CIP 400	+	-	-	-	-	-
Erwinia carotovora subsp. *atroseptica*	CIP 421	+/-	-	-	-	-	-
Erwinia chrysanthemi	CIP 367	+/-	-	-	-	-	-
Pseudomonas syzygii	NCPPB 3792	++	+/-	++	+/-	++	-
Ralstonia pickettii	NCPPB 3899	+	+/-	-	-	-	-
Burkholderia cepacia	NCPPB 2993	+/-	+/-	-	-	-	-
Pseudomonas aeruginosa	NCPPB 1965	+/-	-	-	++	-	-
Pseudomonas putida	NCPPB 1806	+/-	-	-	-	-	-
	NCPPB 1808	-	-	-	-	-	-
Pseudomonas celebensis	UW443	++	++	++	++	++	+/-
	UW 446	++	++	++	++	++	+/-
Unknown bacteria isolated from enriched tuber extracts	11 isolates	+ (6/11)	+/- (7/11)	+/- (6/11)	- (11/11)	Not done	Not done
Unknown bacteria isolated from three different soil extracts	29 isolates	Not done	Not done	+/- (2/29)	+/- (6/29)	- (29/29)	- (29/29)
Unknown bacteria isolated from three different enriched soil extracts	37 isolates	Not done	Not done	+/- (2/37)	+/- (10/37)	- (37/37)	- (37/37)

a. +/-, +, and ++ = coloration intensities; +/- equivalent to those obtained with *R. solanacearum* in citrate buffer at concentration of 10^6 cells/ml, + at concentration of 10^7 cells/ml, and ++ at concentration of 10^8 cells/ml. - = not detected.

cross-reactions in tuber extracts naturally infected with *R. solanacearum* biovar 2A.

Comparison of the detection sensitivity of NCM-ELISA and NASH

Inoculated tuber extracts. The positive samples appeared as bluish purple spots, the coloration ranging in intensity from light pink to dark purple depending on the concentration of *R. solanacearum*. In our work, only the purple coloration obtained with *R. solanacearum* at a concentration of at least 2 x 10^7 cells/ml was rated positive. Unacceptable coloration included a light, pinkish purple (equal to or lighter than that for the concentration of 10^6 cells/ml), similar to that caused by some saprophytic bacteria, and brown (color of the tuber extract). The detection thresholds obtained in NCM-ELISA, NASH, and after plating on MKM are shown in Table 2.

After enrichment, the lowest bacterial concentration that could be detected in NCM-ELISA and NASH varied between 2 and 20 cells/ml among the replications. The efficiency of isolation on MKM after enrichment varied by sample because of the presence of bacterial saprophytes overgrowing *R. solanacearum* colonies. Thus, the plating on MKM was further used to correlate with the results obtained in ELISA before the extracts were enriched. NASH was used as the tool to evaluate the cross-reactivity of the serological *R. solanacearum* method after enrichment, since its sensitivity was similar to that of NCM-ELISA.

Naturally infected tuber extracts. Log_{10} viable counts in the infected tuber and soil extracts were estimated from three MKM plates at the dilution enabling the counting, and are presented in Table 3. The sensitivity in NCM-ELISA after 48 h enrichment averaged 6.45 cells/ml, which is close to the sensitivity obtained with inoculated extracts (Table 2). The same sensitivity was observed in NASH after enrichment (Table 3). NASH was tenfold less sensitive than NCM-ELISA without enrichment, which corresponds to the results obtained with inoculated extracts.

Table 2. Minimum populations of *Ralstonia solanacearum* detected in inoculated tubers by plating on modified Kelman's medium (MKM), NCM-ELISA, and NASH without enrichment (-E) and with enrichment (+E) after 48 h incubation of the inoculated tuber extracts in modified SMSA broth at 30°C, CIP, 1998.

	- E[a]			+ E[a]		
Cells/ml tuber extract	Plating on MKM	NCM-ELISA	NASH	Plating on MKM	NCM-ELISA	NASH
2 X 10^8	+	+	+	+	+	+
2 X 10^7	+	+	-	+	+	+
2 X 10^6	+	+/-	-	+	+	+
2 X 10^4	+	-	-	+	+	+
2 X 10^2	+	-	-	+	+	+
20	-	-	-	+	+	+
2	-	-	-	-	+/-	+/-
0.2	-	-	-	-	-	-
TE [b]	-	-	-	-	-	-

a. + = detected, - = not detected, +/- = variable among the three replications of the whole experiment.

b. TE = R. solanacearum-free tuber extract used for the dilutions of the inoculated tuber extract.

Table 3. Sensitivity of NCM-ELISA and NASH for the detection of *Ralstonia solanacearum* (Rs) in naturally-infected tuber extracts without enrichment (- E) and with enrichment (+ E) in modified SMSA broth for 48 h at 30°C, CIP, 1998.

Original population in the tuber extract			Last dilution in which Rs could be detected in:				Estimated minimum population detected after enrichment
			NCM-ELISA		NASH		
Cells/ml [a]	Log_{10} (cells/ml)	SD [b]	- E	+ E	- E	+ E	Cells/ml
8.66×10^5	5.938	0.015	-	10^{-5}	-	10^{-5}	8.6
6.73×10^5	5.827	0.046	-	10^{-5}	-	10^{-5}	6.7
6.33×10^4	4.801	0.021	-	10^{-4}	-	10^{-4}	6.3
2.30×10^9	9.360	0.055	10^{-2}	10^{-9}	10^{-1}	10^{-9}	2.3
8.40×10^7	7.924	0.021	ND [c]	10^{-7}	-	10^{-7}	8.4
1.00×10^8	8.003	0.005	ND	10^{-7}	-	10^{-7}	10.0
1.66×10^9	9.220	0.015	10^{-2}	10^{-9}	10^{-1}	10^{-9}	1.7
7.60×10^8	8.880	0.023	10^{-1}	10^{-8}	ND	10^{-8}	7.6

a. Estimated from colony counts after plating on three plates containing modified Kelman's medium incubated for 48 h at 30°C.

b. SD = standard deviation.

c. ND = bacteria detected only in the nondiluted extract.

Efficiency of NCM-ELISA for the detection of *R. solanacearum* in field samples

Of 255 tuber samples tested from the germplasm evaluation trial, 56.5% were found negative in NCM-ELISA after 48 h of enrichment. The same result was obtained with NASH and isolation on MKM, demonstrating no lack of sensitivity of NCM-ELISA. In all the samples found positive in NCM-ELISA (42.4%), the presence of *R. solanacearum* has been confirmed either by isolation on MKM or by DNA-hybridization, or both, revealing no cross-reactivity of ELISA.

Detection of *R. solanacearum* in soil

Sensitivities of DAS-ELISA and plating on M-SMSA were greatly increased by the enrichment procedure; as few as 20 and 100 cells/g soil could be detected from inoculated extracts, respectively (Table 4). The enrichment efficiency from soil extracts has been improved by adding potato broth to the M-SMSA broth (1:1) because the bacteria do not grow well in the M-SMSA broth in the absence of potato extract. In preliminary assays to detect *R. solanacearum* in two naturally infested soils, minimum populations detected averaged 17 cells/g soil for San Ramon and 141 cells/g soil for Carhuaz soils (Table 5). The lower sensitivity obtained with Carhuaz soil could be due to slower growth in M-SMSA broth of race-3 strains in Carhuaz soil as compared with the race-1 strains in San Ramon soil. Another possibility is the occurrence of different antagonistic soil microflora, which impaired optimal growth of *R. solanacearum* in the enrichment broth.

Table 4. Minimum populations of *Ralstonia solanacearum* detected by plating on modified SMSA medium (M-SMSA), DAS-ELISA without enrichment (- E) and with enrichment (+ E) after 48 h incubation of the inoculated soil extracts in modified SMSA-potato broth at 30°C. Same results were obtained with the three replications of inoculated soils, CIP, 1999.

	- E[a]		+ E[a]	
Cells/g soil	Plating on M-SMSA	DAS-ELISA	Plating on M-SMSA	DAS-ELISA
10^7	+	+	+	+
10^4	+	-	+	+
10^2	-	-	+	+
20	-	-	-	+
2	-	-	-	-
0.2	-	-	-	-
SE [b]	-	-	-	-

a. + = detected, - = not detected.

b. SE = noninoculated soil extract.

Discussion

R. solanacearum was successfully detected by postenrichment NCM-ELISA (tuber samples) and DAS-ELISA (soil samples) even at low population levels in both inoculated and naturally-infected extracts. Sensitivity and non-cross-reactivity of postenrichment ELISA was demonstrated in 255 field tuber samples and 25 field soil samples. The specificity of ELISA using the adsorbed antiserum was satisfactory, in that no cross-reaction was detected after enrichment (except with *P. celebensis*), without resulting in a failure to detect all strains of *R. solanacearum* as reported by Robinson-Smith et al. (1995).

Postenrichment NCM-ELISA combines the advantages of high sensitivity, low-cost (about $0.30/sample for supplies), ease, and speed (6 h after enrichment of the extracts), and does not require extensive laboratory equipment. The sensitivity of NCM-ELISA after a 48 h enrichment was significantly higher than the one obtained with IFAS, indirect ELISA, and PCR (Janse, 1988; Elphinstone et al., 1996, Caruso et al., 1998; Seal, 1998). The lower sensitivity of postenrichment ELISA obtained by Elphinstone et al. (1996) may be due to the use of PBS buffer for sample extraction, because the same enrichment broth was used in the present study. Indeed, the growth of *R. solanacearum* was much lower in this buffer than in citrate (Gorris et al., 1997). Sensitivity of postenrichment NCM-ELISA corresponded to postenrichment nested PCR (Elphinstone et al., 1996). However, this latter technique is not suitable for seed testing in resource-poor countries. It is expensive ($ 0.70/sample [Seal, 1998]) and requires extensive laboratory facilities, resources, and highly skilled personnel. Moreover, postenrichment ELISA detects only viable cells of *R. solanacearum*, whereas PCR may detect dead cells as well.

An NCM-ELISA kit for the detection of *R. solanacearum* in tuber extracts, including the M-SMSA enrichment broth, has been developed at CIP. It is currently being distributed to national agricultural research institutes and seed programs in developing countries for seed quality testing and for assessing susceptibility of breeding lines to BW. Adequate sampling strategies are being investigated.

Table 5. Sensitivity of DAS-ELISA for the detection of *Ralstonia solanacearum* (*Rs*) in tenfold dilutions of naturally infested soil extracts from two different fields without enrichment (- E) and with enrichment (+ E) in modified SMSA broth for 48 h at 30°C, CIP, 1999.

Original population in soil			Last dilution in which *Rs* could be detected in DAS-ELISA (cells/g)		Estimated minimum population detected after enrichment
Cells/g [a]	Log_{10}	SD [b]	- E	+ E	Cells/g
San Ramon soil					
2.5×10^6	6.398	0.1244	-	10^{-6}	2.5
2.6×10^7	7.415	0.0473	-	10^{-7}	2.6
5.7×10^5	5.756	0.0106	-	10^{-5}	5.7
2.9×10^6	6.462	0.0212	-	10^{-4}	29.0
1.0×10^7	7.000	0.1244	-	10^{-7}	1.0
1.4×10^5	5.146	0.0883	-	10^{-5}	1.4
1.6×10^6	6.204	0.0770	-	10^{-6}	1.6
2.6×10^6	6.415	0.0473	-	10^{-5}	26.0
5.4×10^5	5.732	0.0685	-	10^{-4}	54.0
4.7×10^6	6.672	0.0657	-	10^{-5}	47.0
Carhuaz soil					
3.3×10^6	6.518	0.124	-	10^{-4}	330.0
2.6×10^5	5.414	0.269	-	10^{-4}	26.0
1.2×10^6	6.079	0.061	-	10^{-4}	120.0
2.8×10^6	6.447	0.017	-	10^{-5}	28.0
5.3×10^4	4.724	0.174	-	10^{-2}	530.0
4.5×10^6	6.653	0.013	-	10^{-4}	450.0
1.0×10^6	6.017	0.023	-	10^{-4}	100.0
2.9×10^5	5.462	0.064	-	10^{-4}	29.0
4.5×10^6	6.653	0.097	-	10^{-5}	45.0
2.9×10^6	6.462	0.151	-	10^{-5}	29.0
1.0×10^6	6.000	0.124	-	10^{-4}	100.0
6.2×10^5	5.792	0.100	-	10^{-4}	62.0
1.4×10^6	6.146	0.088	-	10^{-4}	140.0
2.8×10^6	6.447	0.045	-	10^{-5}	28.0
1.0×10^6	6.000	0.000	-	10^{-4}	100.0

a Estimated from colony counts after plating on three plates containing modified SMSA medium incubated for 48 h at 30°C.

b. SD = standard deviation.

For the detection of soil populations of *R. solanacearum*, the sensitivity obtained with postenrichment DAS-ELISA was similar to that reported using plating on specific medium (Granada and Sequeira, 1983; Englebrecht, 1994) with inoculated as well as naturally-infested soils. However, the serological technique is easier to use because it does not require skilled personnel to differentiate between saprophytic and pathogenic colonies. The sensitivity of detection was considerably increased by

the enrichment procedure compared with that reported by Robinson-Smith et al. (1995) for indirect ELISA.

A DAS-ELISA kit is being developed at CIP for the detection of soil populations of *R. solanacearum*. Quantification of soil populations is important in research for the development of control components effective in reducing soil inoculum. Relative semiquantification of soil inoculum potential could be achieved by diluting the soil extract before enrichment and recording the last dilution in which *R. solanacearum* was detected.

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An Improved Method for Fighting Bacterial Wilt: NCM-ELISA Detection Kit and Training Materials

Detecting bacterial wilt disease has become easier for our partners and clients thanks to development of the NCM-ELISA Kit, which can be used to monitor *Ralstonia solanacearum*—the agent that causes bacterial wilt or "brown rot" in potato tubers. Detecting the disease-causing agent is essential for seed production systems and varietal evaluation of resistance to bacterial wilt.

Post-enrichment NCM-ELISA (enzyme-linked immunosorbent assay on nitrocellulose membrane using enriched samples) is as sensitive as the Double-Antibody Sandwich (DAS-ELISA), but is much easier and quicker. Samples and reagents are supported by nitrocellulose membrane instead of micrometer plates and they can be stored for several weeks before testing or sending to outside labs. After NCM-ELISA, the membrane is stable and can be stored for extended periods. *R. solanacearum* in latently infected tubers (those without any visible symptoms) is detected in ELISA after incubating tuber extracts in a semi-selective broth prior to testing. This enrichment procedure increases the sensitivity of the assay by nearly one million. As few as 10 bacteria per milliliter of extract can be detected with this method.

The kit can also be used with roots and stems of potato and other plants for research on disease epidemiology. The package is available complete with an instruction manual and video in Chinese, English, and Spanish. Learning more about the kit or training manual is as easy as contacting Dr. Sylvie Priou (s.priou@cgiar.org) in CIP's Crop Protection Department or accessing CIP-publications on our web page at: www.cipotato.org.

Survey of the Durability of Extreme Resistance to PVY Derived from *Solanum tuberosum* subsp. *andigena*

E. Mihovilovich, L.F. Salazar, F. Saguma, and M.W. Bonierbale[1]

Potato virus Y (PVY), is one of the most important viruses attacking potato (*Solanum tuberosum subsp. tuberosum*). It is distributed worldwide and causes significant crop losses. The most effective strategy for controlling PVY is the use of durable resistance genes. Durable resistance is unlikely to be overcome by diverse pathogen strains or under variable production conditions.

The most complete types of resistance to PVY have been grouped into two main classes: *hypersensitivity* (expressed as a necrotic response to infection), which is conferred by dominant N genes; and *extreme resistance* (with very little or no virus accumulation in the plant) conferred by dominant R genes. PVY can usually be recovered following inoculation from plants carrying N genes, but not from those carrying R genes (Barker 1996). Ry genes are considered durable, since they have proven effective against a range of PVY strains known at present. Ny genes are not considered durable because they are strain-specific. *S. tuberosum* subsp. *andigena* and *S. stoloniferum* are sources of Ry genes. Most breeding for resistance to PVY is based on the introduction into *S. tuberosum subsp. tuberosum* cultivars of Ry genes derived from these two species. The extreme resistance of European varieties comes from *S. stoloniferum* (Ry_{sto}). Conversely, resistance in some varieties and parental clones developed by CIP comes mainly from *S. tuberosum subsp. andigena* (Ry_{adg})

New strains, multiple virus infections, and interactions with subviral pathogens are the main factors leading to the breakdown of virus resistance. During the past 10 yr, a new strain of PVY, tuber necrotic ringspot disease strain (PVY^{nn}), has become established in Europe. It causes severe necrotic symptoms in tubers of PVY-susceptible varieties. It has been reported that the independently replicating potato spindle tuber viroid (PSTVd) has a synergistic effect on PVY multiplication (Querci et al., 1997). They also showed that PSTVd has the ability to decrease resistance to potato leafroll virus (PLRV), and to be encapsidated by this virus and transmitted by aphids. These factors led us to test the durability of the Ry_{adg} gene with respect to its ability to provide protection against PVY^{nn}, and to provide extreme resistance against combined infection by PVY and PSTVd.

Materials and Methods

Four Ry_{adg}-bearing clones, all developed by CIP, were used in this study. They included cv. Costanera and Tacna, which are adapted to the arid Peruvian coast and carry extreme resistance to PVY, and the two parental clones YY.5 and TY.4. Both Peruvian cultivars carry the Ry_{adg} gene in a simplex (Ryryryry) condition. The parental clone YY.5 is duplex (RyRyryry) and TY.4 is triplex (RyRyRyry). These and other multiplex progenitors (possessing more than one copy of the dominant resistance allele) have the ability to transmit resistance to their progeny with a higher frequency than would be the case with simplex clones (Mendoza et al., 1996). A PVY extreme resistance European variety, Pirola, carrying the Ry_{sto} gene, and three PVY susceptible varieties—Bintje (Europe), Desiree (Europe),

1 CIP, Lima, Peru.

and Atlantic (North America)—were used as controls. Plants of all clones were grown from virus-tested in vitro plantlets by first transplanting them to jiffy pots and then to individual plastic pots containing a 1:1:1 mixture of soil, sand, and peat. Three PVY strains, the ordinary (PVY^{o}), necrotic (PVY^{N}), and new tuber necrotic ringspot (PVY^{nn}) strains were used. All were from CIP stock isolates, and were provided in plants of *Nicotiana occidentalis.* PSTVd (severe strain) was provided in tomato plants, where it is maintained for research purposes. Experiments were carried out in the greenhouse at CIP's La Molina Experiment Station from September to December 1997 (primary infection trial), and from March to June 1998 (secondary infection trial). Inoculation in the primary infection trial involved mechanical, aphid, and graft transmission using five plants of each clone for each inoculation method and strain. Mechanical inoculation was performed by rubbing freshly extracted sap from infected *N. occidentalis* plants onto carborundum-dusted potato plants. For graft inoculation, scions (shoot apices) from infected *N. occidentalis* plants were cleft-grafted onto the stems of test plants. Aphid inoculation was carried out by setting 15 infective apterous aphids, previously fed on PVY-infected plants of cv. Atlantic, onto each test plant.

For the PVY-PSTVd combined infection trial, 45 plants of each clone were first mechanically inoculated at the seedling stage using a suspension of sap from PSTVd-infected tomato plants. Infection was verified by nucleic acid spot hybridization (NASH). All of the varieties described above, but not the multiplex parental clones, were used in this cross-infectivity test. Two weeks after PSTVd inoculation, five pre-infected plants (PSTVd) of each genotype were mechanically inoculated with each of the three PVY strains. The 30 remaining PSTVd-infected plants of each clone were graft inoculated (15 plants) or aphid inoculated (15 plants) with PVY 4 wk after PSTVd inoculation, using 5 plants per strain and inoculation method.

Tubers recovered from the primary infection trial of both experiments were used to obtain plants for the evaluation of secondary infection. Visual foliar evaluations and enzyme-linked immunosorbent assay (ELISA) tests for PVY were performed in both experiments, at 30 and 45 days after inoculation during the primary infection cycle, and at the same intervals after tuber planting during the secondary infection cycle. Tubers obtained from the primary and secondary infection cycles were evaluated visually at harvest and after 1 mo of storage at 24°C.

Results

Reaction to PVY inoculation

Plants of the susceptible controls showed mosaic symptoms 7 d after inoculation with all strains (PVY^{o}, PVY^{N}, and PVY^{nn}). During the evaluation period of 45 d, Bintje and Atlantic showed severe mosaic and crinkled symptoms, and a strong hypersensitive reaction, i.e., severe systemic necrosis, and some dead plants. On the other hand, Desiree developed mild mosaic and strong hypersensitivity.

All plants of the susceptible varieties reacted positively to ELISA, except those that showed severe systemic necrosis. Plants infected with PVY^{o} showed much more severe symptoms than those infected with the other strains, which suggests that the PVY^{o} inoculum used in this study represents a highly virulent isolate. More severe symptoms developed after mechanical and graft inoculation than aphid inoculation. Varieties and parental clones carrying Ry_{adg} did not show foliar symptoms against any of the strains, and reacted negatively in ELISA. Conversely, Pirola (understood to carry Ry_{sto}) developed a mild necrosis in some leaves and stems, but virus was not detected in these plants by ELISA.

Table 1. Reactions of selected potato varieties and parental clones against PVY^{o}, PVY^{N}, and PVY^{nn}.

Varieties and parental clones	PVY resistance genotype	Foliage reactions[a]			Tuber reactions
		PVY^{o}	PVY^{N}	PVY^{nn}	PVY^{nn}
Costanera	Ry_{adg}	-; (-)	-; (-)	-; (-)	-
Tacna	Ry_{adg}	-; (-)	-; (-)	-; (-)	-
YY.5	Ry_{adg}	-; (-)	-; (-)	-; (-)	-
TY.4	Ry_{adg}	-; (-)	-; (-)	-; (-)	-
Pirola	Ry_{sto}	H:MN; (-)	H:MN; (-)	H:MN; (-)	-
Desiree	Ny_{tub}	MM; H:SN; (+)	MM; H:SN; (+)	MM; H:SN; (+)	-
Atlantic	$ny_{adg}, ny_{sto}, ny_{tub}$	SM,C; H:SN; (+)	SM,C; H:SN; (+)	M,C; (+)	Necrotic cracking[b]
Bintje	$ny_{adg}, ny_{sto}, ny_{tub}$	SM,C; H:SN; (+)	SM,C; H:SN; (+)	M,C; (+)	-

a. Reaction to PVY by ELISA is shown in parenthesis. Key reactions: MM = mild mosaic, M = mosaic, SM = severe mosaic; C = Crinkle; H:MN = hypersensitivity: mild necrosis, H:SN = hypersensitivity: severe necrosis.
b. Also observed on plants infected with PVY^{N}.

In the secondary infection trial, the susceptible controls reacted with mosaics against all strains. PVY infection was confirmed by ELISA in all cases. The PVY-resistant variety Pirola (Ry_{sto}), however, continued to show a mild hypersensitivity reaction (foliar and stem mild necrosis) in some plants with all strains. Virus was not detected in these plants by ELISA. The resistant varieties and parental clones with Ry_{adg} did not develop symptoms with any strain, and continued to test negative in ELISA. Table 1 summarizes the reactions observed.

Tubers recovered from primary infection did not show any symptom of virus infection, regardless of variety or strain. Conversely, tubers from the secondary infection trial of the susceptible variety Atlantic (inoculated with PVY^{N} and PVY^{nn}) showed severe necrotic cracking lesions typical of virus infection. This symptom was not observed on tubers of any other variety or parental clone harvested from the secondary infection cycle. Ringspot necrosis, reportedly induced by the PVY^{nn} strain, was not found on tubers of any variety or parental clone, either at harvest or after 1 mo of storage at 24°C.

Reaction to combined PVY and PSTVd inoculation

When inoculated with PSTVd and PVY strains, PVY-susceptible varieties developed much more severe mosaic, crinkled, and necrotic symptoms during both infection cycles than those observed under PVY infection alone. Again, more severe symptoms were observed on plants infected with PVY^{o} than the other two strains. PVY infection was confirmed in these varieties by ELISA. In contrast, the doubly inoculated Ry_{adg}-bearing varieties, Costanera and Tacna, did not show any symptom associated with PVY, and reacted negatively in ELISA. The Ry_{sto}-bearing variety Pirola showed the same hypersensitive reaction (mild necrosis of some leaves and stems) as that shown with PVY infection alone and continued to test negative for PVY in ELISA. Severe stunting was observed in plants of this variety as well as in the susceptible controls Atlantic and Bintje. Table 2 summarizes the reactions of varieties against combined inoculation of PVY and PSTVd.

No symptoms of virus infection were observed on tubers of either PVY-resistant or PVY-susceptible varieties recovered from

Table 2. Reactions of selected potato varieties against combined inoculation with PSTVd and PVY.

Varieties	PVY resistance genotype	Foliage reactions [a] PVY^{o}	PVY^{N}	PVY^{nn}	Tuber reactions
Costanera	Ry_{adg}	-; (-)	-; (-)	-; (-)	Spindle shape
Tacna	Ry_{adg}	-; (-)	-; (-)	-; (-)	Spindle shape
Pirola	Ry_{sto}	St; H:MN; (-)	St; H:MN; (-)	St; H:SN; (-)	Spindle shape, and severe size reduction
Desiree	Ny_{tub}	MM; H:SN; (+)	MM; H:SN; (+)	MM; H:SN; (+)	-
Atlantic	ry_{adg}, ry_{sto}, ny_{tub}	SM,C; H:SN; (+)	SM,C; H:SN, St; (+)	SM,C, St; (+)	Necrotic cracking [b]
Bintje	ry_{adg}, ry_{sto}, ny_{tub}	SM,C; H:SN, St; (+)	SM,C; H:SN, St; (+)	SM,C; St (+)	-

a. Reaction to PVY by ELISA is shown in parenthesis. Key reactions: MM = mild mosaic, M = mosaic, SM = severe mosaic; C = crinkle; St = stunting; H:MN = hypersensitivity. mild necrosis, H:SN = hypersensitivity: severe necrosis.

b. Also observed on plants infected with PVY^{N}.

primary or secondary infection, except for the susceptible variety Atlantic. Tubers of Atlantic recovered from plants infected with PVY^{N} and PVY^{nn} again showed necrotic cracking. In addition, tubers from Pirola, Costanera, and Tacna showed severe size reduction as well as deformation (spindle tubers) due to viroid infection. No other variety showed this effect. Ringspot necrosis—the reported symptom of PVY^{nn}—was not found on any of the tubers.

Discussion

Reaction against PVY^{o}, PVY^{N}, and PVY^{nn}

Reactions to PVY^{nn} did not differ from reactions to the other strains. Furthermore, it was not possible to detect PVY^{nn}, PVY^{o}, or PVY^{N} in inoculated plants of Ry_{adg}-containing varieties and parental clones. Some unexpected reactions were observed in plants not carrying this gene. Desiree, understood to carry a gene for hypersensitivity (Ny_{tub}), developed mosaic symptoms with all strains in addition to the expected hypersensitive reaction. *Ny* genes are known to be temperature-sensitive. Temperatures above 22°C during the primary and secondary infection cycles may have accounted for Desiree's overcoming the hypersensitive response toward symptom development. Pirola was not expected to develop symptoms to known strains since it carries the Ry_{sto} gene for extreme resistance. Although virus was not detected in Pirola plants, necrotic spots developed on its leaves and stems in reaction to all of the strains tested in this trial. Barker (1996) described similar necrotic reactions in this cultivar and suggested that they may be caused by difference between isolates and environmental conditions.

Temperatures, above 27°C were encountered during primary infection because of El Niño. That, and fluctuating temperatures between 20° and 25°C during the secondary infection trial, may account for the reaction in Pirola as well as for the uncommon hypersensitive reaction observed in susceptible controls Bintje and Atlantic.

Observation by Le Romancer and Kerlan (1992) of hypersensitivity against the PVY^{nn} strain in an Ry_{adg}-carrying cultivar, V-2, and the Ry_{sto}-carrying variety Corine led them to suggest that this strain behaved as a resistance-breaking strain. However, they did not find the ringspot necrosis symptom that characterizes the pathogenic effect of

PVY^{nn} on the tubers of the cultivars they studied. As mentioned by Barker (1996), that can be caused by the presence of other potyviruses in the isolate.

As the necrotic reaction observed is a nonspecific response of plants to virus infection, and not a damage effect produced in the plant by the virus itself, this reaction cannot be taken as a mechanism of resistance breaking. The necrotic reaction seems to be induced by the replication of virus in a few cells before hosts that possess resistance genes trigger the resistance response. In the case where susceptible cultivars develop this reaction, as in our experiment, the virus succeeds in reaching high levels of replication and the pathogenic effect finally develops. No symptoms associated with PVY multiplication developed in plants containing Ry_{adg}; therefore it can be asserted that resistance to PVY replication of varieties and parental clones carrying this gene is extremely strong and stable.

Tubers recovered from plants of the resistant and susceptible cultivars tested did not develop the tuber necrotic ringspot symptoms reportedly induced by the PVY^{nn} strain. Kus (1992), after testing 40 European and North American cultivars against this strain, concluded that tuber reaction induced by this strain is character-specific for each cultivar. He observed that within susceptible cultivars, the occurrence of ringspot necrosis differed in its incidence, time of appearance, and severity. For instance, Igor, a common European variety, reached 100% tuber symptoms in the first cycle of infection, while Russet Burbank, among other susceptible varieties, never developed symptoms. Conversely, Desiree, which was also tested in our experiment, developed interveinal mosaics, and only 8% of secondarily infected plants exhibited ringspot necrosis on tubers. Although we also observed mosaics on plants of Desiree, we did not find this tuber reaction even on secondarily infected tubers. Our results suggest that susceptible cultivars used in this experiment might be tolerant of this strain, since even though they developed severe foliar symptoms, tubers did not develop necrosis.

No case has yet been reported in which potato plants show tuber reactions against PVY^{nn} without developing foliar symptoms. Hence, there is no evidence to support a resistance-breaking effect. Since no foliar or tuber reaction to PVY^{nn} was found in the Ry_{adg}-bearing cultivars tested, we conclude that Ry_{adg}-mediated resistance is also effective against this strain.

Reaction against combined inoculation of PVY and PSTVd

Combined infection by PVY and PSTVd resulted in much more severe symptoms of PVY in susceptible varieties than those observed under PVY infection alone. This effect and severe stunting were also described by Singh and Somerville (1987). Production of smaller and deformed tubers with a characteristic spindle shape were attributed to the viroid infection, since this symptom is characteristic of PSTVd alone.

There were no differences between the resistance response of either Ry_{adg}- or Ry_{sto}-bearing cultivars under double infection and those observed in the same cultivars infected with PVY alone. No PVY symptoms developed and PVY was not detected by ELISA in the presence of these genes. Hence, there was no evidence to suggest that combined infection by PVY and PSTVd can break Ry_{adg}-mediated extreme resistance.

Conclusions

The durability of the Ry_{adg} gene, with respect to a new strain of PVY (PVY^{nn}), and the presence of PSTVd was demonstrated in this study. The qualitative effect of this gene was confirmed, since one, two, or three dominant alleles provide the same level of protection. Additionally, it was shown that the Ry_{adg}-mediated extreme resistance gene was more effective than

Ry_{sto}. Both resistance genes appear to be stable even in presence of PSTVd, which is known to contribute to very high levels of PVY concentration through its synergistic effect. This desirable feature of Ry_{adg} may also contribute to stability of resistance in the event that PVY might interact with subviral pathogens in nature, whereby vector relations or infectivity may be altered.

Ry genes are frequently used in breeding, and it is expected that they soon will be isolated and used in plant-derived transgenic resistance. The continued testing of the durability of this apparent "frozen vertical resistance" (Robinson, 1976), is important if resistant varieties developed from these programs are expected to replace conventional susceptible varieties. That is particularly true if deployment on a long-term, global scale is envisioned.

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The Leafminer Fly in Potato: Plant Reaction and Natural Enemies as Natural Mortality Factors

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The pea leafminer fly (LMF) species, *Liriomyza huidobrensis* (Blanchard) is highly polyphagous, attacking many vegetables and ornamental plants (Spencer, 1990). LMF has become a key pest in all the countries where it has been introduced and is resistant to many insecticides. In many places, the pest has shown significant levels of resistance to most carbamate, organophosphate, and pyrethroid insecticides commonly used to kill larvae and adult flies (Parrella et al., 1984, Macdonald, 1991). LMF is capable of completely destroying potato crops in the absence of adequate control measures.

Originating in the neotropics, it was restricted to Central and South America until the 1980s. Since then, *L. huidobrensis* has rapidly spread to other areas, and is reported in several African, European, and Asian countries. Specifically, *L. huidobrensis* is reported to be a serious potato pest in Argentina, Brazil, Chile, Indonesia, Israel, Kenya, Malaysia, Mexico, and Peru, and in Central America and North Africa (IIE, 1996).

LMF occurred at low populations on the central coast of Peru and had no negative economic effect on the potato crop until the 1950s (Wille, 1952). In the following decade, potato fields were sprayed with organic insecticides (DDT, parathion, BHC) against the tomato pinworm (*Tuta absoluta)* (Campos, 1976). Although in most cases, these sprays were unnecessary, as there was no evidence of pinworm infestations reaching economic thresholds in potato. During that decade, however, LMF populations had begun to increase (Herrera, 1963; Campos, 1978). At this point, the insecticides used were primarily to fight LMF infestations rather than pinworms. Since the 1980s, 10-13 sprays/season have been used against LMF in potato. The cost of spraying has become the most expensive component of potato production (Ewell et al., 1990; Mujica and Cisneros, 1997). Most research over the last 20 yr has been oriented toward finding new compounds to replace insecticides that have lost effectiveness in controlling LMF larvae and adult flies.

The resurgence of LMF as a pest has been attributed to the destruction of its natural enemies by insecticides (Cisneros, 1986; Yabar, 1988; Ochoa and Carballo, 1993). For farmers, the presence of adult flies early in the cropping season elicits early sprays that create a treadmill effect. Secondary effects of such frequent spraying are the occurrence of heavy infestations of the white mite, *Polyphagotarsonemus latus* (Banks), and the budmidge, *Prodiplosis longifila* (Gagne).

This paper reports results of the study of the reaction of the potato plant to LMF infestation and the occurrence and role of natural enemies of LMF with a goal of using this knowledge to determine how to break the cycle of high LMF incidence.

Material and Methods

Reaction of the potato plant to LMF infestation

In the study of LMF potato plant interactions, five aspects were investigated: (1) adult feeding and oviposition behavior, (2) pattern of LMF damage in the potato plant,

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(3) hypersensitivity reaction of potato leaves (egg extrusion), (4) LMF population density and potato plant phenology, and (5) seasonal variation of LMF population.

Adult feeding and oviposition behavior. Adult feeding and oviposition was studied in the greenhouse using caged (potted) plants of cv. Canchán. Plastic tubing (cellulose membrane, 49 mm av diam) was used to isolate small groups of flies on leaflets. Newly emerged male and female flies were introduced into the tubing. Daily observations were made on the occurrence of oviposition and feeding punctures to describe adult behavior.

Pattern of LMF damage in the potato plant. Evaluation of larval damage was carried out with cv. Revolución in an experimental field in the Cañete Valley from August to October 1995. No insecticide was applied. Leaf samples were taken from the bottom, middle, and top parts of the potato plants. Occurrence of mining in potato foliage by LMF larvae was recorded by observing fresh and dry tunnels in the sampled leaves.

Hypersensitivity reaction of the potato plant. The occurrence of egg extrusion was recorded in greenhouse trials in La Molina in 1996 using Canchán. Two pairs of male and female flies per leaflet were isolated in plastic tubing for oviposition. The flies were removed after 24 hr. Leaflets were then observed daily in the laboratory. The number of eggs extruded was recorded as well as the number of alive and dead neonate larvae.

LMF population density and potato plant phenology. Adult and larval populations were evaluated in a potato field (cv. Canchán) using no insecticide applications (Cañete Valley, June to November 1996). The adult population was determined by counting the number of flies/plant on 25 plants. Damage was determined by recording the percentage of infested foliage area on each plant. Larval infestation in leaves was determined by counting the number of larvae per leaflet on 25 infested leaflets. Samples were taken weekly throughout the growing season.

Seasonal variation of LMF population. Population studies were conducted in three sites (Cañete, Callao, and Carabayllo on the central coast of Peru) from January to December over 3 yr, 1996-1998, to look at the seasonal variation. Potato fields and other host crops (celery, chinese onion, lettuce, tomato, bean, pea, spinach, and cucumber) were evaluated. Adult populations were determined by using a yellow sticky trap (20 x 20 cm) in each field. Infested foliage was taken to the laboratory for further observations (emergence of flies and parasitoids). Samples were taken weekly over the 3 yr.

Occurrence and role of natural enemies of LMF

Parasitoids. Yellow sticky traps were used to determine the occurrence of adult parasitoids. The percentage of parasitism was evaluated weekly by collecting leaves infested with LMF larvae. The leaves were stored in petri dishes in the laboratory and kept for 30 d. Adult flies that developed from healthy larvae and the number of parasitoids (ectoparasitoids and endoparasitoids) recovered from fly larvae and puparia were recorded.

Predators. *Soil-inhabiting predators.* Soil inhabiting predators were captured in pitfall traps (1-L plastic cups with 500 cc formaldehyde (5%)) placed in potato and other host crop fields. Traps were collected weekly and the number of predators recorded.

Foliage-inhabiting predators. For recording the presence and number of predatory flies (*Condylostylus similis* and *Drapetis* sp.), 25 plants/field were sampled weekly.

Results and Discussion

Reaction of the potato plant to LMF infestation

Numerous field observations (unpublished data) confirm that short-cycle (early) potato cultivars suffer more severe damage by LMF than long-cycle (late) cultivars. The most likely explanation is that late cultivars produce new leaves that compensate for damaged leaves. Glandular trichomes have been mentioned as a potential protection mechanism against LMF (Mujica et al., 1993), but commercial cultivars with high densities of such trichomes are not available. Previous studies (Gonzales, 1994) and our own observations, however, suggest that a hypersensitivity mechanism could be involved.

Adult feeding and oviposition behavior. The female produces two types of lesions in the potato leaf, a feeding lesion and an oviposition lesion. As soon as they emerge, adult females make superficial feeding lesions in the upper surface of the leaf with their ovipositor. Lesions are round (1 mm diam). Both females and males feed on the exudate of the lesion. Mating occurs 6 to 24 h after flies emerge from puparia. Oviposition lesions are about the same size as feeding lesions, but are deeper because the female lays the egg inside the leaf tissue. Eggs newly laid on the lower surface of the leaf are not readily visible to the naked eye.

Pattern of LMF damage in the potato plant. Newly hatched larvae burrow inside the leaf surface, making a serpentine mine. Mine diameter increases as the larva grows. A large proportion of grown larvae remains close to the midrib. Leaf tissue affected by larval mining becomes necrotic and brownish colored. The length of time before the damaged area becomes necrotic depends on the cultivar, physiological condition, and age of the plant. As necrotic areas coalesce in highly-infested leaves, the whole leaf dries out and dies. Highly-infested potato fields appear burned. Fly infestations may start at plant emergence and continue to plant senescence.

Larval damage in a growing plant follows a fairly well established pattern. Leaf lesions, for both feeding and oviposition, are scattered over the plant. Lower leaves are the first to show damage. Middle and upper leaves are progressively damaged as the plant grows and infestation continues. Damage in the upper leaves usually occurs when the canopy stops growing. Necrosis of the infested leaves follows the same pattern, until the whole plant dries out.

Hypersensitivity reaction of potato plant. Females oviposit in potato foliage as soon as the plant emerges, but larval mines are scarce. At this stage of plant development, the lack of correlation between the number of adult flies and the number of larval mines on leaves is evident. In fully grown plants—up to preflowering—there are more mined leaves in the lower part of the plant than in the upper part.

During growth phases, flowering to senescence, larval mines develop in leaves anywhere on the plant. This is the period that infestation flares up in potato fields. Differences in larval infestation depend on where on the plant eggs were deposited. When an egg is laid in a mature leaf and hatches, almost all the neonate larvae successfully start burrowing into the palisade tissue of the leaf surface. That explains why larval infestations start in the mature, lower leaves of a growing plant, and cover the whole plant after all foliage is mature.

When an egg is laid in a growing leaf, a hypersensitivity reaction makes many neonate larvae fail to burrow into the leaf tissue. Tissue surrounding the encrusted egg starts hypertrophic growth (abnormal multiplication) of cells that push the egg to the leaf surface. Extruded eggs are exposed to adverse weather conditions that result in dehydration and exposure to predators.

Neonate larvae of surviving eggs experience the same fate, thereby reducing their chances to burrow into the leaf tissue.

In the laboratory and greenhouse, more than 90% of eggs were extruded; 60% of those died from dehydration (Sotomayor and Cisneros, 1996). That explains why potato plants with growing foliage show small numbers of mined leaves despite high adult fly populations. Egg extrusion is higher in vigorously growing potato plants that are well fertilized and irrigated.

LMF population density and potato plant phenology. It is important to differentiate between the population densities of adult and larval LMF. Immigrant adults initiate infestations in small potato plants.

Despite relatively large numbers of adult flies, larval populations initially are low because of egg extrusion. As more leaves mature (beginning at the lower part of the plant), more larvae are able to develop and the larval population increases gradually. When the plant stops growing, about 1 wk before flowering, larval population reaches its peak and remains at a plateau until initiation of plant senescence. That is the time when larval outbreaks may be extremely injurious and the whole plant dries out (Figure 1).

Differentiating adult fly from larval populations helps to monitor LMF populations for management purposes. Monitoring adult populations usually leads to early applications of insecticides that could be avoided considering the low larval populations during vegetative growth of the plant. Early applications adversely affect a comprehensive pest management strategy.

Seasonal variation of LMF population. LMF host plants are present in the Cañete Valley of Peru year-round because of its favorable climate. In normal years (those not affected by El Niño), monthly average summer temperature is 23.6°C (18.4°C - 28.7°C); av winter temperature is 15.6°C (13.2°C - 18.0°C). Still, there are clear seasonal trends in LMF population levels as data from 1994-96 observations suggest. Highest populations are recorded in June (winter) and September (spring). Lowest populations occur in the warmer months (December to April) (Figure 2). An increase in larval parasitism seems to be the most important factor in reducing the LMF population during the warm months of the year. In November, parasitism rates as high as 92% are common.

Another factor that may affect population fluctuation is a reduction in the rate of oviposition during the warmer months (Lizarraga, 1989). However, populations remain high under intensive insecticide treatments, confirming the stronger effect the presence of natural enemies has on reduction of the fly population.

Atypical weather in 1997 and 1998 caused by El Niño resulted in drastic changes in LMF population densities (Figure 2). Temperatures higher than normal were recorded up to June 1998, followed by a return to normal beginning in July. Minimum daily temperatures took longer to reach normal levels. That explains the low LMF population during the period of warmer temperatures. As temperature decreased, the first LMF peak was recorded in September. But in two other sites on the central coast (San Agustin and Carabayllo) where vegetable crops are produced under heavy use of insecticides, LMF populations remained fairly high despite higher temperatures. Population density peaks were recorded in May and June and in September and October. Records in 1997-98 suggest that factors such as the occurrence of other LMF plant hosts may also play a role in the dynamics of the LMF population (Figure 3).

Occurrence and role of natural enemies of the LMF

The occurrence of low populations of LMF up to the 1950s cannot be explained by unfavorable climate or lack of suitable hosts, as it was in the case of El Niño in 1997-98. The temperature range on Peru's

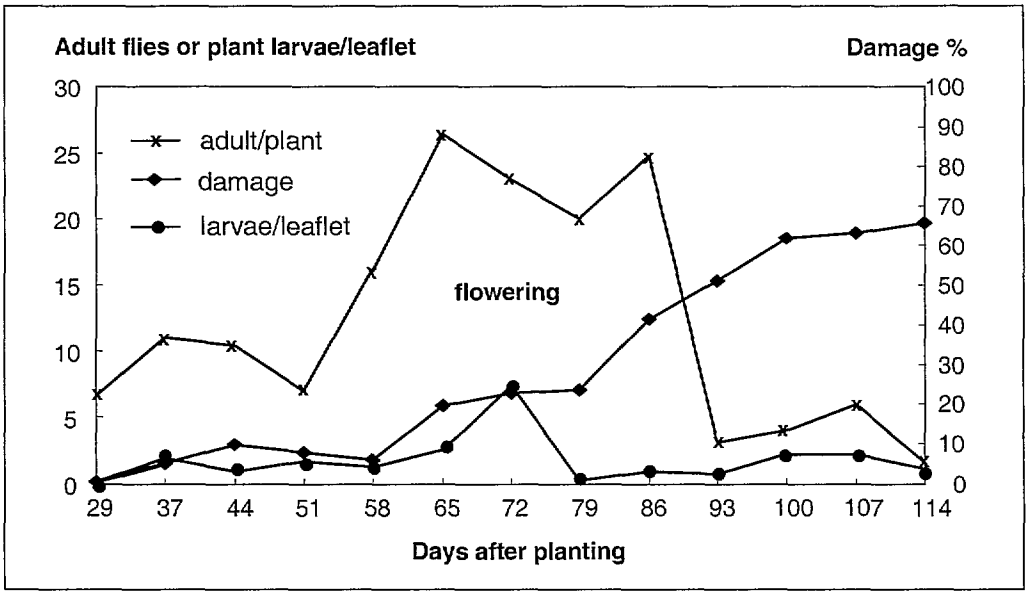

Figure 1. Variation of leafminer fly adult and larvae populations and damage in one cropping season, Cañete, Peru, 1996.

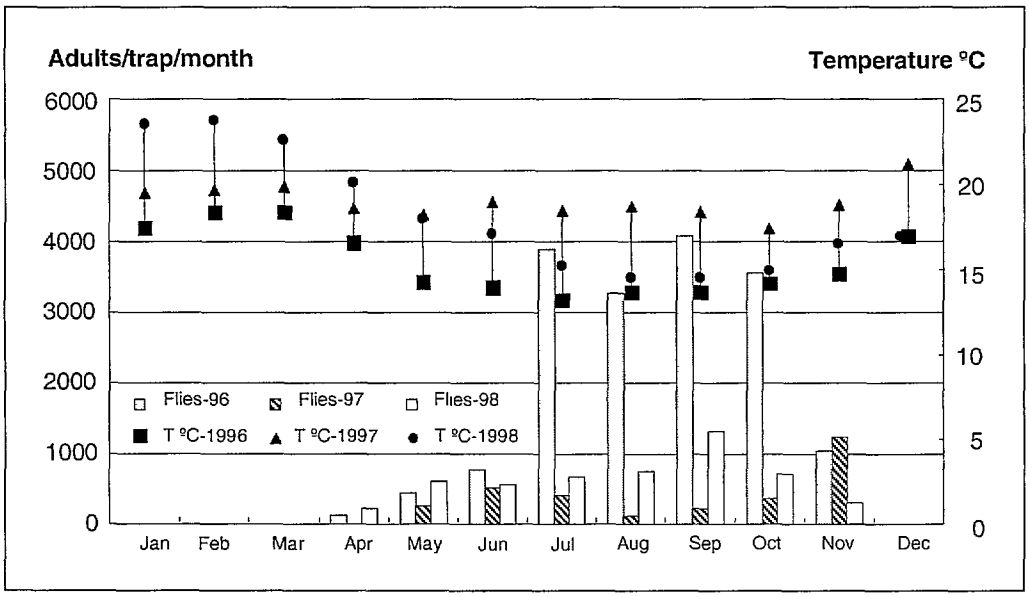

Figure 2. Population densities of the leafminer fly in potato fields, and monthly av min daily temperature for three consecutive yr (1996-97-98) in the Cañete Valley, Peru.

central coast is favorable for the development of LMF as well as its host plants. The most likely scenario is that until the 1950s natural enemies kept LMF populations below economic thresholds. For several years, LMF parasites and predators have been recorded in potato fields and, to a limited extent, in fields of other host crops on the central coast (Redolfi et al., 1985;

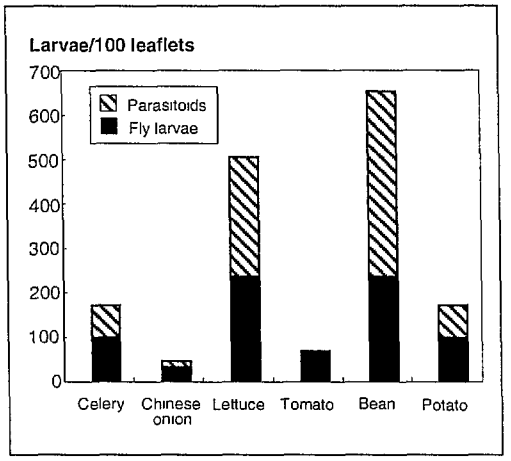

Figure 3. Seasonal av leafminer fly larval infestation and parasitoids in several vegetable crops, including potato, Carabayllo, Lima, Peru, 1998.

Sanchez and Redolfi, 1988; Fonseca and Sanchez, 1996).

Parasitoids. ***Identification of species.*** There is a rich complex of parasitoid species that attack LMF larvae on Peru's central coast (Table 1). Some have been identified; others are in the process of being identified or characterized. Most parasitoid species (17) belong to the Eulophidae family. The most abundant species are the ectoparasitoid, *Diglyphus* sp. and the endoparasitoids, *Halticoptera arduine*, and *Chrysocharis* spp. Other parasitoids are present but are less abundant under the conditions found on the central coast (Figure 4).

Relative effectiveness of parasitoids. The two most important parasitoids seem to be largely responsible for the seasonal variation of the LMF population. Females of *H. arduine* lay their eggs inside the body of the LMF larva by introducing their ovipositor through the epidermal layer of the leaf mine. The parasitoid larva develops inside the LMF pre-pupal larva. The parasitized fly larva survives until pupation, allowing the parasitoid larva to complete its development. Emergence of parasitoid adult wasps occurs 1 wk after the emergence of flies from nonparasitized puparia. Level of parasitism (measured as percentage of fly puparia) by *H. arduine* commonly reaches 55-78% from June to August.

Females of *Diglyphus* sp. paralyze the LMF larva inside the leaf mine and lay their eggs next to the larva. The parasitoid larva feeds on the juices of the fly larva from outside, resulting in the death of fly larva before pupation. The parasitoid pupae are formed inside the leaf mine. Adult wasps emerge from the dry mined leaves. The level of parasitism by *Diglyhus* sp. was estimated to be around 60-82% of fly larvae from September-November.

Seasonal occurrence of parasitoids. In Cañete, the potato planting season starts in March and extends for several months depending on weather. Late plantings are harvested in December. When little or no insecticide is used, parasitism of LMF larvae from April to August usually varies from 35% to 55%. But, from September onward, total parasitism increases steadily until November when parasitism nears 100%. High temperatures recorded in 1997-98 changed this pattern (Figure 5). The occurrence of new pests, whiteflies, budmidges, and cutworms, led farmers to use insecticides more frequently than normal. Parasitoids in Cañete were drastically affected; total parasitism was even lower than in other valleys on the central coast.

Predators. Leafminer flies in the study area are attacked by many predators belonging to five insect orders (Coleoptera, Hemiptera, Diptera, Dermaptera, and Hymenoptera) and by spiders. Most predators are general feeders and prey indiscriminately on several insect pests. Some predatory flies of the families Dolichopodidae and Empididae tend to prefer LMF.

All developmental stages of LMF were subject to predation. The most exposed stages, however, were most vulnerable—the extruded egg in the foliage and the pupa in the soil. Direct evaluation of the role played

Table 1. Species of parasitoids of the order Hymenoptera that attack leafminer fly larvae and pupae in the central coast of Peru, 1998.

Hymenoptera	Subfamily	Species	Parasitism
Ichneumonnoidea			
Braconidae	Opiinae	*Opius scabriventris*	Endoparasitoid
		Opius sp.	Endoparasitoid
Cynipoidea			
Eucoildae			
		Ganaspidium sp.	Endoparasitoid
Chalcideoidea			
Eulophidae	Eulophinae	*Diglyphus websteri*	Ectoparasitoid
		Diglyphus begini	Ectoparasitoid
		Diglyphus sp.	Ectoparasitoid
	Tetratischinae	*Diaulinopsis sp.*	Endoparasitoid
	Entedontinae	*Chrysocharis phytomyzae*	Endoparasitoid
		Chrysocharis ainsliei	Endoparasitoid
		Chrysocharis sp. A	Endoparasitoid
		Chrysocharis sp. B	Endoparasitoid
		Chrysocharis sp. C	Endoparasitoid
		Chrysocharis sp. D	Endoparasitoid
		Chrysocharis sp. E	Endoparasitoid
		Chrysonotomyia sp. A	Ectoparasitoid
		Chrysonotomyia sp. B	Ectoparasitoid
		Chrysonotomyia sp. C	Ectoparasitoid
		Closterocerus cinctipennis	Ectoparasitoid
		Closterocerus sp.	Ectoparasitoid
	Elachertinae	*Zagrammosoma multilineatum*	Ectoparasitoid
Pteromalidae	Miscogasterinae	*Halticoptera arduine*	Endoparasitoid
		Halticoptera sp. A	Endoparasitoid
		Halticoptera sp. B	Endoparasitoid

by specific predators in the dynamics of the fly is extremely difficult. For the time being, efforts are centered on identifying these species and describing their predatory activity. Table 2 lists the most common predators of LMF found in coastal Peru.

Soil-inhabiting predators. The importance of soil-inhabiting predators is usually underestimated. That is particularly true in the case of LMF, because its larval stage is always protected inside leaf mines. It is only when larvae abandon the mine to

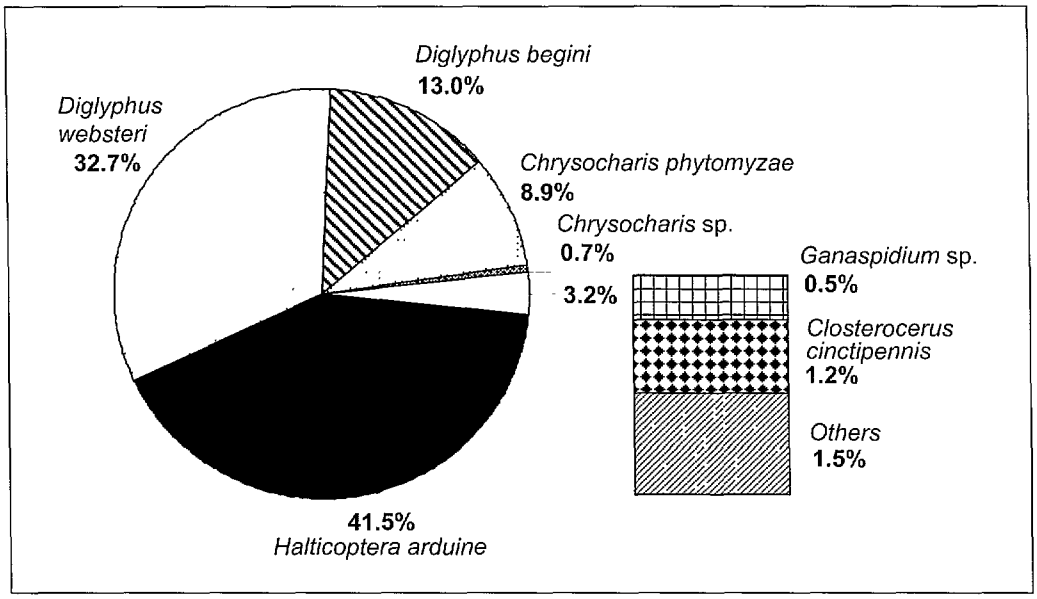

Figure 4. Distribution of species of parasitoids of leafminer fly larvae in potato and other crops in the Cañete Valley, Peru, 1998.

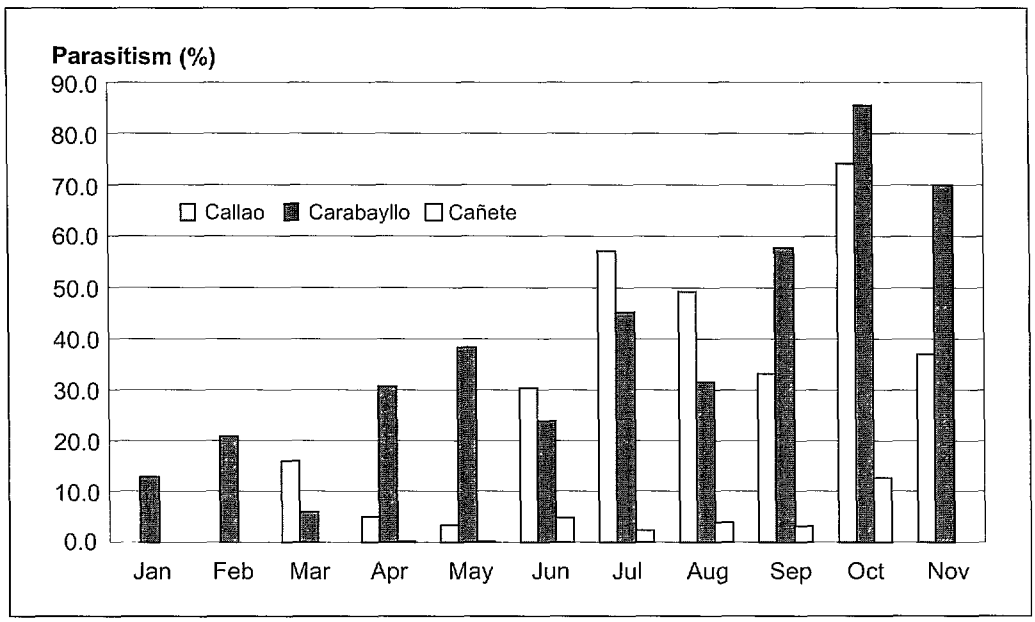

Figure 5. Occurrence of leafminer fly parasitism in potato and other host plants at three sites on the central coast of Peru, 1998.

pupate that they become vulnerable to predators in the soil. In some fields, the most abundant predators were *Pterostichus* sp. and *Calosoma abbreviatum*. *Pterostichus* sp. crawls rapidly on the soil surface searching for prey, including LMF puparia. *Calosoma abbreviatum* are also present, but in smaller numbers.

Table 2. Predaceous arthropods reported to feed on leafminer fly eggs, larvae, pupae, and adults in the central coast of Peru, 1998.

Class	Order	Family/species	Prey
Insecta	Coleoptera	Carabidae	
		Calosoma abbreviatum	Pupae
		Pterostichus sp.	Pupae
		Cicindellidae	
		Megacephala carolina-chilensis	Pupae
		Staphilinidae	
		Undetermined spp.	Pupae
	Hemiptera	Anthocoridae	
		Orius insidiosus	Egg
		Nabidae	
		Nabis punctipes	Larvae
		Lygaeidae	
		Geocoris punctipes	Egg
	Dermaptera	Labiduridae	
		Undetermined spp.	Pupae
	Diptera	Dolichopodidae	
		Condylostylus similis	Adult
		Empididae	
		Drapetis sp.	Adult
	Hymenoptera	Formicidae	Pupae
Arachnida	Araneida		
		Theridiidae	Adult, pupae
		Argiopidae	Adult, pupae
		Lycosidae	Adult, pupae
		Anyphaenidae	Adult, pupae
		Salticidae	Adult, pupae

Megacephala carolina-chilensis was fairly common from December through March. A nonidentified species of the family Staphilinidae was commonly trapped throughout the year.

The seasonal abundance of soil predators was associated with higher temperatures (Figure 6). Several species of ants are active predators in the soil and foliage. Finally, several species of spiders (general predators) occurred on the soil surface and in the foliage.

Foliage-inhabiting predators. Eggs, larvae, and adult LMF are exposed to predators in the plant foliage. Adult and nymphs of small to minute true bugs, *Geocoris punctipes* and *Orius insidiosus,* prey upon LMF eggs, especially extruded eggs. Another true bug, *Nabis punctipennis,* prey on eggs and larvae, penetrating the leaf epidermis with its proboscis to reach larva inside the leaf mine. Their predatory effect on LMF has not been quantified directly, but the presence of these voracious

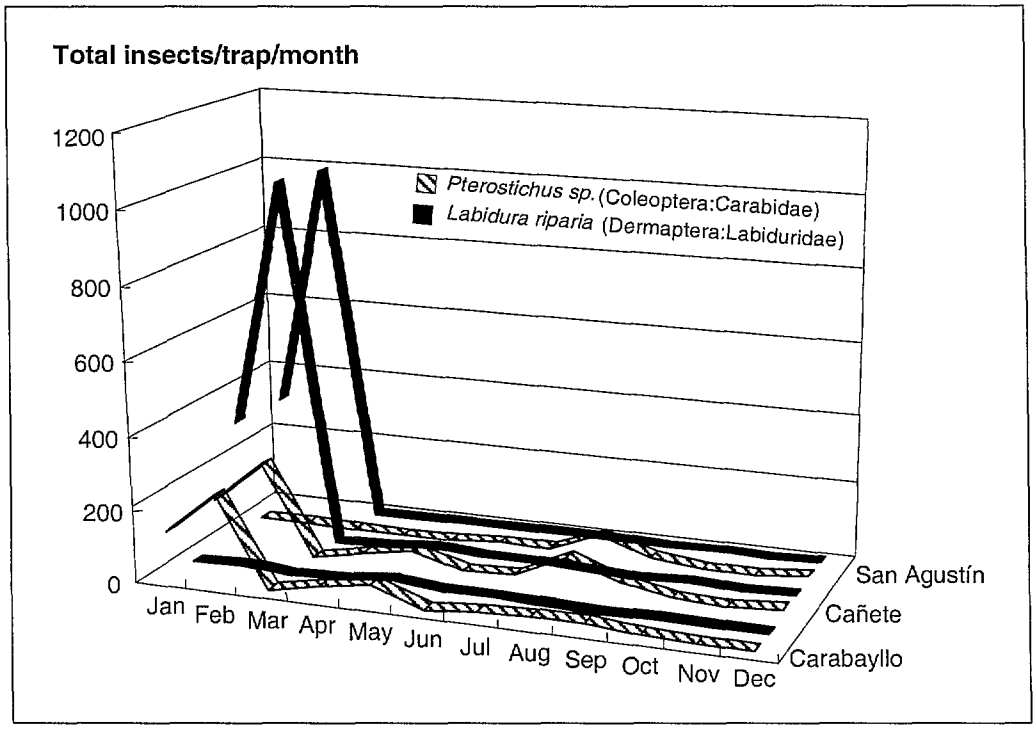

Figure 6. Seasonal occurrence of the most abundant predators captured in pitfall traps at three sites on the central coast of Peru, 1998.

predators coincides with slower population growth.

Even more difficult to evaluate is the role of predatory flies that capture and kill LMF adults. Species of Dolichopodidae and Empididae occur in large numbers near humid areas with abundant vegetation along the central coastal valleys of Peru. When insecticides are not used, they are abundant in potato, beans, and other crops infested by LMF. They actively hunt LMF at rest and in flight. Similar behavior is exhibited by black fly (*Drapetis* sp.). Predatory true bugs are constantly present, whereas predatory flies occur only occasionally, but usually in large numbers.

Conclusions

There are important natural mortality factors in the potato plant and in potato fields that affect LMF populations. These factors constitute the basis for the management of the pest. Hypersensitivity of the growing potato leaf that results in egg-extrusion can be further selected for as a mechanism of resistance against the fly. The complex group of parasitoids plays an important role in regulating LMF populations on the Peruvian central coast. Their introduction to other areas, particularly where there is little rain, might help to manage LMF infestations.

Although it was not possible to quantitatively evaluate the mortality produced by predators of LMF, their presence was a sign of good biological control and coincided with low LMF populations.

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Taxonomy and Bionomics of the Andean Potato Weevil Complex: *Premnotrypes* spp. and Related Genera

J. Alcázar and F. Cisneros[1]

Andean potato weevils (APW) are the most serious pests of potato (*Solanum* spp.) at high altitudes (above 2,800 m) in the Andean region, where wild and cultivated potato species are their only hosts. They are distributed from Argentina to Venezuela covering a mountain territory about 5,000 km long. When no control measures are used, a common situation for subsistence farmers, more than 50% of tubers are commonly infested at harvest. Commercial production is subjected to the use of highly toxic insecticides applied to the foliage or incorporated into the soil. Even then 15-30% of harvested tubers are infested.

In a few cases where ancient agricultural systems are still practiced, as in communal agriculture, APW damage is negligible. That is because of distant rotations in time (5-7 yr) and space (potato fields spaced several kilometers apart), a system that can rarely be practiced today.

Most work on APW has been devoted to the study of chemical control of the pest, forced by the need to combat the pest and reduce damage. Other, more basic, aspects such as identification of the various weevil species, their geographical distribution, and similarities/differences in their life cycles and seasonal history have been only partially or nonsystematically addressed.

The APW Complex

Farmers collectively designate a group of weevils whose larvae bore into potato tubers as Andean potato weevil ("gorgojo de los Andes") or white grubs ("gusanos blancos"). Taxonomists have described several species, but it is uncertain if there still remain undescribed species, particularly in southern Peru and Bolivia.

Taxonomy of APW

Although species of the genus *Premnotrypes* are the most widely distributed, the first taxonomic descriptions of APW were of species in two different genera. The first species described was *Phyrdenus muriceus* Germar in 1824. The second was *Rhigopsidius tucumanus* Heller in 1906 (Pierce, 1914). Both were collected in Argentina.

Pierce (1914) described two new APW species from infested tubers in Peru: *Premnotrypes solani* and *Trypopremnon latithorax*. They were considered the most important potato weevil species in the Peruvian entomological literature for many years (Wille, 1952). In the interim, four new species had been described: *Trypopremnon sanfordi* Pierce (1918), *Solanophagus vorax* Hustache (1933), *Plastoleptops solanivora* Heller (1935), and *Premnotrypes fractirostris* Marshall (1936).

Kuschel (1956) included the genus *Premnotrypes*, within a new tribe (Premnotrypini), and presented a key for the identification of 11 valid species within the genus. An additional species was described by Alcalá (1979a), making a total of 12 valid *Premnotrypes* species. They are: *P. vorax* (Hustache), collected in Colombia, Ecuador and Peru; *P. latithorax* (Pierce), collected in Peru, Bolivia and Chile; *P. solaniperda* Kuschel, collected in Peru and Bolivia; *P. clivosus* Kuschel and *P. zischkai* Kuschel, collected in Bolivia; and

1 CIP, Lima, Peru.

P. fractirostris Marshall, *P. piercei* Alcalá, *P. pusillus* Kuschel, *P. sanfordi* (Pierce), *P. solani* Pierce, *P. solanivorax* (Heller), and *P. suturicallus* Kuschel, all collected in Peru.

Some authors dealing with potato pest problems included other genera within the APW complex, but these species are not able to complete their life cycles in potato. Yaya (1971) reported *Scotoeborus* sp. and a species near *Adioristus* sp. in potato in the central mountains of Peru. Other reports referred to *Hyperodes* sp. (Delgado, 1975); three species of *Adioristus* (*A. subsquameus* Hustache, *A. ebenus* Hustache, and *A. leprus* Hustache); and *Listroderes* sp. from the central mountains of Peru (Valencia and O'Brien, 1976). *Naupactus* sp. has been reported in internal documents of the Instituto Nacional de Investigacion Agraria, Huancayo, Peru.

Identification of APW Species

Genera and higher categories

The three genera involved in the APW complex belong to different subfamilies of family Curculionidae (Wibmer and O'Brien, 1986): genus *Premnotrypes*, tribe Premnotrypini, subfamily Entiminae; genus *Phyrdenus*, tribe Cryptorrhynchini, subfamily Chryptorrhynchinae; and genus *Rhigopsidius*, tribe Rhytirrhinini, subfamily Rhytirrhininae.

Tribe Rhytirrhinini is formed by only one genus (*Rhigopsidius* Heller), with two species (*R. tucumanus* and *R. piercei*). Van Emden (1952), however, considers them as synonyms. Tribe Crytorrhynchini is divided into several subtribes. The subtribe Cryptorrhynchina contains several genera of which one is related to the APW complex, *Phyrdenus* LeConte syn. of Cryptorrhynchus Germar.

Kuschel (1956) described tribe Premnotrypini, which includes three genera: *Rhinotrypes* Kuschel, *Microtrypes* Kuschel, and *Premnotrypes* Pierce. Only species of genus *Premnotrypes* are related to the APW complex. Synonyms recognized for genus *Premnotrypes* are *Trypopremnon* Pierce, *Solanophagus* Hustache, and *Plastoleptops* Heller.

Characterization of genera

The following characterization of genera of APW species is based on conventional taxonomic grouping of species. But the first premise is that the weevils are adults of larvae that developed in potato tubers.

1. Beak rather short. Hind wings vestigial. 2
   Beak long. Hind wings well developed. *Phyrdenus muriceus*
2. Prosternum grooved for reception of beak. Mandibles lacking deciduous piece. Pronotum with a deep median furrow widened angulary at middle and also behind. *R. tucumanus*
   Prosternum not grooved for reception of beak. Mandibles have deciduous piece. Large compound eyes with more than 80 facets. *Premnotrypes* spp.

Characterization of *Premnotrypes* species

External morphological characteristics and the male's aedeagus are valuable for identifying weevil species. The principal characters used for identification are those of the head (compound eye), rostrum or beak (epistome, groove for reception of antennal scape, mandibles, mandibular cusp or deciduous piece (Figure 1A)), antennae (antennal scape and antennal club), thoracic sclerites, and elytra (grooves

and intergrooves, posterior upper [bending] part). Complementary characters are scales, pubescence, setae, grooves, tubercles, and callus. (See Figure 1B.)

All *Premnotrypes* species show sexual dimorphism; females are larger than males. Average lengths recorded for females and males are as follow: *P. vorax* females 6.8 mm, males 5.6 mm; *P. latithorax* females 6.7 mm, males 5.6 mm; *P. suturicallus* females 8.0 mm, males 7.5 mm. The apex of the 5th sternite is blunt in males, pointed in females. The end portions of elytra are strongly declivous in females, less declivous in males.

Key to *Premnotrypes* species (modified from Kuschel, 1956)

1. Antennal scape with abundant scales. Dorsal scales and setae of rostrum mostly oriented forward. 2
   Antennal scape without scales. Dorsal scales and setae of rostrum oriented backward. 9

2. Eighth groove of elytron irregular, as with supernumerary points. 3
   Eighth groove normal; points in a definite simple line. 4

3. Base of prothorax with six nodules widely separated forming an arch. Pronotum densely pointed. Rostrum wide. Ocular lobes very prominent. Peru. *P. solani*
   Base of prothorax apparently with only four nodules; lateral ones are fused in a prominent body. Pronotum sparsely pointed. Rostrum narrow, with a deep suprascrobal naked groove. Ocular lobes slightly prominent. Peru. *P. solanivorax*

4. Rostrum epistome elevated 5
   Rostrum epistome almost flat, only slightly convex. In the high part of the elytron with six major tubercles, two on the third intergroove and one on the fifth. The latter is located equidistant between the other two. Peru and Bolivia. *P. solaniperda*

5. Antennal scape short and very thick, does not reach the anterior margin of the eyes. Tibia scaly in the lower border. Anterior margin of pronotum with a strong elevated structure that divides in two backward, imparting a sigmoid form to the whole structure. (See Figure 1C.) Peru. *P. fractirostris*
   Antennal scape slender, reaching somewhat beyond the anterior margin of the eyes. Tibia without scales in the lower border. Structure of pronotum different from that described above. 6

6. Frons without swelling near the eye. Rostrum with strong to moderate dorsal curvature. 7
   Frons with a swelling near the eye. Rostrum with a dorsal curvature less pronounced than above. Elytra transversally convex up to the 7th intergroove, whose tubercles are similar to those of the 5th intergroove. Elytra fold vertically to the sides at the 7th intergroove. The 5th intergroove generally ends in a larger tubercle, but without forming a true callus. 8

7. Rostrum with strong dorsal curvature. Elytra flat up to the 5th intergroove and then almost vertical to the side. Tubercles of the 7th intergroove much smaller

than those of the 5th intergroove. This one generally ends in thick callus in the upper part of the bending part. (Figure 1D). Colombia, Ecuador, Peru, and Venezuela. *P. vorax*

Rostrum with moderate curvature. Elytra transversally moderately convex. Third intergroove with a large tubercle on the upper posterior (bending) part. (See Figure 1E). Peru. *P. piercei*

8. Prothorax with the lateral swelling of the base blunt, and as prominent as the anterior lateral swelling. Lower tooth of the mandibles pointed. (See Figure 1F). Peru, Bolivia, and Chile. *P. latithorax*

   Prothorax with the lateral swelling of the base pointed and prominent. Lower tooth of mandibles blunt. Peru. *P. sanfordi*

9. Antennal scape thin and reaching beyond the anterior margin of the eyes. The 3d intergroove ends in the upper posterior (bending) part with an elevated tubercle. Bolivia. *P. clivosus*

   Antennal scape at most may reach the anterior margin of the eyes. The 3d intergroove does not have a tubercle larger than the upper posterior (bending) part. 10

10. Suture in the upper posterior (bending) part with a callus. Peru. *P. suturicallus*

    Suture in the upper posterior (bending) part without a callus. 11

11. Prothorax more or less rough and scaly. The 7th intergroove forms a strong disc ridge. The 3d and 5th intergrooves each have a large tubercle. Behind it the elytra fall vertically. Bolivia. *P. zischkai*

    Prothorax somewhat irregular but smooth. Few scales in the disc. The 7th intergroove does not form a pronounced border that limits the disc. Tubercles in odd intergrooves small and blunt. Peru. *P. pusillus*

Geographical Distribution of APW Species

All species of genera *Premnotrypes, Rhigopsidius,* and *Phyrdenus* that attack potato are native to the Andes. They commonly occur between 2,800 and 4,700 m where the number of plant species is somewhat restricted. Practically the only crop that can be grown at those altitudes is potato (*Solanum andigenum* and other species of tuber-forming *Solanum*, including bitter potatoes at higher altitudes). The Andean mountains extend along Chile, northwest Argentina, Bolivia, Peru, Ecuador, Colombia, and part of Venezuela.

The APW species are not evenly distributed along the Andean mountains. Most species are concentrated in Peru and Bolivia, which could be considered the center of origin for these weevils. Ten of the 12 species of *Premnotrypes* occur in Peru. *P. clivosus* and *P. zischkai* have been reported only in Bolivia. *P. vorax* occurs in Colombia, Ecuador, Venezuela, and Peru. *Rhigopsidius tucumanus* occurs in northwest Argentina, Bolivia, and the south of Peru. *Phyrdenus muriceus* occurs in Bolivia and northeast Argentina.

Alcalá (1979) made the first study on the distribution of Andean weevils in Peru. We have updated that work and present it in Figure 2 along with distribution of APW species throughout South America. *R. tucumanus* has been reported in Argentina (Tucumán, Santiago del Estero, Jujuy, Catamarca, and Salta) (Agostini and Vilte, 1982), Bolivia (Potosí, Chuquisaca, Tarija, Cochabamba, and La Paz) (PROINPA,

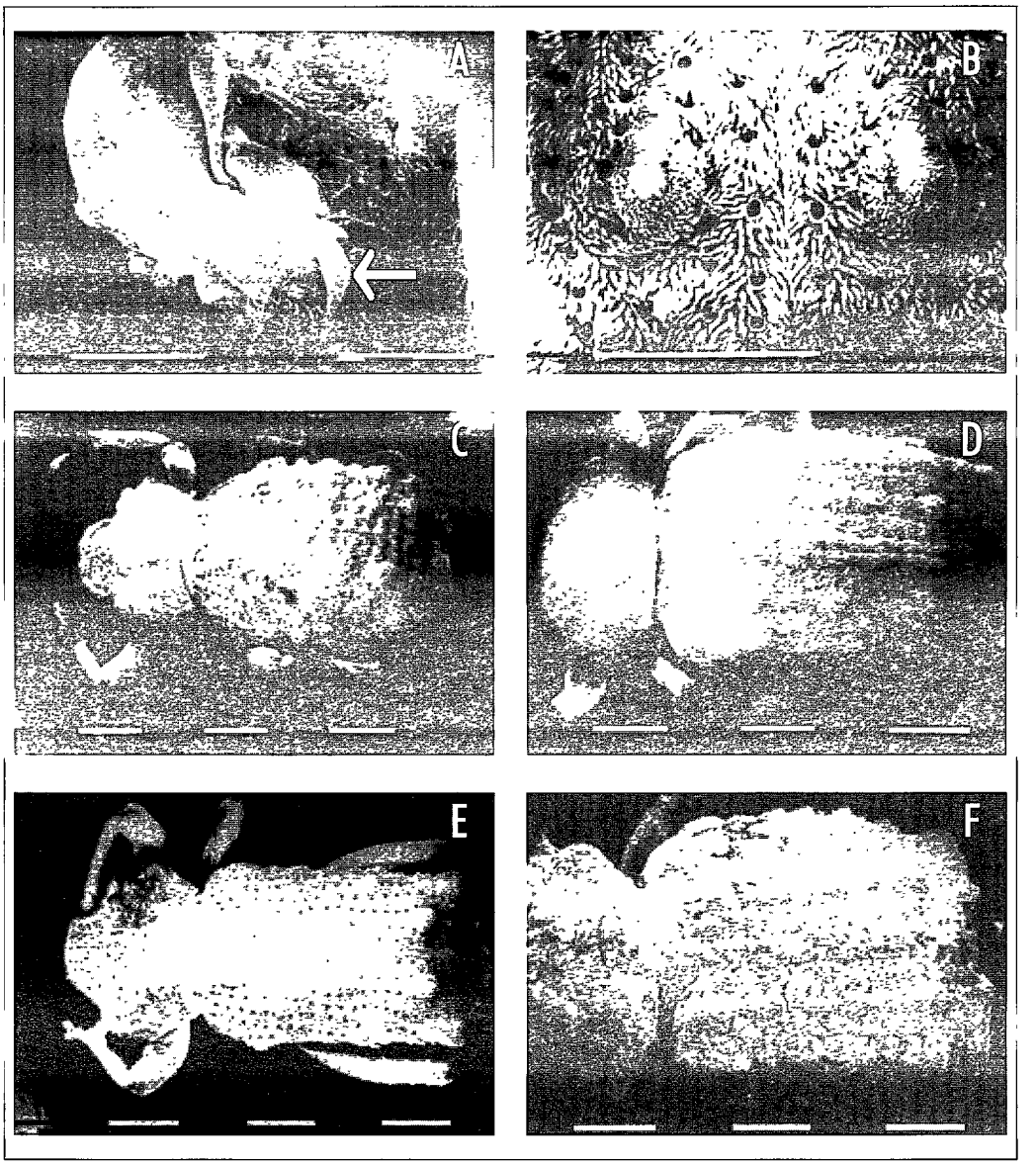

Figure 1. Morphological characteristics of *Premnotrypes* spp. A) mandibular deciduous piece, *P. latithorax*; B) elytra: tubercles and scales, *P. piercei*; C) dorsal view, *P. fractirostris*; D) dorsal view, *P. vorax*; E) dorsal view, *P. piercei*; F) dorsal view, *P. latithorax*. White lines = 1 mm.

1994), Chile (Agostini and Vilte, 1982), and Peru (restricted to Puno at the border with Bolivia).

Phyrdenus muriceus occurs at relatively low altitudes, not more than 2,000 m and is distributed in the mesotermic valleys of Bolivia (Cochabamba, Tarija, Chuquisaca, and Santa Cruz) (PROINPA, 1994). The original description of the species was based on material collected in Argentina.

Life Cycle and Seasonal Occurrence

The most widespread and important pests of the high Andes by far are *P. latithorax*,

Figure 2. Geographic distribution of species of the Andean potato weevil complex in the Andean Region.

P. suturicallus, and *P. vorax*. They are allopatric species in Peru. Their life cycles and the seasonal histories in Peru were studied in their respective areas of distribution (*P. vorax* in Cajamarca, *P. suturicallus* in Huancayo, and *P. latithorax* in Cusco.

Behavior

The three main species of *Premnotrypes* show similar behavior. It is expected that the same may be true for the other nine species of the genus; however, distinct differences have been observed for *Phyrdenus* and *Rhigopsidius*.

Premnotrypes. Adult males and females remain hidden during the day beneath soil clods, stones, dry leaves, or any other shelter including soil cracks near the potato plant. In the evening weevils climb to the

foliage to eat the border of the leaves and to mate. Females lay their eggs inside straw or other plant debris near the plants. As eggs hatch, neonate larvae make their way into the soil seeking potato tubers. The larva bores into the tuber and remains there feeding until it is ready to pupate. Then the larva abandons the tuber and digs into the soil to make a pupal cell and prepare a tunnel for its emergence as an adult. Weevils remain in the pupal cell until their emergence with the onset of rains. The weevil in the pupal cell is called an overwintering weevil. Overwintering weevils can be identified by the presence of the deciduous pieces of the mandibles. These pieces are detached when weevils become active and emerge from the soil.

Although this synchronization is evident for weevils in the field, rain is not the only stimulus to emergence. Adults also emerge from stores where rain is not a factor. In this case, however, the emergence period is extended.

Because the period of initial larval infestation of tubers extends over several weeks, larvae commonly reach maturity and abandon the tuber for pupation before harvest. In that case, pupation cells are scattered all over the field. Larvae that reach maturity at harvest, when tubers are piled, concentrate underneath the piles. Finally, the last group of larvae abandons the tubers during storage. Here, during the first 30 d, 97% of larvae leave the tubers for pupation. Pupation areas are the sources of new infestations.

Rhigopsidius tucumanus. The behavior of *R. tucumanus* differs from that of *Premnotrypes* spp. in that pupation occurs inside the tuber. As a result, adults emerging from the planted seed tubers initiate field infestations. Females lay eggs in the soil near the potato plants.

Phyrdenus muriceus. *Phyrdenus muriceus* adults migrate to the potato fields, either by walking or by flying (this species is the only one in the group that can fly). Feeding weevils make small holes in the leaves. Females lay eggs in the soil near the stem of the plant, and larvae feed on both tubers and roots. Pupation occurs in the soil.

Life cycles

Life cycles of APW have been reported by several authors with different levels of detail: Carrasco (1961), Tisoc (1989), and Carbajal (1992) on *P. latithorax*; Calvache (1986) and Muñoz and Alcázar (1998) on *P. vorax;* Alcázar (1976) on *P. suturicallus*; Carhuamaca and Tovar (1987) on *P. piercei*, and Gil (1991) on *P. solaniperda*. They show many similarities and few differences.

The life cycles of *P. suturicallus*, *P. piercei*, and *P. vorax* are given in Table 1. The most remarkable differences are in the number of larval instars (five for *P. vorax* compared with only four for the other two species), and the smaller quantity of eggs laid by *P. vorax*. Differences in time to complete larval instars and developmental stages may be due to species-related differences or different environmental conditions, particularly temperature.

Seasonal occurrence

There is one generation a year for the species of *Premnotrypes* studied and for *R. tucumanus*. The developmental stages of these weevils are synchronized with climatic conditions, the cropping system, and the phenological development of the potato plant. Our records in Peru; studies by Gil (1991) with *P. solaniperda* in Puno, Peru; and Carbajal (1992) with *P. latithorax* in Bolivia all indicate the occurrence of one generation a year. However, Gallegos (1995) in Ecuador and Calvache (1986) in Colombia, working with *P. vorax*, consider that there is more than one generation a year when potato cropping is continuous.

Potato production in the high mountains is essentially rainfed. There are two well-defined seasons: the dry, cold, winter season and the rainy, moderately warm

Table 1. Life cycle of three species of Andean potato weevil in days: *Premnotrypes suturicallus, P. piercei,* and *P. vorax*, Peru.

Stage	*P. suturicallus*	*P. piercei*	*P. vorax*
Egg (d)	33	26	43
Larva I	11	8	16
Larva II	9	7	14
Larva III	12	9	17
Larva IV	57	56	18
Larva V	-	-	58
Pupa (d)	54	52	50
Overwintering adult (d)	115	135	66
Cycle (Egg-adult) (d)	291	293	282
Longevity male (d)	159	277	168
Longevity female (d)	126	233	193
Total cycle (d)	434	549	463
Ovipositing period (d)	106	127	119
Eggs/female (no.)	631	521	374

growing season (spring-summer). The weevil overwinters successively as prepupa, pupa, and overwintering adult in a pupal cell in the soil (or in the tuber in case of *R. tucumanus*). When spring rains begin, overwintering weevils become active and emerge from the soil. Weevils remain in the field if potato plants are available, or migrate to new potato fields.

When immigration occurs, infestations are heavier near the border than in the center of the field. The seasonal history of adults and immature stages of *P. vorax* was studied in Cajamarca in the field and in stores. Adult emergence starts by the last week of October and continues until the end of February. Migration to potato fields occurs from December to February. Highest adult populations in the field were observed in February with population density reaching as high as four weevils/plant. Larval damage to tubers starts by the middle of March and increases until April. Twenty-five to 72% of tubers were infested at harvest in the evaluated fields. Prepupae occur from April to September; pupae from May to October; and overwintering adults from June to November (Figure 3).

Natural Enemies

Contrary to what might be expected of a native pest complex, natural enemies for APW are scarce. For many years tens of thousands of larvae have been collected and observed for the occurrence of parasitoids. None have been recorded.

Predators are also restricted in number, occurrence, and effectiveness. The only reference to effective predators in the literature is an ant of the genus *Iridomirmex* (Garmendia, 1961). That has not been confirmed in the areas where CIP has developed integrated pest management programs, including those where insecticides are not used or are used on a limited scale. Among vertebrates, toads and birds act as weevil predators. But toad populations in potato fields are so small that their effect is meaningless. Birds have been observed looking for weevil larvae in recently harvested potato fields. Again, bird populations are low and their effect on weevil populations is limited. A practical use of this experience has been the utilization of chickens as effective predators at harvest or shortly thereafter.

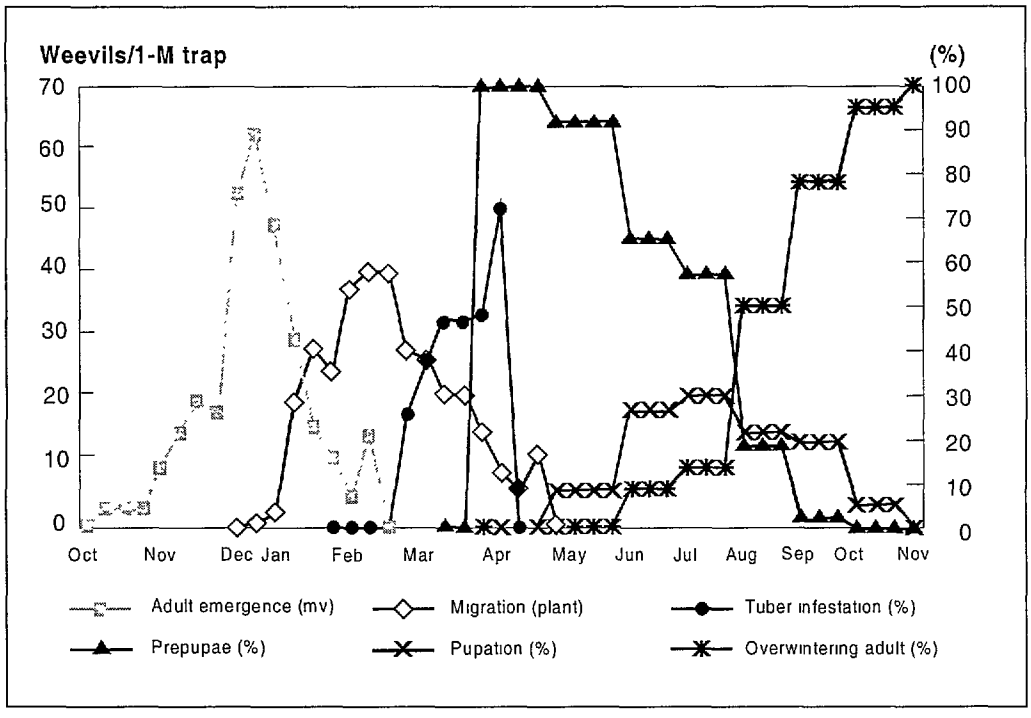

Figure 3. Seasonal history of the Andean potato weevil (*Premnotrypes vorax*) in Cajamarca, Peru. 1997.

Some soil-inhabiting ground beetles (Carabidae and Tenebrionidae) are general predators (*Harpalus turmalinus, Hylitus* sp., and *Metius* sp.). Ground beetle have a limited chance to capture neonate larvae because larvae are exposed for only a short time before they penetrate the soil. Although ground beetles readily eat weevil eggs when they are offered, in nature the eggs are inside straw or other plant debris and safe from predation.

The only pathogen able to develop disease in APW is the fungus *Beauveria brongniartii*. Conditions favorable for the epizootic are heavy rains and concentrated weevil populations. The multiplication and practical use of the pathogen is under study.

Host Plant Relations of Potato Weevils

There are two, commonly accepted misinterpretations related to the host range of the two groups of weevils present in potato fields.

1. It is believed that members of the APW complex can survive and multiply in other host plants present in potato fields or rotation fields.
2. It is also believed that other weevils that inhabit potato fields (as adults in the foliage or larvae in the soil) can damage potato tubers.

A series of tests have demonstrated that *Premnotrypes* spp. cannot survive as larvae on plants other than potato. That has been demonstrated with *P. suturicallus, P. vorax,* and *P. latithorax* on oca (*Oxalis tuberosa*), ulluco (*Ullucus tuberosum*), and mashua (*Tropaeolum tuberosum*) (Vera et al., 1994). Adults may eventually feed on leaves of several plants, but in no case can a life cycle be completed. As for other species of weevils present in potato fields, our tests indicate that they cannot damage potato tubers. These weevils survive by feeding on weeds in potato fields (Table 2). Adults feed on foliage; larvae live in the soil and feed on roots (Lazaro, 1999).

Table 2. Host plant relations of the Andean potato weevil and other species of weevils commonly found in potato fields. Huancayo, Peru, 1998.

Plant species[a]	Weevil species			
	Premnotrypes suturicallus	*Adioristus sp.*	*Scotoeborus sp.*	*Naupactus sp.*
Kikuyo (*Pennisetum clandestinus*)	(-)	(+)	(+)	(+)
Lengua de vaca (*Rumex crispus*)	(-)	(+)	(+)	(+)
Puka puncho (*Rumex acetocella*)	(-)	(+)	(+)	(+)
Garbanzo (*Astragalus sp.*)	(-)	(+)	(+)	(+)
Yuyo (*Brassica campestris*)	(-)	(+)	(-)	(-)
Aguja-aguja (*Erodium cicutarum*)	(-)	(+)	(-)	(-)
Sara-sara (*Gamochaeta sp.*)	(-)	(+)	(+)	(-)
Potato cv. Yungay	(+)	(-)	(-)	(-)

a. (+) = host plant, (-) = nonhost plant.

Conclusion

Controversial aspects in the literature related to the taxonomy and bionomics of the APW complex have been clarified with this work. Reviewed taxonomic keys will help to identify APW species. The updated geographical distribution of the species life cycles and host range will help to interpret the evolution of the weevil complex.

Acknowledgement

The authors are grateful to Professor Giovanni Onore, Departamento de Biología, Pontificia Universidad Católica del Ecuador for reviewing this paper.

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Population Dynamics of the Andean Potato Tuber Moth, *Symmetrischema tangolias* (Gyen), in Three Different Agro-ecosystems in Peru

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Andean potato tuber moth, *Symmetrischema tangolias*, is one of the most serious pests of potato, *Solanum tuberosum*, in Peru and Bolivia. It is considered a pest of economic importance in potato stores in both countries (Ewell et al., 1994; Palacios and Cisneros, 1997; Arenas et al., 1998). Damage is caused by larvae, which mine tubers making them unsuitable for human consumption or for seed. To prevent damage to tubers in storage, farmers use highly toxic insecticides, thereby jeopardizing their health and the environment. *S. tangolias* is also a potato pest in the field where larvae mine stems and tubers. In dry years, a high incidence of the pest in the field can reduce tuber production. Knowledge of Andean potato tuber moth survival and behavior in field and storage is minimal. The objective of this research was to study the population dynamics of *S. tangolias*, its seasonal trends, life cycle in storage, survival, and behavior.

Materials and Methods

The study was carried out in three Andean communities in Peru: Urquillos (Cusco, southern highlands), Carhuapaccha (Huancayo, in the central highlands), and Santa Clotilde (Cajamarca, in the northern highlands).

Urquillos is situated at 2,800 m. Potato is grown year-round. During the rainy season (October-May), potato is grown at altitudes of from 3,600-3,800 m. During the dry season, potato is grown under irrigation in rotation with other crops at lower altitudes (2,800 m). Potato production in this region is for both commercial use and local consumption.

Carhuapaccha is situated at 3,175 m. Cultivated areas extend up to 3,800 m. Irrigation is available at lower elevations allowing farmers to produce other commercial vegetables. Potato is produced once a year during the rainy season (October-May) in the upper lands of the community (3,500 - 3,800 m.). Potato production is commercially oriented and insecticides use is intensive.

Santa Clotilde is situated at 3,020 m. Potato is grown from June to December and from January to May in rotation with wheat, barley, and peas. Production is basically for home consumption.

Populations dynamics

Seasonal patterns of PTM abundance. Moth populations were monitored in potato fields and storage sites using experimental sex pheromone traps in Santa Clotilde and Urquillos, and light traps in Carhuapaccha. Five fields, two in Santa Clotilde and three in Urquillos, were selected for the field trials. Five storage sites were monitored, two in Carhuapaccha and three in Urquillos. One trap by each field and store was used. Modified water pan traps (Bacon et al., 1976, Raman and Booth, 1983) were placed at ground level. Rubber septa impregnated with a 2:1 mixture of (E,Z) 3,7 tetradecadienyl acetate and (E)-3-tetradecenyl acetate (Griepink et al., 1995)

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suspended in each trap. Adult moths trapped were collected weekly throughout the year. Match catch data was expressed as the average number of moths/trap/night.

Life cycle in stores

Pupae collected from the fields were used to start a moth colony to study its life cycle in rustic potato stores. Couples of emerging adults were placed in 0.5 L plastic containers (12 cm diam, 6 cm high) and covered with a 50-mesh cloth held in place by a rubber band). Eggs laid by females were collected daily. Newly hatched larvae were released on potato tubers to complete their developmental cycle reaching the pupa and adult stages. Adults were sexed based on abdomen size and then isolated in egg-laying containers. Observations were made for one year. Data were collected over the pre-oviposition and oviposition periods from adult emergence until laying of the last egg batch. Natural mortality was evaluated for each developmental stage.

Survival

Fields and stores were sampled to assess damage to potato plants and tubers, and to determine the fate of the surviving population. At harvest, 13 fields were sampled: 4 in Urquillos, 5 in Carhuapaccha, and 4 in Santa Clotilde. Each field was divided into 5 representative sections. A 1 m^2 area was evaluated in each section for number of plants and for moth damage in stems and tubers. Four weeks after harvest, five 1 m^2 areas in the same fields were sampled for number of larvae, and pupae in stems, tubers, and soil.

At the end of storage period, damage in tubers was evaluated in four stores in Urquillos and five stores in Carhuapaccha. A sample of 100 potato tubers was evaluated and scored as healthy or damaged in each store. A second evaluation, conducted 1 month after potato tubers were taken from storage, consisted of three 1 m^2 areas in the roof and walls in the store. Numbers of pupae and adults in cracks and crevices were recorded.

Behavior

Egg-laying preference. The oviposition preference of the moth was investigated on three levels. These included preference of soil vs plant, parts of the plant (lower, middle, and upper), and the microhabitat preferred (axillae, stems, leaves). We also evaluated the effect of potato development stages (vegetative growth, tuber initiation, tuber bulking) on oviposition. The experiment was carried out in the greenhouse in the CIP station in Huancayo. Twelve potato plants in pots (cv Yungay) were used per development stage. Potato plants were planted sequentially every 30 d so that plants of different ages could be infested at the same time. Each group of plants was put in cages where fifty mated couples of *S. tangolias* were released. After 10 d, plants were cut at the base of the stem and evaluated to determine number of eggs laid in the upper, middle, and lower third of the plant. Once all plant material was removed from pots, potato slices were put on the soil surface to determine the number of eggs laid in the soil. For this experiment, a factorial design with three factors (2x3x3) was used. Data on the number of larvae per plant was analyzed by ANOVA and means were compared using Fisher's least significant difference (LSD) procedure.

Plant infestation preference. The objective of the infestation preference experiment was to determine the location of initial plant damage (lower, middle, or upper level) caused by neonate larvae according to the stage of development of the potato plant (vegetative growth, tuber initiation, tuber bulking). This experiment was carried out in the greenhouse at the CIP station in Huancayo. Twenty potato plants (cv. Yungay) were planted in pots for each developmental stage; the plants were planted sequentially every 30 d so that plants of different stages could be infested at the same time. Each 20-plant group was subdivided into 4 subgroups of 5 plants; each plant was a replicate. In each group 50 neonate larvae of *S. tangolias* were released on soil, and on the lower, middle, and upper parts of the plant. The evaluation

was made 15 d later. For this experiment a completely randomized design was used with three factors: A = development stage, B = zone of release of neonate larvae, and C = zone where initial damage was found. The number of larvae damaging the plant was analyzed by ANOVA and means were compared using Fisher's least significant difference (LSD) procedure.

Tuber infestation in the soil. The depth that neonate larvae penetrate the soil to infest potato tubers was determined by placing tubers at 5 depths (0, 3, 5, 10, and 15 cm) in boxes containing soil. Each treatment was replicated 3 times with exposure to artificial infestation with 25 neonate larvae of *S. tangolias*. Tuber damage was assessed after 35 d. Data were subjected to ANOVA and means were separated by the LSD test.

Pupation in the soil. To determine the depth at which pupation occurs, three calibrated boxes (50 x 50 x 50 cm) containing field soil were used. Fifty fully-grown *S. tangolias* larvae were released in each box. Penetration was evaluated at 45 d by checking soil layers in increments 1.0 cm thick. Data were subjected to ANOVA and means were compared using Fisher's least significant difference (LSD) procedure.

Flight height. Flight height for monitoring and management was determined by using sticky traps (transparent plastic sheets 1 m wide x 2 m high smeared with Tangle Trap (Tanglefoot ®, Grand Rapids, MI) in potato fields of two communities in Cajamarca. The traps were marked at 20 cm-intervals. Evaluation was based on eight records/trap, taken weekly. Catch data were subjected to ANOVA, mean separation was done using Duncan's new multiple range test (DMRT).

Results and Discussion

Seasonal trends

Urquillos. Population data taken from October 1994 until October 1996 showed *S. tangolias* was present in potato fields, even in the absence of the crop (Figure 1A). During the 1st yr, the number of adult moths reached 505/trap/wk between October and February when the potato crop was present. The number decreased to 17/trap/wk between May and September in the absence of the crop. During the 2nd year, December 1995 - December 1996, the moth population fluctuated in like manner, but numbers were lower.

Moths were present in potato stores throughout the year (Figure 1B). Minimum capture was 23 moths/trap/wk; maximum, 186. Moths were present throughout the year because tubers were stored year-round as a result of the two-crop seasons/yr in Urquillos; the first at 3,500 m and the second at 2,800 m altitude.

Carhuapaccha. The pest was monitored in farmer's stores using light traps from December 1995 until December 1996. The moth was present throughout the year, but populations were low between January and May when no tubers were stored. Populations started to increase in June, peaking first in August (30 moths/trap/wk) and then again in November (145 moths/trap/wk). The second peak corresponds to the end of the storage period. Damage caused by *S. tangolias* in potato tubers increased from 0.8% after 1 mo of storage to 90% 3 mo later (end of the storage period) (Figure 2). Results suggest that the pest could have entered the stores on or within tubers as eggs or early larval instars. Development of a second generation in stores is believed to be responsible for the damage in tubers.

Santa Clotilde. Monitoring farmers' fields from February 1996 to May 1997 showed that the moth was present throughout the year (Figure 3). Population peaked twice during the year (deep drop during March in first peak was due to low temperatures and rain which affected adult moth activity). Both peaks corresponded to the flowering stage of the crop. Maximum capture in the first population peak was 807 moths/trap per week and 596 moths/trap per week in

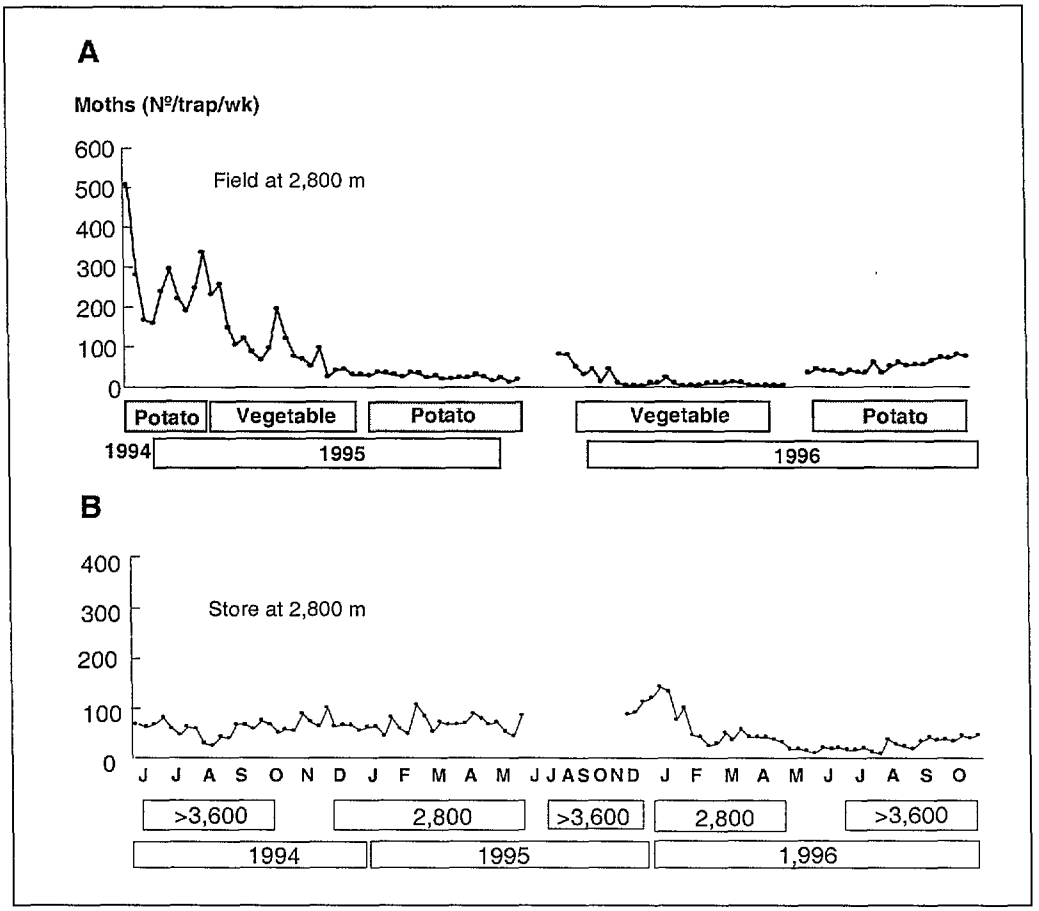

Figure 1. Andean potato tuber moth population in Urquillos, Cusco, Peru, 1994-1996.

the second peak. Adult population drastically decreased when there was no potato crop in the field due to lack of food and low temperatures at night (frost).

Life cycle

Studies show that, in rustic storage, *S. tangolias* completes its life cycle in 105 days at 13°C (Santa Clotilde and Carhuapaccha) and only 70 days at 17.4°C (Urquillos). Egg laying capacity was not significantly different (P=0.05) between locations, averaging 178-185 eggs/female. Accumulated natural mortality of immature stages was high averaging 75% in Santa Clotilde and Urquillos and 57% in Carhuapaccha (Table 1). *S. tangolias* was found to develop three to five generations in a year (Table 1).

Pest survival

In Urquillos, potato stems and tubers showed no damage at harvest. That might be the result of the adequate use of cultural practices such as irrigation, hilling up, and timely harvest. In addition, stores close to the fields may be a source of food and refuge for the pest throughout the year. That may have had an influence on the low level of damaged tubers in the field. Samples from the field that had been rotated (Urquillos) averaged 6.4 potato tubers/m^2, but they were not damaged by *S. tangolias* (Table 2). Observations from the remaining population in the field showed the presence of larvae and pupae in dried tubers and stems 3 months after harvest.

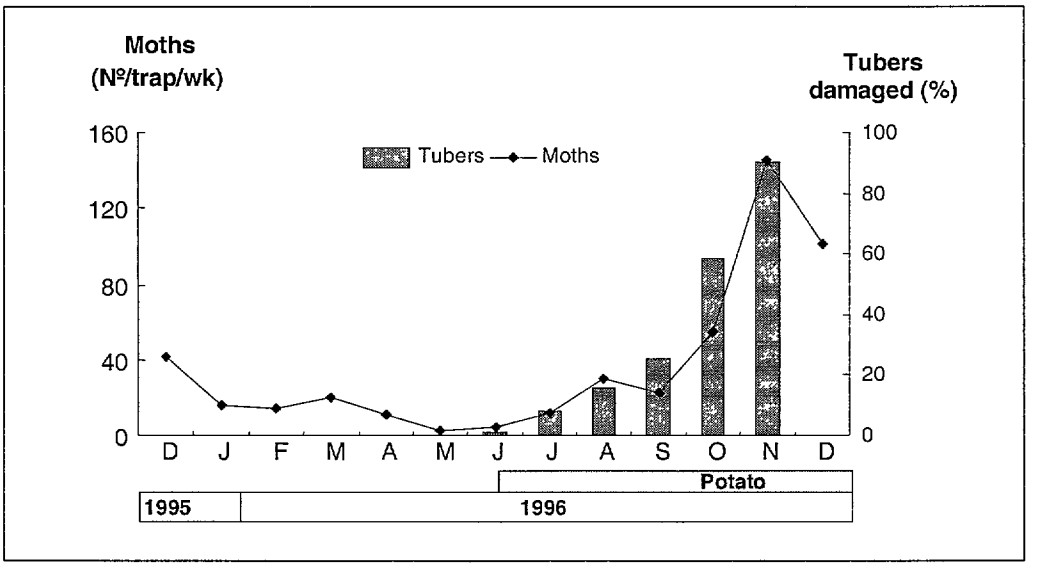

Figure 2. Andean potato tuber moth store population and tuber damage, Carhuapaccha, Junin, Peru, 1997.

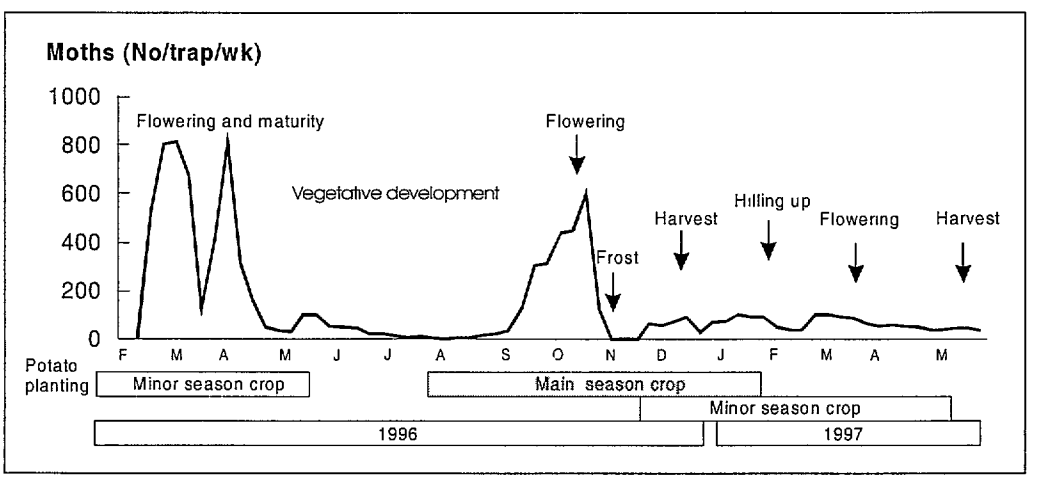

Figure 3. Andean potato tuber moth field population in Santa Clotilde, Cajamarca, Peru, 1996-97.

Moths remaining in storage facilities when there are no stored tubers ensure pest persistence in stores. At higher altitudes, the moth is introduced to potato fields every year with the seed.

Evaluations in the fields and stores in Carhuapaccha showed that the pest had spread from 3,020 to 3,800 m. Moths are transported to the stores in harvested tubers and returned to the fields in seed tubers. Prevalence of the pest in the absence of a crop suggests that the pest survives in crop residue between field plantings. Tubers kept by farmers for their own consumption usually serve as a food source for the moth to complete its cycle.

Behavior

Egg-laying preference. The moth lays eggs almost exclusively on the plant (92%), independent of crop age (Figure 4). Egg-

Table 1. Life cycle (in days) and natural mortality (%) of Andean potato tuber moth in stores, Peru.

Department/Community	Cusco/Urquillos	Junín/Carhuapaccha	Cajamarca/Santa Clotilde
Av. Temp. (°C)	17.4	12.6	13.0
Stage			
Egg	9	16	17
Larva	40	58	57
Pupa	22	32	31
Total	**71**	**106**	**105**
Longevity	24	23	33
Oviposition period	25	23	25
Egg/female	184	178	185
Mortality			
Egg	31	4	12
Larva	28	28	46
Pupa	15	26	18
Total	**74**	**58**	**76**
Generations/year	5	4	3

Table 2. Damage and remaining population of Andean potato tuber moth in the field and in stores, Peru.

Department/Community	Cusco/Urquillos	Junín/Carhuapaccha	Cajamarca /Santa Clotilde
Fields			
Fields with damaged plants (%)	0	100.0	90.0
Plants with damaged stems (%)	0	61.6	82.0
Damaged tubers (%)	0	2.1	21.8
Remaining tubers/m^2 (no.)	6.4	4.1	4.3
Remaining population/m^2 (no.)	0	16.9	9.4
In stems	0	11.8	4.5
In tubers	0	3.3	4.9
In soil	0	1.8	
Stores			
Damaged tubers (%)	88.0	90.0	80.0
Remaining population (no.)	13.0	14.8	—
In roofs	8.0	5.8	—
In walls	5.0	9.0	—

laying distribution analysis showed that the middle third of the plant is the preferred area for oviposition and that adults select a microhabitat for egg-laying. The preferred microhabitat is the axilla (Figure 4). Eggs laid in the axillae of the plant are protected from adverse environmental factors, hence ensuring penetration of the larvae into stems.

Plant infestation preference. Since *S. tangolias* moths prefer to lay eggs on the

middle part of the plant, the analysis was concentrated on larvae released in that area. The results show the effects of plant development stages on larval distribution. During vegetative growth, damage was concentrated on the middle level of the plant. Damage was limited to the lower part of the plant during tuber initiation and tuber bulking. (Figure 5).

Tuber infestation in the soil. Larvae penetrated the soil to a depth of 5 cm. Tuber damage decreased with depth, from 80% at ground level to 40% at a depth of 5 cm. Tubers at deeper levels are not damaged by moths (Figure 6A), probably because of the moth's limited penetration ability and its low egg-laying rate in the soil.

Pupation in the soil. Sixty-three percent of larvae pupated in the soil and 37% in the tuber (Figure 6B). Under these circumstances, damaged tubers remaining in the field are pest reservoirs and also the means of transferring infestation from field to store and back to field. Pupation in soil occurred from 0.1 to 3.5-cm depth, with 82% of pupation in the first 2.5 cm (Figure 6C).

Flight height. The number of adult moths captured in sticky traps showed that adults could fly to a height of 200 cm. But most flight activity (about 67%) was concentrated between 20 and 80 cm. That could be explained by the adult preference for ovipositing on the plant.

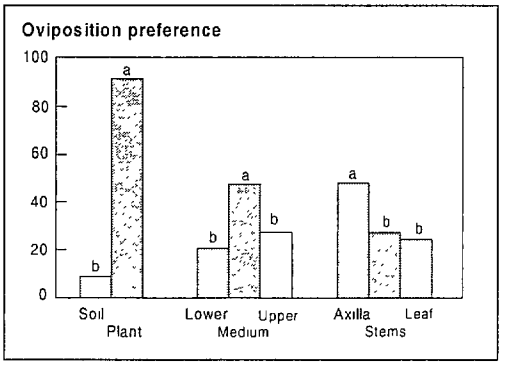

Figure 4. Oviposition preference of Andean potato tuber moth in potato, Peru, 1998. (In each group, bars with the same letter are not significantly different [P<0.05, LSD test].)

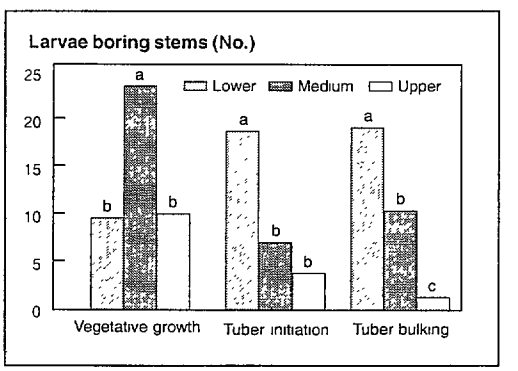

Figure 5. Plant age preference of Andean potato tuber moth neonate larvae for infestation, Huancayo, Peru, 1998. (In each group, bars with the same letter are not significantly different [P<0.05, LSD test].)

Conclusions

Adults of *S. tangolias* were found in the fields and in stores in the three communities under study. The pest damaged potato stems and tubers. Damage in harvested tubers was more important in Santa Clotilde, a community where potato is grown twice a year. Tuber damage in stores was significant in all study sites. The moth population can survive in crop residue in the absence of a host plant. Thus, timely sanitation to collect and destroy plant residues and volunteer plants is an important management option. In storage, the moth survives in crevices and in tubers stored for home consumption. Hence, cleaning and disinfecting storage areas is needed to break the moth cycle to prevent re-infestation of newly harvested and stored potatoes.

The adult preference for laying eggs in the plant and larval preference for lower and middle parts of the plant explain the low percentage of tuber damage and the high incidence of the pest in stems. This could be a practical monitoring tool to

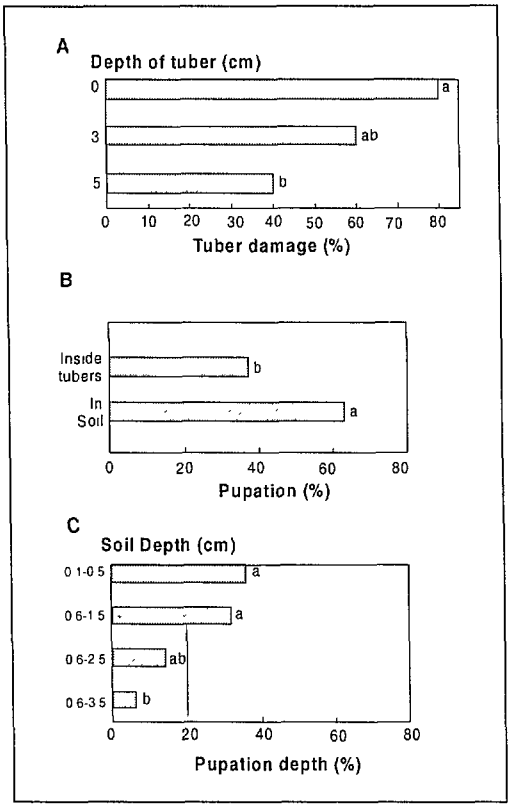

Figure 6. Ability of Andean potato tuber moth larvae to reach tubers at different depths, and their pupation inside and outside tubers, Cajamarca, Peru, 1997. (Fig. A and C: bars with the same letter are not significantly different [$P<0.05$, LSD test]; Fig. B: bars with the same letter are not significantly different [$P<0.05$, Student's t-test].)

detect the presence of the pest in plants and assess potential damage. The limited penetration capacity of larvae into the soil demonstrates the importance of planting depth and hilling-up in the management of this pest. Preventing access to tubers limits tuber infestation.

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Assessing Bt-Transformed Potatoes for Potato Tuber Moth, *Phthorimaea operculella* (Zeller), Management

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The potato tuber moth (PTM) *Phthorimaea operculella* (Zeller) is one of the most damaging pests of potatoes, *Solanum tuberosum* L., in warm temperate and subtropical climates (Fenemore, 1988). During the growing season, the potato tuber moth mines into foliage and stems, while at plant senescence adults lay eggs in soil cracks and on exposed tubers. At harvest, tubers do not always show signs of damage but may harbor eggs and early instar larvae. This may result in severe postharvest losses in the absence of adequate control measures. The PTM is the single most significant insect pest of potato (field and storage) in North Africa and the Middle East (Fuglie et al., 1992). In the absence of cold stores, farmers must rely on chemical insecticides to protect tubers from tuber moth damage during the storage period (Roux et al., 1992). Storage losses reported from India vary from 30 to 70% (Saxena and Rizvi, 1974). In Latin America, a complex of three tuber moth species is known to infest potatoes. Farmers routinely apply chemical insecticides to protect their crops (Raman, 1988). This reliance on chemical insecticides not only increases production costs but also has serious deleterious effects on human health and the environment.

Faced with this serious pesticide problem, scientists started to seek safer alternatives such as the use of *Bacillus thuringiensis* to replace toxic chemicals in their integrated pest management (IPM) strategies. Proteins of spore-forming soil bacterium are toxic to larvae of different orders of insects (Lepidoptera, Diptera, Coleoptera, Hymenoptera, Homoptera, Orthoptera, and Mallophaga) and to nematodes, mites and protozoa (Feitelson et al., 1992). Spores of *B. thuringiensis* are already widely used as biopesticide in commercial agriculture to control several key pests. However, field applications of this biological pesticide have not always provided a cost-effective control of insect pests. A more efficient way to deliver Bt can be achieved by genetically engineering crop plants to produce the active component of this biopesticide. The crystal protein CryIIIA was expressed in potato and provided resistance against the most serious defoliating pest, *Leptinotarsa decemlineata* (Say) (Adang et al., 1993; Perlak et al., 1993). Similarity, the expression in potato of the crystal protein CryIA(b) resulted in resistance to potato tuber moth (Peferoen et al., 1990; Jansens et al., 1995).

At CIP, we have developed potato tuber moth resistant clones suitable for most agroecologies of developing countries where PTM is a severe pest. The Bt technology (gene constructs) was acquired from the Belgian company, Plant Genetic Systems (PGS). The insertion and expression of the *cryIA(b)* gene is reported here as well as its effect on potato tuber moth in laboratory and field experiments. This leads us to suggest future steps that should be taken to effectively and safely deploy such cultivars in developing country.

Materials and Methods

Transformation, regeneration, and selection

Two *Agrobacterium tumefaciens* strains were used for potato transformation

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C58C1RifR(pGV2260)(pTFD16) and C58C1RifR(pGv2260)(pTRVA1) containing truncated *cryIA(b)* gene from *Bacillus thuringiensis* subsp. *berliner* 1715 (Hofte, et al. 1986). These Bt genes are under the control of a single (referred to as Bt-1) and double (referred to as Bt-2) 35s promoter, respectively.

Potato plantlets were propagated in Magenta boxes (Sigma) by subculture of single leafy node cuttings on solid Murashige and Skoog (MS) basal medium (GIBCO) supplemented with vitamins, 3.0% sucrose and solidified with 0.3% phytagel (referred to as MSA medium). The medium was sterilized at 120°C for 20 min. Cultures were grown in an incubation room under 16 hours photo-period at 2000 lux, 22-24°C and 70% relative humidity. Potato transformation was done following the method of De Block (1988) with several modifications.

DNA extraction and hybridization

Genomic DNA was isolated from leaf tissues following the method of Dellaporta et al. (1983). Presence of the Bt gene was determined by Southern blot analysis using the EcoRV fragment of 650 bp from pTFD16 plasmid as a probe (Sambrook et al., 1989).

CryIA(b) protein determination

Monoclonal antibodies specific against the *B. thuringiensis* subsp. *berliner* 1715 crystal protein, provided by PGS, were used to quantify by ELISA CryIA(b) protein in soluble protein extracts of tubers. Total protein was determined using a Bio-Rad protein assay.

Leaf and tuber bioassays

Greenhouse experiments were conducted on 3 different cultivars (Sangema, Cruza 148, and LT-8) over three years. Treatments corresponded to the transformed lines of each cultivar. A total of 85 different lines have been tested against PTM, 31 transgenic lines of Cruza 148; 37 transgenic lines of LT-8, and 17 lines of Sangema. Treatments were exposed to 25 neonate PTM larvae. Each treatment was replicated 10 times. Evaluations were made 7 and 10 days after infestation where larval mortality was recorded.

In 1994, harvested tubers from different Cruza 148 lines (25 out 31 lines), were divided into three groups of 50 g each representing three replications for tuber assays. Each treatment (50 g of tuberlets) was exposed to 10 neonate larvae.

In 1997, harvested tubers from the different Sangema lines (14 out 17 lines) were used in tuber assays. Treatments consisted of a single tuber (Ca. 30 g) replicated six times. Each treatment was exposed to five neonate larvae.

Tests were carried out in an insect mass-rearing room under controlled temperature and humidity conditions (25 ± 2°C and 70 ± 5% relative humidity). Larval mortality was recorded after 25 days and expressed in percentage.

Larval development

The bioassay consisted of testing the effects of transformed potatoes on larval development. Tubers of three transgenic lines of the clone LT-8/Bt2 (44.9, 34.1, and 34.2) plus an untransformed control were exposed in a sliced form to 30 neonate larvae each. Each treatment was replicated 5 times. Larvae were counted, measured and weighed daily until they died or pupated.

Storage

Harvested tubers were evaluated for stability of Bt gene expression over the length of the storage period (4 months) in CIP's San Ramon Station (mid-elevation jungle). A free-choice test was conducted under diffuse-light store conditions, using 10 lines in 1995 and 27 lines in 1996 of the cultivar LT-8. Treatments consisted of 5 tubers replicated four times in a completely randomized block design.

All treatments included exposure to an artificial PTM infestation. Newly emerged

adult tuber moths were released in the storage area to simulate natural infestation. Evaluations of tuber infestation were made 120 days after infestation using a 1-5 scoring scale (1 = non-damaged tuber, 5 = 100% damage) Tubers were cut to assess damage.

Field trials

Selected transgenic lines were field tested to evaluate resistance to potato tuber moth and assess their morphological characteristics. Field tests were conducted under strict biosafety regulations (CIP, 1993). Trials were carried out in two locations, San Ramon and Tacna (winter, main potato season) in order to evaluate resistance to potato tuber moth and non-target pests.

In San Ramon, field trials consisted of several treatments with three replications in a completely randomized block design. Each experimental unit was five rows (of 15 plants), 4.5 m long, 0.9 m row-spacing, and 0.30 m plant-spacing. With the transformation process, plants from the same clone/cultivar may present different morphological characteristics. To assess this potential change, plant growth was evaluated by plant height and leaf ratio (leaf length/leaf width) according to Vaughan and Gatehouse (1991).

In Tacna (1997-98), trials consisted of nine treatments (representing 9 lines of LT-8). Experimental plots were of the same size and design as the field plots of the summer crop in San Ramon. Evaluations for potato tuber moth were made in the same manner. Data were collected also on the incidence of non-target species (*Tuta absoluta, Liriomyza huidobrensis, Russelliana solanicola,* and *Myzus persicae*) on transgenic lines. At harvest, tubers were evaluated for PTM damage using samples of 25 tubers per plot. Yield data was also recorded.

Results and Discussion

Development of transgenic potato using developing country cultivars

Transformation experiments were initiated with three important potato cultivars adapted to a relatively warm climate: LT-8, which is immune to PVX and PVY; Sangema, important in Rwanda; and Cruza-148, which has moderate resistance to bacterial diseases and is also important in Rwanda and Burundi. A large series of transgenic plants have been obtained through *Agrobacterium*-mediated transformation. In total, 42 transgenic clones with Bt-1 and 7 with Bt-2 were generated for LT-8, 46 and 42 transgenic clones of Bt-1 and Bt-2, respectively, for Sangema cultivar, and 114 transgenic clones of Bt-2 for Cruza-148.

Gene insertion and assessment of copy number

A sample of transgenic clones was tested for the presence of the Bt gene by Southern blot analysis. The band pattern indicates independent insertion events (Figure 1). In other experiments the number of the Bt genes was estimated to range from 1 to 3 copies per haploid genome (Table 1).

CryIA(b) protein quantification

The amount of CryIA(b) protein in tubers was determined by ELISA tests of 10 transgenic lines of LT-8 and 4 of Sangema cultures. A range of 1 to 11 ng of CryIA(b) per mg of total soluble protein was found (Table 1). In agreement with other studies, no correlation was found between Bt gene copy number and amount of CryIA(b) protein expressed in tubers. However, the amounts of CryIA(b) protein in three out of four transgenic clones transformed with the Bt-2 construct carrying the Bt gene with double promoter 35S were much higher than those carrying the Bt-1 construct (single promoter) (Table 1). This result suggests that the double 35s promoter leads to higher protein accumulation in potato.

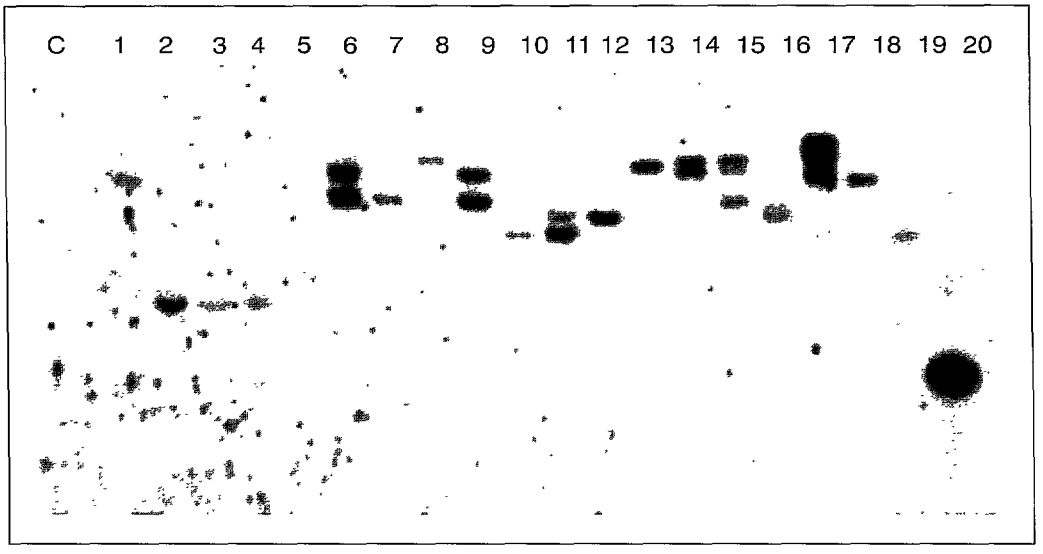

Figure 1. Hybridization of genomic DNA of transgenic LT-8 lines with the Bt gene:Lane C: DNA of non-transformed LT-8. Lanes 1 to 19: DNA of transgenic LT-8 lines. Lane 20: positive control (isolated *bt* probe).

Table 1. Molecular characterization of transgenic lines by quantification of CryIA(b) protein (means of 2 assays in ng/mg soluble proteins) and by copy number of *cryIA(b)* gene.

Clone	CryIA(b) protein[a]	*cryIA(b)* gene copy number
LT-8 /Bt-1 /DST 24-2	5.64	1
LT-8 /Bt-1 /DST 24-3	2.50	3
LT-8 /Bt-1 /DST 34-1	1.99	1
LT-8 /Bt-1 /DST 34-2	4.86	1
LT-8 /Bt-1 /DST 34-3	6.26	1
LT-8 /Bt-1 /DST 34-5	3.55	2
LT-8 /Bt-2 /DST 36-1	10.87	1
LT-8 /Bt-2 /DST 36-4	1.18	1
LT-8 /Bt-2 /DST 36-5	6.00	nd
LT-8 /Bt-2 /DST 36-8	9.37	2
Sangema /Bt-1 / DST 39-1	2.28	1
Sangema /Bt-1 / DST 39-2	1.94	1
Sangema /Bt-1 / DST 39-3	4.71	2
Sangema /Bt-1 / DST 39-4	nd[b]	2

[a] ng bt toxin/mg protein.
[b] Not determined.

Leaf and tuber bioassays

Evaluations of larval mortality on transformed Cruza 148, at seven days, showed 100% mortality. Twenty-three out of 31 lines tested were significantly different from the non-transformed check (P = 0.01) (Table 2). The eight remaining lines were not significantly different from the control (P = 0.01). Mortality ranged from 36.30 to 49.48%. After one month, the susceptible lines still harbored live larvae, suggesting that the Bt gene was not expressed properly in the foliage.

Evaluations of tubers, one month after harvest, were conducted on 25 out of 31 lines of Cruza 148. Larval mortality was high (100%) in 16 lines of the 25 tested. Eight out of the nine lines showed a mortality around 50% as compared to the check with 22.22% of mortality (Table 2). A high mortality of PTM in transgenic lines indicated the presence of Bt toxins in leaves and tubers.

Evaluations of larval mortality on foliage (10 days after infestation) on transformed LT-8 indicated excellent results with 100% mortality on all transformed lines. The non-transformed check showed 37.2% mortality (Table 2). Evaluations of 17 transformed Sangema at 10 days showed high mortality (100%). All lines showed better larval control than the non-transformed check. Larval mortality in the check was 20% (Table 2). The damage caused by larvae in the transgenic lines was very low. The neonate larvae have to feed on the leaves for the Bt toxins to work. The effect of the toxin on the larvae often causes stunted growth and feeding inhibition, leading to death (Figure 2).

Larval development

Infestation with neonate larvae on transgenic lines showed no effect for the first 3 days. The fourth day, mortality increased drastically until all larvae had died at the seventh day. Larvae fed on non-transformed plants were still alive after 10 days (Figure 3).

Durability of tuber resistance storage

Transgenic potatoes resistant to PTM larvae according to leaf and tuber bioassays were also tested for durability of the tuber

Table 2. Mortality in potato tuber moth foliage and tuber assays of potato transgenic lines expressed as percent of infested larvae.

Clone	Leaf[a]	Tuber[a]
	7 days	1 month
Cruza 148/Bt2/(8 lines)	±50% bc	±50% cde
CRUZA-148/Bt2/ (1 Line)	100.00 a	86.67 b
CRUZA-148/Bt2/ (+ 22 lines)	100.00 a	100.00 a
CRUZA-148 (control)	47.55 bc	22.22 e
	10 days	
LT-8/Bt1/ (37 Lines)	All 100%	NT
LT-8 (control)	37.2	NT
(Only foliage was tested)		
	10 days	
Sangema/Bt2/ (+ 17 lines)	100.00	100.00
Sangema (control)	20.00	20.84

[a] Means followed by the same letter are not significantly different (Waller-Duncan test, p = 0.01).
NT = not tested.

Figure 2. Damage produced by *Phthorimaea operculella* on leaves of untransformed (left) and transformed plants (right) of Sangema clone. At the left corner shows the initial PTM damage in transgenic lines.

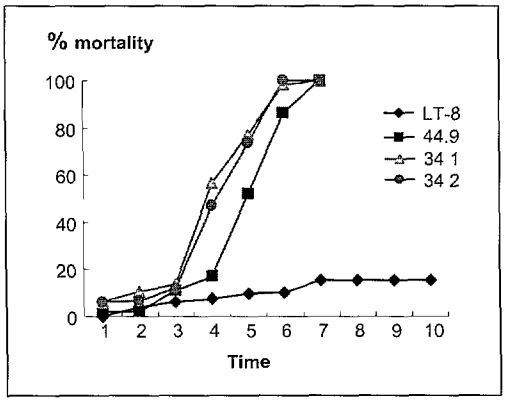

Figure 3. Mortality of neonate larvae reared on potato transgenic lines. La Molina, Peru, 1998.

resistance in storage. All transgenic lines tested (37 of LT-8 and 4 of Sangema) remained uninfested over at least 6 months of storage while the non-transformed plants were seriously damaged. (Figure 4). Hence, resistance can be considered durable in storage.

Assessment of field resistance and impact on non-target pests

Field trial at San Ramón, 1995. Ten transgenic LT-8 and 19 Cruza-148 lines that scored well for PTM resistance under greenhouse conditions were evaluated for PTM resistance in the field under high PTM pressure. The trials were carried out at CIP's experimental station during the summer season when no potato is grown in that area. All transgenic plants of LT-8 and Cruza-148 showed a high resistance level against PTM attack (zero larvae per plant) under these conditions, whereas the nontransformed ones showed higher numbers of PTM larvae.

Morphological characteristics (plant height and leaf L:W ratio) of LT-8 were scored and found, for the majority, to be within the normal range of variability compared to control plants. However, means of plant height of six transgenic lines of Cruza 148 out of a total of 26 were significantly lower than control plants, whereas one was significantly higher than the control Cruza 148.

Results from field data showed the same trends as those from laboratory and greenhouse experiments. There were some phenotypic variations with respect to plant height and leaf length/weight (L:W) ratio. These field trials allowed lines to be selected that were phenotypically similar to the non-transformed control.

Field trial at Tacna, 1997-98. Nine lines of LT-8, showed adequate levels of resistance (no infestation) to PTM in field trials in Tacna. The transgenic lines were found to be resistant to the tomato pinworm, *Tuta absoluta*. Effects on non-target species *Liriomyza huidobrensis*, *Russelliana solanicola*, and *Myzus persicae* were all non-significant (P= 0.05). Hence, this Bt gene affected both PTM *Phthorimaea*

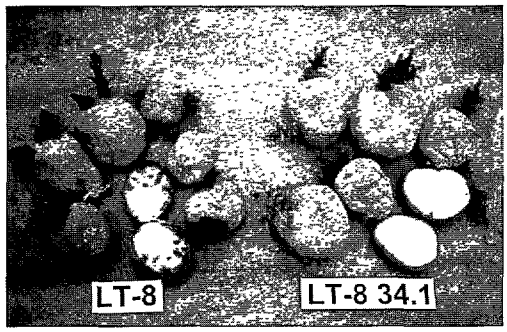

Figure 4. PTM damage on tubers from transformed plants (right) and non-transformed plants (left), after 4 months of storage.

operculella and the tomato pinworm *Tuta absoluta*. Both pests are commonly found in potato fields.

At harvest, PTM infestation on tubers was limited to control plots; no transformed lines showed damage. Yields were not significantly different between transformed and non-transformed lines. Jansens et al. (1995) using the same *cryIA(b)* gene obtained similar results. Ebora et al. (1994) used a different *cryIAc* gene and obtained much lower PTM mortality (1.03%).

Deploying Transgenic Potatoes: Special Consideration

Potential for insect resistance

Insects have shown their ability to overcome the various insecticides-based control measures by developing resistance to all major classes. Resistance to Bt has already been reported for Indian meal moth, *Plodia interpunctella* (Hubner) (McGaughey, 1985) and for the Diamond-back moth, *Plutella xylostella* (L.) (Tabashnik et al., 1990; Shelton et al., 1993). It is commonly accepted that deployment of Bt-transformed crops should be handled with utmost care to reduce or delay the potential of insect resistance to Bt (Tabashnik et al., 1991; McGaughey and Whalon, 1992, Wearing and Hokkanen, 1994). Bt toxins deployed at a high rate and for an extended duration in the field present a situation highly conducive to the development of resistance. This could be alleviated by the use of tissue and time-specific promoters of Bt gene expression (van Rie, 1991) and the inclusion of multiple Bt and other resistance genes (Brattsten, 1991).

Resistance management

Based on past experience with insecticides, there are several options available for managing potential resistance to Bt.

Refugia. This consists of providing a "refuge" for susceptible insects for dilution of selection pressure by planting non-transformed cultivars or other host plants within and/or around the crop. Also, the use of time and tissue-specific promoters allows the gene expression in targeted areas only.

Seed mixtures or mosaics. Mixing susceptible and resistant seed at planting provides unprotected plants harboring susceptible insects within the field.

Rotation. The impact of crop rotation on selection intensity contributes to the persistence of the Bt gene in the ecosystem, thus influencing the potential development of resistance. This will have to be evaluated in relation to the target pest population dynamics and dispersal to other host plants.

Evaluations of other systems indicate that under sound IPM programs, the incorporation of Bt genes in potato is feasible from the Bt resistance potential. However, special care will have to be taken to avoid cross-resistance as the same genes are used for Lepidoptera on several crops as bio-pesticide sprays. Also, broad-spectrum insecticides should never be used against adults to preserve susceptible immigrants and natural enemies in the system. Time and tissue-specific promoters (i.e., expressing Bt genes in tubers) may be able to minimize the major drawbacks associated

with the deployment of Bt in the potato crop (persistence, gene flow).

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Participatory Needs and Opportunity Assessment for Potato IPM Development Planning: The Case of Indonesia

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Potato (*Solanum tuberosum*) production in Asia has increased tremendously over the past decades as a result of increased area planted to potato and increased yields (CIP/FAO, 1995). Indonesia is among the countries showing the highest growth rates for potato production. Harvested area of potato almost tripled from an average of 19,442 ha over the period 1970-79 to an average of 53,436 ha in the period 1990-97. Yields almost doubled from 7.9 to 15.1 t/ha (CBS, 1998).

Potatoes in Indonesia

Potato in Indonesia is typically grown in the uplands under humid tropical conditions. Production has increased, but at the cost of environmental degradation due to unbalanced and heavy use of external inputs (fertilizers and pesticides) and indiscriminate forest clearing as potato farmers sought disease-free and nutrient-rich, virgin soils. Pest and disease problems have become so serious that farmers commonly apply mixtures of pesticides to the potato crop at intervals of only 2-4 d. The leafminer fly (LMF) (*Liriomyza huidobrensis* Blanchard), an exotic pest introduced into Indonesia in 1994, is spreading rapidly and has become a major threat to potato cultivation. Its presence triggers frequent, mostly broad-spectrum insecticide applications, but with little success (Rauf and Shepard, 1999).

This trend of increasing pesticide application, aggravated by the monetary crisis that hit Indonesia in 1998, caused farmers to spend a larger proportion of their potato cultivation budget on pest control. On the other hand, products with high pesticide residues are being rejected at the export markets in Singapore and Malaysia. Farmers are beginning to realize that they need to look for alternatives to chemical control. However, national research and extension efforts have been limited and research results generally do not reach the majority of farmers. Several nongovernmental organizations (NGOs) conducted potato integrated pest management (IPM) farmer field schools, but they lacked effective technical alternatives to tackle the complex on-farm problems. Through the implementation of a participatory needs and opportunities assessment, CIP aims to establish effective IPM approaches for potato growers in Indonesia. Those involved in the needs assessment were farmers, NGOs, Indonesian agricultural research institutes, and the national IPM program. We are presenting here the preliminary results of the first phase of this on-going study.

Participatory Needs Assessment Methodology

The needs assessment consisted of a participatory study with the following objectives:

- To understand the importance and constraints of potato cultivation for farm households in major potato growing areas in Indonesia.
- To inventory potato cultivation practices, problems, and output relating to crop management in general and pest management in particular.

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- To identify opportunities and partners for sustainable improvement of the potato enterprise, prioritize needs, and set the agenda for a collaborative potato IPM research and development program in Indonesia.

Major potato growing areas in Indonesia are the provinces of West and Central Java and North Sumatra, accounting for 77% of national potato production (CBS, 1998). Four sites in these three provinces were selected for the needs assessment exercise. Selection criteria were the coverage of varied cultivation and marketing systems and the availability of local partners, i.e., NGOs, and organized farmer networks (Table 1). The following seven methods and activities were applied to achieve the objectives.

Village profiling and problem ranking using participatory rural appraisal (PRA) methods including transects, group discussions, ranking exercises, seasonal calendar, and informal individual interviews with men and women farmers, village officials, and traders.

Season-long record keeping of the potato enterprise, including quantitative technological and economic cultivation data, by 45 farmers.

Individual interviews with potato farmers on production and marketing.

Regular field monitoring throughout the season using direct observation of pest, disease, and natural enemy occurrence and damage, and the use of sticky traps in fields subject to the record-keeping activity.

Assessment of the rate of parasitism of the LMF through rearing of larvae collected from the field in funneled containers.

Data analysis meeting with participating farmers and partner organizations at each site at the end of the season.

National Potato IPM Program Planning Workshop with representatives of all national stakeholder groups to present the results of the needs assessment and other previous work, and to plan a collaborative potato IPM development program.

Not all data were available at the time of this writing. Therefore results are presented in a descriptive manner; advanced statistical analysis will be done later.

Table 1. Profile of the four needs assessment sites, Indonesia, 1998.

Province	West Java	Central Java	North Sumatra	
District	Bandung (BD)	Banjarnegara (BN)	Simalungun (SI)	Tanah Karo (TK)
Vicinity to city	Near	Far	Far	Near
Cultivation system	Intensive vegetable crops	Intensive vegetable crops, extensive subsistence crops	Intensive vegetable crops, extensive subsistence crops	Intensive vegetable crops, extensive subsistence crops
Potato marketing	Local market	Local market	Export	Export
Major potato cultivation constraints (farmers' perception)	Leafminer fly, late blight, bacterial wilt	Leafminer fly, late blight, viruses	Bacterial wilt, late blight, leafminer fly	Bacterial wilt, late blight, leafminer fly
Local partner[a]	TP4 (farmer trainer network)	YPPSE (local NGO)	YCD/WE (local/int'l NGO)	JTTK/WE (farmer network/int'l NGO)

a. TP4 = Pangalengan IPM Farmer Trainers Team, YPPSE = Foundation for Development and Socioeconomic Progress, YCD = Foundation "Love the Village", JTTK = Tanah Karo Farmers' Network, WE = World Education.

The study covered the 1998 dry season in Central Java and the 1998/99 wet season in all four sites. Farmers appreciated their involvement in the needs assessment data collection, analysis, and planning process. They were reported to have benefited from the activities by having analyzed and increased their understanding of their own potato enterprise. Their participation in the needs assessment is expected to facilitate farmer collaboration in the upcoming technology and training development phase.

Results

Potato cultivation opportunities and constraints

Farmers at the study site in West Java ranked potato first in importance, whereas at the other three sites potato was ranked third, following subsistence crops such as maize and sweetpotato, and other cash crops such as chili peppers (*Capsicum* sp.). Farmers pointed out that the advantage of potato over other commonly cultivated crops is its potential for high productivity, easy and profitable marketing, and relatively stable market prices. Disadvantages include its susceptibility to a range of pests and diseases resulting in high production cost, intensive crop care, and high risk. Potato cultivation therefore is limited to a select group of farmers who can afford the investment and risk. An economic analysis of the data collected in this study suggests the diverse perspectives of farmers. Some obtain a relatively high net return from potato, while others lose money when local conditions are unfavorable during a particular season. One way of reducing the risk of crop loss is by cultivating potatoes only on a small plot. The field size planted by farmers in the study ranged from 0.03 to 0.65 ha, with an average of 0.22 ha. Considering total cultivated land area averages about 0.5 ha per farm family in Java and 1-2 ha in North Sumatra, farmers obviously reduced the size of their potato plots in response to rising costs of external inputs due to the 1998 economic crisis.

The most severe production constraint perceived by farmers was LMF in West and Central Java, and bacterial wilt (BW) caused by *Ralstonia solanacearum* in North Sumatra (Table 1). High LMF incidence and damage was confirmed in all areas through field observations. Data are being analyzed to assess crop loss. In addition to high incidence, which caused considerable yield reduction, the LMF problem was considered most serious because farmers did not have adequate control measures. The chemical measures taken were expensive but ineffective. BW was more common in North Sumatra than in the other areas, but incidence was relatively low compared to LMF and late blight (LB) caused by *Phytophthora infestans*. Farmers, however, ranked BW as their most serious problem because there is no way to control it when it occurs.

The second most important problem mentioned in all areas was LB. LB incidence was generally high, especially during the wet season, but farmers considered it relatively manageable by means of intensive fungicide use. Other production constraints considered important by farmers included thrips (*Thrips* spp.), especially under dry conditions, potato tuber moth (PTM) (*Phthorimaea operculella* Zeller), and the lack of good seed. The predominant potato cultivar planted in all areas is Granola, which, though more susceptible to LB and LMF than other cultivars, is preferred by consumers. Furthermore, most farmers did not practice good seed selection, nor was high quality seed always available on the market. Although farmers initially neglected to mention it, we analyzed the seriousness of soil fertility degradation as a result of high-level, unbalanced, inorganic fertilizer applications and poor soil conservation practices. We believe that could be a major threat to sustainable potato cultivation, especially in West Java and North Sumatra.

Potato yields

Potato yields obtained by the respondents during the 1998 dry season and the 1998/99 wet season varied greatly across and within study sites (Figure 1), ranging from 1.0 to 28.0 t/ha with an average of 10.5 t/ha, 0.4 t/ha of which was unmarketable due to tuber rot, mainly caused by *R. solanacearum*. Normally, the wet season is considered the best season for growing potatoes in the study areas in West Java and North Sumatra. Farmers cultivate under rainfed water supply, with a yield potential 25-30 t/ha. In the study site in Central Java, where rainfed water supply is abundant throughout the year, the dry season is considered the best season for potato cultivation, with a yield potential of around 20 t/ha. The relatively high incidence of LB during the wet season is tackled with higher frequencies of fungicide application, although not always very effectively. Figure 2 shows this ineffectiveness by the frequency of cases where LB was identified as a major cause of low yields during the wet season despite intensive pesticide use. The 1998/99 wet season was an extraordinary season for LB, particularly in North Sumatra, due to increased rain as a result of the La Niña phenomenon. Furthermore, LMF, commonly regarded as a dry season pest and despite recent quiescence, reoccurred during the North Sumatran wet season. In West and Central Java, the 1998/99 wet season was considered relatively favorable for potato production. LMF occurrence, however, continued to increase causing major damage to potato crops for the majority of participating farmers. Several farmers who had planted before the onset of rains reported thrips damage. Early crop growth was poor due to drought, aggravated by the high incidence of thrips during the first part of the growing season.

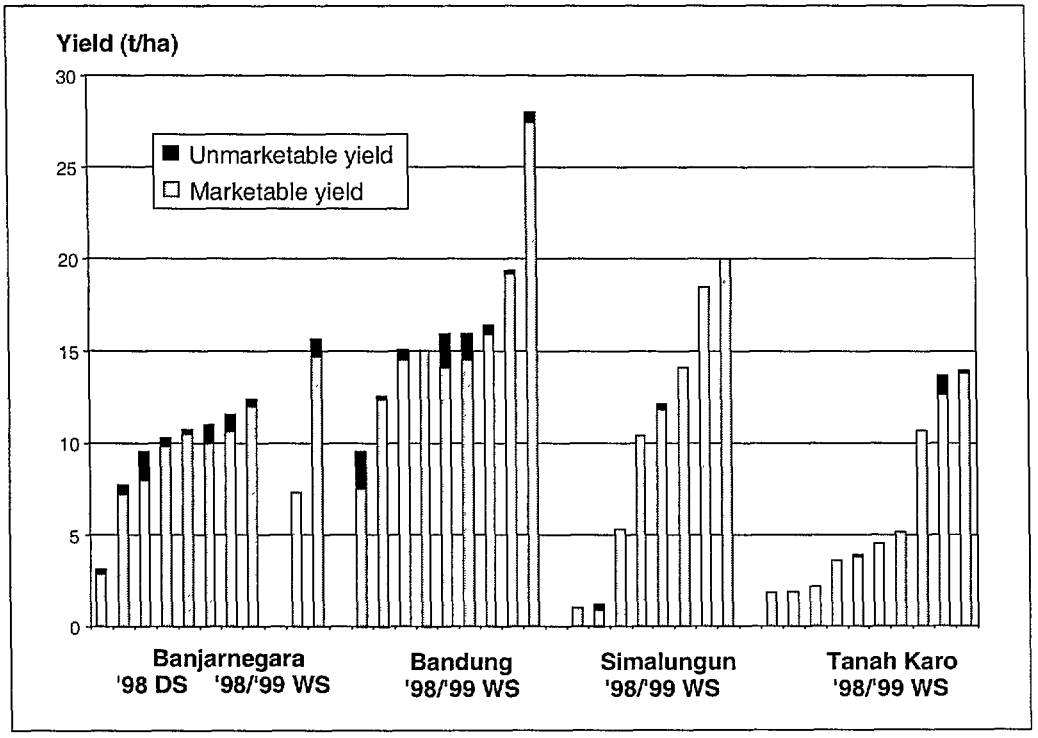

Figure 1. Potato yields in Indonesian study sites during the 1998 dry season (DS) and 1998/99 wet season (WS). Each bar represents the crop of one farmer.

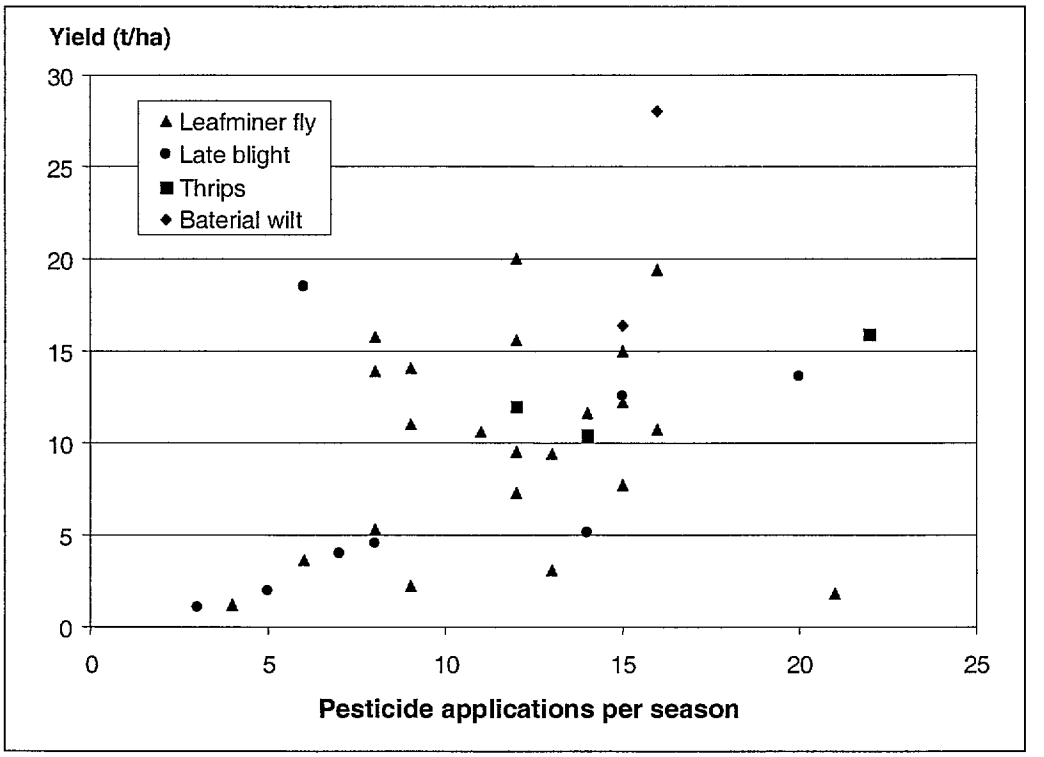

Figure 2. Relation between number of pesticide applications per season and yield. One data point represents one farmer. The marker style for each data point indicates the major production constraint identified by the farmers.

Farmers' cultivation practices were poorly related to yields, indicating that farmers had no sound technologies and practices to increase yields and manage their production constraints. Labor allocation to the potato crop, including hired labor and an opportunity cost for household labor, ranged from US$46 to 604/ha. That implies low labor efficiency for a large portion of farmers, particularly those with small fields.

Fertilizer management practices varied widely, with total inorganic NPK doses ranging from 25 to over 2,000 kg nutrients/ha with an average of 609 kg/ha. Average fertilizer application rates were 245 kg N/ha, 215 kg P/ha, and 178 kg K/ha. Farmers obtaining the highest yields applied fertilizer at moderate rates. In the absence of adapted, recommended rates, farmers depend on their own experience and perceptions. Yet their knowledge about plant nutrition and crop health is generally poor. For example, one farmer reported adding extra fertilizer to compensate for water shortage during the early growth stage of the crop.

Pesticide use averaged 12 applications/season, ranging from a low of 3 to a high of 22. Farmers giving only a few applications faced total crop failure (Figure 2). The data from the study sites, however, showed neither higher yields nor better control of pests at higher pesticide application frequencies. This strongly indicates injudicious and erroneous pesticide application practices.

Practices perceived by farmers to favor high crop yield include 1) the use of healthy seed, 2) balanced fertilizer management, 3) effective pest and disease manage-

ment, and 4) good cultural practices. But farmers lacked information and resources to use these practices. They would like to see them as topics for collaborative adapted technology development.

Pest management practices

Farmers' primary alternative for controlling pests and diseases of potato was pesticides. Only a few farmers reported trying other methods, such as yellow sticky traps, to control LMF albeit with undetermined success. Farmers spent an average of US$378/ha on pesticides or 23.8% of total production cost for potato cultivation. Their major sources of information regarding pest management were pesticide retailers and agrochemical salesmen who regularly visit even the remotest villages where vegetables are grown. Information is normally limited to promotion of the type of chemical to be applied, and does not include advice about proper application methods. As a result, farmers tend to mix several types of pesticides for one application. One woman in North Sumatra was observed spraying a cocktail of two insecticide and five fungicide brands, some with the same active ingredient. Farmers normally do not consider recommended doses or intervals between applications.

Across areas, farmers began applying pesticides to the crop 11-38 d after planting, and continued at an interval of once every 2-4 d until the crop was 40-83 d old, depending on how soon it died off. Taking into account the multiple doses given through cocktails of several pesticides in one application, an average of 27 doses/field per season were applied to the potato crop, with a maximum as high as 58 doses. Only one farmer reported monitoring pest and disease status before deciding on a chemical control measure. He never mixed different types of chemicals in one application, and applied 20 doses throughout the season. He obtained among the highest yields in his area.

Not surprisingly, natural enemy populations in these ecologically disturbed systems are extremely low, particularly for newly introduced pests such as LMF. Three parasitoids of LMF were identified in the study areas: *Hemiptarsenus varicornus* (Girault), *Neochrysocharis formosa* (Westwood), and *Opius* sp. The rate of parasitism, however, was low (1.6% during the wet season in North Sumatra). Farmers were eager to develop more effective and sustainable pest control methods, particularly for those pests and diseases for which they have no adequate control measures, i.e., LMF, thrips, and BW.

Economic return from potato cultivation

Potato cultivation in the study areas during the 1998 dry season and the 1998/99 wet season resulted in an average gross income of US$2,621/ha. However, there was large variation between individual farmers (see Figure 3) due to wide variability in yields and market prices. Average price received for potato was US$0.24/kg, but fluctuated from US$0.06 to 0.37/kg, depending on the season, type of market, tuber quality (including size and shape), and the distance from the field to the main road.

Production cost varied widely with regard to total amount and to allocation of budget items. The net return, measured as the gross income minus production cost (including inputs, hired and household labor, and rent for land), averaged US$1,032/ha. Net return ranged from a loss of US$2,151/ha to a profit of US$5,842/ha (see Figure 3). Although the average profit was three to four times that of what farmers could earn from a good rice crop, the large variation emphasized the high risk of potato growing. Thirty percent of participating farmers lost money on potato cultivation during the study seasons, which they attributed to unfavorable weather contributing to low yields and high production costs.

Discussion and Conclusions

The participatory needs and opportunities assessment for potato IPM provided us with an overall picture of potato growing

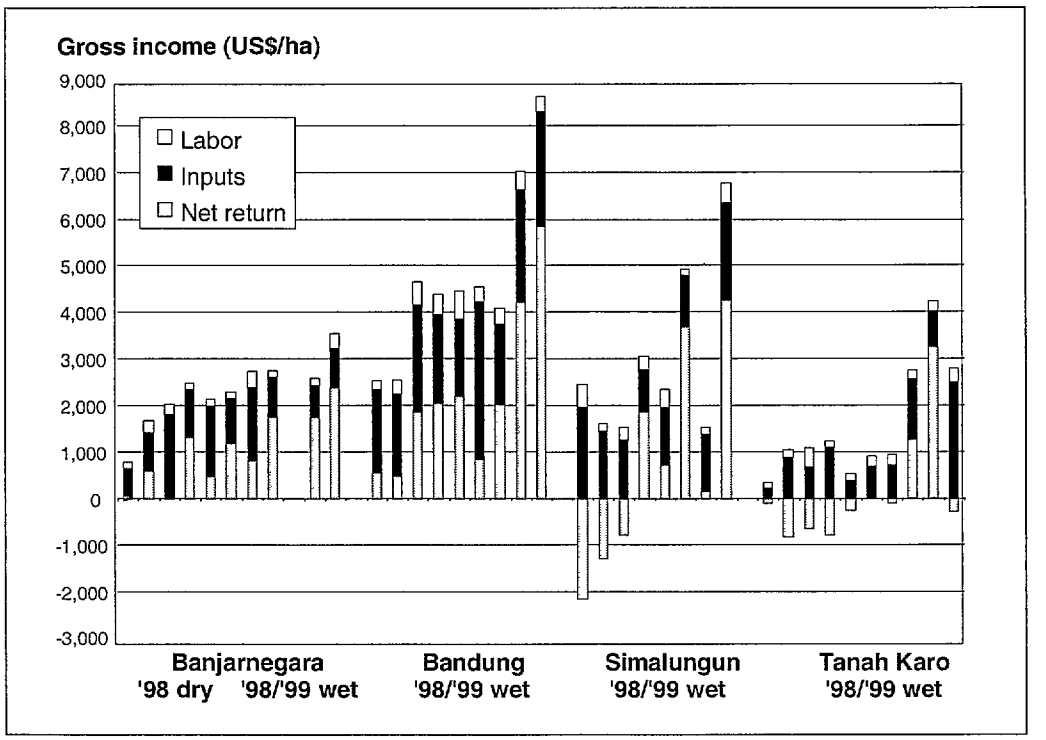

Figure 3. Economic analysis of the potato enterprise in Indonesian study sites during the 1998 dry season (DS) and 1998/99 wet season (WS). Gross income consists of the sum of production cost (labor and inputs) and net return (US$1 = 8,500 Rp in 1998). Each bar represents the crop of one farmer.

systems in the major production areas in Indonesia, the problems farmers face, the effort they expend, and opportunities for improving potato cultivation. The need to develop more ecologically and economically sustainable cultivation practices became an apparent overarching concern. In particular, farmers demanded new, more effective pest management measures to (1) provide better opportunities to benefit from the potential of potato cultivation, and (2) make potato cultivation less polluting. This study provides the foundation for future collaborative IPM development program planning. We identified major research areas that need attention (LMF, thrips, and BW management; soil nutrient management; and a healthy seed supply system). In addition, the assessment triggered high interest in participating in follow-up adapted technology development activities within the farming communities.

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Interaction of Maternal Clones of Potato (*Solanum tuberosum*) with Pollinator Clones of *S. phureja* for Induced Parthenogenesis

M. D. Upadhya and R. Cabello[1]

Induced parthenogenesis (pseudogamy) has been used in potato, *(Solanum tuberosum)* to extract matroclinous dihaploids (2x = 24) from tetraploids using *S. phureja* as the pollen parent (Hougas et al., 1964; Hermsen and Verdenius, 1973). The use of dihaploids for genetic research and breeding is well-documented (Bradshaw and Mackay, 1994). More dihaploids from a wide range of cultivars or advanced selections would be desirable, and even essential to fully realize their potential for breeding and genetic research (Kotch and Peloquin, 1987). At CIP production and use of dihaploids from cultivars or advanced clones is being pursued as a breeding approach to produce parental lines for hybrid true potato seed (TPS) families.

Although parental lines now available produce hybrid TPS families, which are fairly homogenous in tuber shape and color, there is still a certain degree of heterogeneity in haulm morphology and tuber composition. Furthermore, incorporating into parental lines resistance to late blight (LB), caused by *Phytophthora infestans*, using major and minor genes from divergent sources is required to ensure stability of resistance in hybrid families. Parental lines should carry genes that result in the least segregation for haulm and tuber characteristics in hybrid families and provide stable resistance to diseases such as LB.

The first step is extracting a large number of dihaploids from a wide range of clones belonging to *S. tuberosum* subsp. *tuberosum* and *S. tuberosum* subsp. *andigena*, and selecting for desired characters. The selections can then be used to resynthesize tetraploid lines carrying the desired genes in multiplex condition. That is expected to provide a higher order of homogeneity in the hybrid TPS families.

A significant influence on the frequency of haploids induced by both the pistillate and pollinator parents has been demonstrated (Hougas et al., 1964). Monogenic dominance of low seed set in the pollinator has been postulated along with the idea that seed set/berry by pollinators shows no correlation with haploids/berry (Hermsen and Verdenius, 1973). Literature dealing with haploid induction efficiency of *S. phureja* clones has not considered the important role the maternal parent might play in the induction of parthenogenetic seeds.

However, such a role has been noted in *Nicotiana* (Pandey and Phung, 1982) and other species and strains of plants (Asker, 1979; Gustafsson, 1947; Hermsen and Ramanna, 1981), where parthenogenesis could proceed with or without fertilization. Also, there has been no study to evaluate the role of cytoplasm in the promotion of parthenogenetic seed development. Therefore, we undertook to estimate the following:

- Dihaploid induction efficiencies of two *S. phureja* clones thought to be efficient inducers.
- Dihaploid production ability of a number of tetraploid varieties and parental lines as seed parents.

1 CIP, Lima, Peru.

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- Interaction between maternal clones and the pollinators for the induction of parthenogenetic seeds.
- The possible role of cytoplasm in promoting parthenogenetic seed production.

Materials and Methods

The pollinator clones of *S. phureja* used for comparison in this investigation were IVP-35 and IVP-101. Both are homozygous for the dominant seed marker *embryo-spot*. The maternal clones consisted of two groups: (1) 12 cultivars and TPS parental lines of diverse background, and (2) 14 sister clones selected from a single cross (CFK-69.1 x CEW-69.1) sharing common cytoplasm.

Maternal and pollinator clones were grown in pots in a protected nethouse at CIP's Huancayo Station (3,280 m) in Peru. The natural photoperiod was extended by 4 h using sodium vapor lamps providing ~50 lux at the plant level to promote flowering. The plants were drip irrigated and fertilized with 5 split applications of N totaling 250 ppm with basal applications of 200 ppm P and 150 ppm K.

The seed parents were trimmed to retain one inflorescence with six buds/stem and were emasculated at the ripe bud stage. Two successive pollinations at 4-h intervals were carried out when the flower opened (Thakur and Upadhya, 1991). Pollen from the pollinator clones was collected and preserved until used following the procedure of Thakur et al. (1994). Berries were collected 8 wk after pollination and allowed to ripen at room temperature for 2 wk before manual extraction of seeds.

True seeds (TS) were surface treated with 0.5% sodium hypochlorite for 10 min, rinsed, and dried to <5% moisture content. Seeds with embryo spots and without embryo spots (i.e., those not resulting from a sexual cross) were separated and counted. Seeds without embryo spots were stored at 30°C for 2 mo to break dormancy. Seedlings grown from these seeds were checked for nodal pigmentation at the 4-5 true leaf stage to segregate the hybrids in case some seeds were undetected by the embryo marker. The embryo spot in the hybrid seeds denotes pigmentation of the node between the cotyledons and the radical. The dominant gene governing this pigmentation also produces pigmentation of the nodes in the plant and the eyebrows of the tubers (Hermsen and Verdenius, 1973). Seedlings without nodal pigmentation were transplanted in 12-in. diam. pots and after 30 d were checked for ploidy, first by stomatal chloroplast counts and then by chromosome counts using root tip squashes. The number of dihaploids and tetraploids were recorded for each of the seed parents from pollinations with respective pollinator clones.

Results and Discussion

Number of seedlings tested, diploid plants identified, and the percentages for each of the pollinator clones used for each of the 14 seed parents are given in Table 1. The average dihaploid frequency was higher when IVP-101 was used as the pollinator, compared with the use of IVP-35. That confirmed the results of Hermsen and Verdenius (1973) that IVP-101 exhibited higher dihaploid inducing efficiency than other clones studied. In Table 1, the seed parents are arranged in three groups according to their response to the two pollinator clones with respect to percentage of dihaploids recovered. The data clearly show a differential maternal response to parthenogenetic haploid induction by the pollinator clones. These observations confirm previous reports that seed parents used for the extraction of dihaploids, using different pollinator clones of *S. phureja*, differ significantly in their dihaploid production ability. (Hutten et al., 1994).

In maize, Chase (1949, 1952) postulated that the differential behavior of the seed parents for monoploid production efficiency could be due to 1) frequency of recessive lethal genes in the seed parent,

Table 1. Comparison of dihaploid induction efficiency of *S. phureja* pollinator clones IVP-35 and IVP-101 in tetraploid clones/lines of *S. tuberosum*, Peru, 1997-98.

Males	Nonspotted seeds sown (no.)		Plants grown to maturity (no.)		Survival (%)		Dihaploids (no.)		Dihaploids (%)	
Females	IVP-35	IVP-101	IVP-35	IVP-101	IVP-35	IVP-101	IVP-35	IVP-101	IVP-35	IVP-101
Group 1										
Achirana	569	134	569	134	99.1	80.7	44	32	7.7	23.8
Ccompis	73	247	73	247	91.2	68.0	9	39	12.3	15.8
Desiree	97	4	81	4	83.5	100.0	4	3	4.9	75.0
MF-1	133	65	133	296	80.1	93.1	0	5	0.0	7.7
Serrana	70	74	70	74	39.3	44.8	6	11	8.6	14.8
Stirling	14	73	14	73	38.9	61.3	4	39	28.6	53.4
TPS-13	13	6	13	6	68.4	50.0	3	4	23.1	66.7
TPS-67	57	24	57	24	49.1	32.4	2	2	3.5	8.3
Group 2										
Atzimba	206	435	206	435	89.6	92.2	11	14	5.3	3.2
TPS-7	6	60	6	60	17.6	53.6	3	2	50.0	3.3
Group 3										
MF-11	21	15	21	15	84.0	100.0	0	0	0.0	0.0
TS-9	14	4	14	4	73.7	40.0	0	0	0.0	0.0
Average									12.0	22.7

and 2) the tendency of particular genotypes of the seed parent to favor monoploid development.

Hougas et al. (1964) later confirmed the two postulates of Chase from their results with tetraploid potatoes. Our results also support postulate (1) (Table 1). Here it is clear that the survival of seedlings from nonspotted seeds varied by female parent involved and the pollinator clone used. Low survival from certain female parents may point to a higher load of lethal recessives. The data also show that, in certain crosses, the pollinator clone influences survival. In crosses with cv. Stirling and TPS-7, survival was markedly lower with IVP-35 as the pollinator than with IVP-101. With TS-9 and Ccompis, the reverse was true. This differential behavior cannot be explained only on the basis of Chase's postulate (1). Possibly the genotypes of the two pollinator clones differentially interact through the endosperm (4x from the seed parent + 2x from pollinator (Hougas et al., 1964) to suppress lethal factors and enhance embryo viability, or enhance lethal effects by synergy. Present data on differential emergence/survival from nonspotted seeds involving the two pollinator clones do not agree with results of Hutten et al. (1994) who report a similar percentage of nonemerging seeds involving 3 pollinator clones in crosses with 26 female parents.

The significant differences in dihaploid production ability between seed parents could be explained on the basis of inducibility factors present in the female parent. They are similar to the heritable factors found for the culturability/regeneration capacity of pollen for haploid production through anther culture (see Wenzel, 1994). Hence we propose that such heritable

factors controlling the response of parthenogenetic seed production are present but need confirmation through further investigations.

The above discussion still leaves the question of what part cytoplasmic influence plays on the inducibility of parthenogenetic haploids. Therefore, we pollinated 14 sister clones from a cross carrying identical cytoplasm with the two pollinator clones. Data on seeds set/berry, and the percentage of seeds without the embryo spot are given in Tables 2 and 3. The results clearly show that seeds set/berry varies widely between the sister clones in response to the two pollinator clones (Table 2). Similarly, the percentages of seeds without the embryo spot also vary widely between the sister clones in response to the two pollinator clones (Table 3). That suggests the role of cytoplasm probably is not such that it can influence nuclear factors determining the parthenogenetic induction ability of the seed parent.

Table 3 indicates that nuclear factors govern the induction of parthenogenetic seeds in a genotype. That is due to wide segregation among sister clones for the percentage of seeds without the embryo spot in response to the two pollinator clones.

Pandey and Phung (1982) showed the presence of the *Hertwig effect* in plants through induced parthenogenesis using irradiated pollen. They postulated that *N. alata* has specific genes that, when transferred to the egg in segmented fashion, promote parthenogenetic diploidy. *N. glutinosa* has, in addition, genes that promote parthenogenetic haploidy. Therefore, it is reasonable to expect the genetic constitution of the seed parent and the pollinator clone to figure significantly in the successful induction of parthenogenetic seeds. The present data demonstrate that the genotypes of both the maternal clones and the pollinator clones are crucial for the induction of parthenogenetic haploids. If what has been shown in *Nicotiana* can be applied to the present case, the following would be true. Inducer genes in the pollinator clones, when present in the 6x endosperm (4x of maternal + 2x of pollinator)

Table 2. Comparative seed set/berry with *S. phureja* pollinator clones IVP-35 and IVP-101 involving 14 tetraploid female sister clones of *S. tuberosum*, Peru, 1997-98.

Males	Seeds/berry (no.)		Ratio
Females	IVP-35	IVP-101	35:101
C95LB-22.9	28	7	4.2:1
C95LB-22.14	49	12	4.2:1
C95LB-22.8	37	9	3.9:1
C95LB-22.15	39	11	3.5:1
C95LB-22.3	63	20	3.2.1
C95LB-22.2	57	18	3.1:1
C95LB-22.6	61	21	2.9:1
C95LB-22.7	44	16	2.8:1
C95LB-22.5	24	9	2.6:1
C95LB-22.11	35	15	2.3:1
C95LB-22.12	30	13	2.3:1
C95LB-22.13	51	28	1.8:1
C95LB-22.1	25	21	1.3:1
C95LB-22.10	6	10	0.6:1

Table 3. Comparative percentage of seeds without embryo spot with *S. phureja* pollinator clones IVP-35 and IVP-101 involving 14 tetraploid female sister clones of *S. tuberosum*, Peru, 1997-98.

Males	Total seeds (no.)		Seeds without embryo spot (no.)		Seeds without embryo spot (%)	
Females	IVP-35	IVP-101	IVP-35	IVP-101	IVP-35	IVP-101
C95LB-22.1	1,247	636	143	164	11.5	25.8
C95LB-22.2	1,552	441	7	63	0.5	14.3
C95LB-22.3	1,315	237	9	30	0.7	12.6
C95LB-22.5	723	101	73	30	1.0	29.7
C95LB-22.6	2,803	415	31	60	1.1	14.4
C95LB-22.7	221	140	0	22	0.0	15.7
C95LB-22.8	402	224	4	46	1.0	20.5
C95LB-22.9	303	197	3	16	1.0	9.6
C95LB-22.10	30	206	3	26	10.0	12.6
C95LB-22.11	1,214	346	178	135	14.7	39.0
C95LB-22.12	2,043	293	184	57	9.0	19.4
C95LB-22.13	1,112	550	9	47	0.8	8.5
C95LB-22.14	1,181	591	2	119	0.2	20.1
C95LB-22.15	426	300	4	45	0.9	15.0
Average					3.7	18.4

in synergy with the genes in the egg, can initiate parthenogenetic development of the 2x/4x (unreduced egg cell) embryo and the seed.

Hermsen and Verdenius (1973) reported polyploids from nonspotted seeds in the progenies of cultivars x homozygous pollinators of *S. phureja*. They reported a frequency of 1.9% for matroclinous tetraploids. Their data, however, clearly indicate the 13 phureja pollinator clones homozygous for embryo spot had differential parthenogenesis induction efficiency. The cultivars Gineke and Radosa produced matroclinous tetraploids although the frequency in Gineke (27) was higher than in Radosa (14).

Such matroclinous tetraploids could originate only from unreduced (4x) egg cells produced during megasporogenesis. It has been shown that restitution, either in the first meiotic division (FDR) or in the second meiotic division (SDR), in *Solanum* diploids and dihaploids is genetically controlled (Mok and Peloquin, 1975). Hence, it is reasonable to assume that the gene or genes controlling restitution will also be operative at the tetraploid level. The 4x egg cells would result from FDR or SDR, premeiotic/postmeiotic doubling, or apospory. Such 4x egg cells would then give rise to matroclinous tetraploids through the inducer effect of the *phureja* pollinator coupled with the inducible effect in the seed parent. The frequencies of such matroclinous tetraploids produced depend on the genotype of the seed parent as well as the pollinator.

That matroclinous tetraploids originate in this manner is supported by the data in Table 1. Chromosome counts confirmed the remaining plants raised from nonspotted seeds were tetraploids. There are marked differences in the frequencies depending on the seed parent and the pollinator clone.

That confirms parthenogenetic seeds are produced by the interaction of genotypes of maternal clones (inducibility factors) with the pollinator genotypes (inducer factors). These would have either a dihaploid or a tetraploid embryo of matroclinous origin.

Conclusions

The results of these investigations show that the pollinator clones, IVP-35 and IVP-101 have differential efficiency for dihaploid induction. The overall average for the two pollinators shows that IVP-101 is more efficient than IVP-35. However, the dihaploid induction efficiency is also governed by the genotype of the seed parent.

Crosses involving 14 sister clones with the two pollinators indicated the absence of cytoplasmic factors influencing the proportion of parthenogenetic seeds without embryo spot. Based on these studies and information on other species, it is postulated that the inducibility of parthenogenetic seeds seems to be determined by nuclear genes of the seed parent in response to the inducer effect of the pollinator clones. Moreover, at the tetraploid level unreduced 4x egg cells are produced through restitution. That could give rise to matroclinous tetraploids through parthenogenesis.

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A Proposed *Solanum tuberosum* subsp. *andigena* Core Collection

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Although, potato is known worldwide as *Solanum tuberosum*, in Latin America there are thousands of farmer cultivars that have been grown in the Andes for centuries. They are classified as *Solanum tuberosum* subsp. *andigena* [hereinafter called *andigena*] and S. *tuberosum* subsp. *tuberosum* (*tuberosum*) (2n = 4x = 48); *S. stenotomum, S. phureja, S. goniocalyx*, and *S.* x *ajanhuiri* (2n = 2x = 24); *S.* x *chaucha* and *S.* x *juzepczukii* (2n = 2x = 36); and *S.* x *curtilobum* (2n = 5x = 60) (Hawkes, 1990). The primary center of diversity of cultivated potato is in the highlands of Andean South America where all cultivars except *S. tuberosum* subsp. *tuberosum* are native. The Chiloé Archipelago of Chile is a secondary center of diversity. There hundreds of farmer cultivars of *S. tuberosum* subsp. *tuberosum* adapted to long photoperiods still grow under cool environments at or near sea level (Hawkes 1990, Huamán et al., 1997).

CIP assembled a potato collection of more than 15,000 farmer-selected accessions of cultivars from Argentina, Bolivia, Chile, Colombia, Ecuador, Guatemala, Mexico, Peru, and Venezuela, largely from 1971 to 1989. Since then, some selected donations were received from nongovernmental organizations (NGOs) working to conserve on-farm Andean cultivars. Many of the accessions in the collection were donated to CIP by institutions in South American countries. A large number of them were gathered and shared by joint CIP-NARS (national agricultural research system) collecting expeditions.

Since potatoes are clonally propagated, the tubers collected in different farmer's fields were expected to duplicate numerous accessions of the same cultivar. In many cases, the same cultivar was collected under different vernacular names along its area of cultivation. In addition, donations from national or institutional collections added further duplication because the same cultivar could be maintained in more than one potato collection. Therefore, it could have several identification codes. A process of identifying duplicate accessions of the same cultivar, using morphological and electrophoretic criteria of total proteins and esterases, reduced this potato collection to about 3,500 different farmer cultivars (Huamán, 1986, 1994).

Farmer selected cultivars of *andigena* are predominant in the collection and represent about 75% of the total cultivated accessions. With the exception of *S. stenotomum,* accessions that include several hundred farmer cultivars, and *S. phureja* with more than one hundred, all other cultivated species have fewer cultivars and are more restricted geographically (Huamán et al., 1997).

The core collection concept was put forward in Frankel and Brown (1984). A core was defined as a limited set of accessions derived from an existing germplasm collection, chosen to represent the genetic spectrum in the whole collection. The core should contain the maximum genetic diversity available in the collection. The remaining accessions in the collection are called the reserve collection.

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Brown (1989a, 1989b, 1995) also indicated that the accessions in the core are chosen primarily to be representative, and are ecologically or genetically distinct from one another. Within the primary constraint of covering the genetic diversity and ecological range, the aim should then be to maximize genetic diversity. This implies that the core should not contain duplicates and should minimize similarity between its entries.

The fundamental role of the core, then, is as a workable guide or point of entry to the whole collection. Therefore, the selection of a core subset of *andigena* cultivars in the collection maintained at CIP is essential to increase the use of the genetic diversity available in the entire collection. Core collections have been defined for many crops in the last decade (Ortiz et al., 1998). This paper reports the process of selecting the *andigena* core collection.

Materials and Methods

The original number of *andigena* accessions collected in the highlands of Latin America and assembled in the genebank at CIP was 10,722. These accessions were collected in eight countries from Mexico to Argentina. Over the years, a process of identification of duplicate accessions of the same cultivar was undertaken in this collection. Accessions with similar tuber, stem, and floral characters were morphologically compared when grown side by side in the field at CIP's highland experiment station in Huancayo, central Peru (3,200 m). Accessions that were morphologically identical were also compared by analyzing total proteins and esterases extracted from their tubers by polyacrylamide gel electrophoresis. Those that were morphologically and electrophoretically identical were considered duplicates.

One clonal accession of each duplicate group was selected to represent the group for further comparisons with other accessions in the collection. The other duplicate accessions were converted to true seed (Huamán and Stegemann, 1989). The output of this work was to reduce the *andigena* collection from 10,722 to 2,427 accessions. Further comparisons in 1998 showed 48 additional duplicates, reducing the number of cultivars in the collection to 2,379. That represents about 22% of the original collection. The number of duplicates of the same cultivar ranged from 1 to 276 accessions (Table 1).

Morphological data were recorded from these 2,379 *andigena* cultivars grown in the field at Huancayo. Data were recorded using a 0 to 9 scale for 25 key cultivated potato descriptors selected from an internationally accepted descriptor list (Huamán et al., 1977). Of the 25 descriptors, 9 are related to tuber characters; 6 to plant habit, stems, and leaves; 8 to flowers; and 2 to fruit characters (Table 2). Corolla, tuber skin, and flesh colors were recorded using two color charts that combine color and intensity. They were developed to match color diversity in flowers and tubers shown by Andean potato cultivars. The codes used

Table 1. Number of duplicate accessions found in the original *andigena* potato collection maintained at CIP, Lima, Peru, 1998.

Duplicates within groups	Duplicate groups
None (unique)	1,204
1-2	747
3-5	482
6-10	194
11-15	60
16-20	27
21-30	37
31-50	19
51-75	11
76-100	7
101-125	4
126-150	1
276	1

Table 2. Means (χ), standard error (SE), and χ^2 tests of frequency distribution for morphological descriptors for the whole (2,379 accessions) and core collection (306 accessions) of *andigena* potato cultivars. Descriptor states transformed into a 0 to 9 scale[a] except for predominant flower and tuber skin color, which combined color and intensity in a two-digit score. R^2 values were calculated for each morphological character in the whole collection considering a maximum of six clusters and the highest values are shown in bold face, CIP, Lima, Peru, 1998.

Morphological Character		Whole		Core		Classes	χ^2	$P > \chi^{2b}$	R^2
		X	SE	*X*	SE	(no.)	calculated		In clusters
Phb	Plant habit	2.77	0.014	2.79	0.042	5	1.75	0.781	0.008
Stc	Stem color	2.93	0.035	3.00	0.107	7	2.86	0.827	**0.175**
Stw	Stem wing shape	1.25	0.010	1.30	0.030	3	1.03	0.598	0.026
Pln	No. pairs primary lateral leaflets	5.32	0.018	5.34	0.053	7	1.61	0.952	**0.359**
Pin	No. primary interjected leaflets on rachis	12.82	0.128	13.17	0.382	9	18.94	0.015	**0.560**
Sin	No. secondary interjected leaflets on petiolules	7.06	0.161	6.70	0.466	9	3.44	0.904	**0.763**
Pdc	Pedicel color	4.70	0.036	4.74	0.103	9	6.90	0.547	0.061
Klx	Calyx color	4.57	0.027	4.36	0.085	7	10.56	0.103	0.046
Fw1	Predominant flower color	17.92	0.096	17.72	0.301	8	5.74	0.570	**0.102**
Fw2	Secondary flower color	4.45	0.596	4.36	0.183	8	10.87	0.144	0.022
Fw2d	Distribution of secondary flower color	1.01	0.038	1.23	0.115	10	12.28	0.198	0.004
Fwsh	Corolla shape	5.80	0.023	5.68	0.072	7	16.18	0.003*	0.003
Ant	Anther pigmentation	0.28	0.015	0.35	0.049	6	4.293	0.508	0.008
Pst	Pistil pigmentation	1.65	0.034	1.67	0.104	8	3.684	0.815	**0.229**
Frc	Fruit color	1.26	0.018	1.31	0.061	8	9.156	0.242	0.003
Frsh	Fruit shape	2.17	0.023	2.13	0.070	8	12.98	0.073	0.008
Tsk1	Predominant tuber skin color	16.17	0.164	16.67	0.467	9	17.51	0.025	**0.859**
Tsk2	Secondary tuber skin color	3.93	0.065	3.84	0.193	10	8.69	0.466	0.045
Tsk2d	Distribution of secondary tuber skin color	3.76	0.053	3.75	0.157	8	1.09	0.993	0.066
Tsh1	Tuber shape outline	5.85	0.032	5.81	0.099	8	7.05	0.424	0.001
Tshx	Odd tuber shape	0.96	0.054	0.73	0.136	10	17.79	0.038	0.004
Tey	Tuber eye depth	5.09	0.031	5.02	0.093	5	0.60	0.897	0.005
Tf1	Predominant tuber flesh color	2.27	0.018	2.32	0.061	7	7.87	0.248	0.015
Tf2	Secondary tuber flesh color	1.30	0.058	1.59	0.185	7	5.55	0.475	0.056
Tf2d	Distribution secondary flesh color	0.55	0.028	0.69	0.090	8	7.88	0.343	0.045

[a] According to Huaman et al. (1977)

[b] $P > \chi^2$ means the probability of χ^2 greater than χ^2 calculated. If the value is ≥ 0.05, there is no significant difference between whole and core collections.

for tuber skin color were white-cream (1 = pale, 2 = intermediate, 3 = dark); yellow (4, 5, 6); orange (7, 8, 9); brown (10, 11, 12), pink (13, 14, 15), red (16, 17, 18); red-purple (19, 20, 21); purple (22, 23, 24); purple-black (25, 26, 27). The codes for flower color were white (1 = pale, 2 = intermediate, 3 = dark); red-pink (4, 5, 6); red-purple (7, 8, 9); blue (10, 11, 12); blue-purplish (13, 14, 15); lilac (16, 17, 18); purple (19, 20, 21); and violet (22, 23, 24).

Cluster analysis of the morphological data was done with NTSYS-pc v1.70 (Rohlf, 1992) using the simple matching coefficient and the unweighted pair group method arithmetic mean algorithm (UPGMA). The phenogram produced was used to determine accessions with similarity coefficients below 0.75. One accession from each of these clusters was selected for the core subset.

A proportional sampling strategy aimed to maximize geographical representation was adopted. The goal was to retain potential differences in ecological adaptation to the niches where potato is grown. Therefore, the number of accessions to be selected for the *andigena* core collection was based on the square root of the number of different cultivars from the main geographical division (state, department, or province) of each country (Table 3). The goal for total sample size of the core was 10% of the original number of accessions as suggested by Brown (1995) for clonal crops. As much as possible, we intended to include in the core those cultivars with desirable genes for breeding. Therefore, we used all available data from evaluations conducted at CIP to identify sources of resistance to diseases and pests as well as other desirable traits (Huamán, 1987; other data in the potato database at CIP).

The strength of association between the 22 morphological characters scored as 1-9 (3 characters were scored as actual numbers of leaf parts) was determined using Cramer's V coefficient

$$V = \sqrt{\frac{\chi^2}{N * \min(r-1, c-1)}}$$

where c^2 = chi square value from the contingency table, N = total number of accessions analyzed, r = row, and c = column. R^2 values were also calculated for the whole collection to determine the most important morphological characters to form a maximum of six clusters using the FASTCLUS procedure (SAS Institute, 1985).

The mean phenotypic diversity between the collection of 2,379 (whole) and the subset of 306 accessions (core) was compared by Student's *t* test for all descriptors. Similarly, the homogeneity of the frequency distributions between whole and core collections was analyzed by chi-square test as suggested by Ortiz et al. (1998).

Results

Analyses of morphological data

Cramer's V coefficients between pairwise comparisons of the 22 morphological characters scored as 1-9 showed only 3.6% of them to be correlated at values of 0.30-0.56. This means that these characters are independent and therefore suitable for these analyses of cultivated potatoes (Table 4). The highest values found were V = .56 between secondary tuber flesh color (Tf2) and distribution of secondary tuber flesh color (Tf2d), which are expected to have some association. The same was true for predominant tuber flesh color (Tf1) and secondary flesh color (Tf2) with V = 0.50; predominant flower color and secondary flower color with V = 0.49; secondary tuber skin color and distribution of secondary tuber skin color with V = 0.48; and for primary and secondary tuber flesh color (Tf1 and Tf2d) with V = 0.40. These associations could be explained by the high percentage of accessions in the collection that do not show secondary colors in either the flowers or tubers.

Table 3. Number of accessions in the whole (W) and core (C) collection of *andigena* potato cultivars according to geographic data from their collection site, CIP, Lima, Peru, 1998.

Country	State, department, or province	W	Square root W	C
Argentina	Catamarca	3	1.7	2
	Jujuy	42	6.5	7
	Salta	41	6.4	6
	Unknown	6	2.4	0
Bolivia	Oruro	50	7.1	7
	Potosi	59	7.7	10
	La Paz	35	5.9	6
	Chuquisaca	4	2.0	2
	Cochabamba	8	2.8	3
	Tarija	3	1.7	1
	Unknown	161	12.7	24
Colombia	Boyaca	39	6.2	6
	Cundinamarca	13	3.6	3
	Quindio	3	1.7	1
	Santander	6	2.4	2
	Santander del Norte	4	2.0	1
	Cauca	13	3.6	3
	Nariño	46	6.8	7
	Tolima	2	1.4	1
	Valle	4	2.0	2
Ecuador	Bolivar	18	4.2	4
	Cañar	11	3.3	3
	Chimborazo	34	5.8	6
	Cotopaxi	15	3.9	3
	Tungurahua	10	3.2	3
	Carchi	25	5.0	5
	Imbabura	31	5.6	6
	Pichincha	6	2.4	2
	Azuay	8	2.8	2
	Loja	16	4.0	4
	Unknown	20	4.5	1
Guatemala	Huehuetenango	6	2.4	3
	Quezaltenango	9	3.0	2
	San Marcos	10	3.2	3
	Solola	2	1.4	1

Continued on next page.

Table 3 (cont.)

Mexico	Mexico	2	1.4	1
	Puebla	11	3.3	3
	Veracruz	7	2.6	3
Peru	Ancash	109	10.4	10
	Huanuco	85	9.2	9
	Lima	50	7.1	7
	Junin	99	9.9	10
	Pasco	53	7.3	7
	Apurimac	88	9.4	11
	Ayacucho	152	12.3	12
	Huancavelica	39	6.2	6
	Amazonas	10	3.2	4
	Cajamarca	42	6.5	6
	La Libertad	19	4.4	4
	Lambayeque	4	2.0	2
	Piura	6	2.4	2
	Cusco	288	17.0	22
	Puno	110	10.5	13
	Unknown	455	21.3	23
Venezuela	Merida	12	3.5	4
	Trujillo	23	4.8	5
Total		**2,427**		**306**

Cluster analyses showed the most important morphological characters to form the most different six clusters of accessions were predominant tuber skin color (Tsk1), number of secondary interjected leaflets on the petiolules (Sin), number of primary interjected leaflets on the rachis (Pin), number of pairs of primary lateral leaflets (Pln); pistil pigmentation (Pst), stem color (Stc), and predominant flower color (Fw1). The R^2 values ranged from $R^2 = 0.001$ to 0.859 (Table 2).

Selection of a core subset

The frequency distributions of data from the collection sites of accessions in the whole and core collections were determined by country and state (Table 3). As much as possible, the number of accessions in the core subset for each state was equal to the square root of the number of accessions in the whole collection from that state. The number of accessions from Argentina and Ecuador with unknown collection sites was reduced in the core to favor accessions with known collection sites. But, in the case of accessions from Bolivia and Peru with unknown collection sites, the proportions in the core were retained because of the relatively high number of those accessions.

From a dendrogram generated by cluster analysis of the morphological data, accessions for the core were selected to assure at least one representative accession from the most different morphological clusters (data not shown). First priority was given to select accessions from the main geographical division of each country represented in very low frequencies. From those clusters containing many accessions, the representative accessions were selected on the basis of their resistance to diseases and pests and their dry matter content. Another criterion was to favor the most widespread cultivars

Table 4. Matrix of measures of association between the morphological descriptors[a] recorded in the whole *andigena* collection using Cramer's V method; values above 0.30 are in boldface, CIP, Lima, Peru, 1998.

	Phb	Stc	Stw	Pdc	Klx	Fw1	Fw2	Fw2d	FwSh	Ant	Pst	FrC	FrSh	Tsk1	Tsk2	Tsk2d	Tsh1	Tshx	Tey	Tf1	Tf2	Tf2d
Phb	1																					
Stc	0.07	1																				
Stw	0.07	0.07	1																			
Pdc	0.08	0.21	0.12	1																		
Klx	0.08	0.17	0.08	**0.37**	1																	
Fw1	0.13	0.17	0.10	0.26	**0.34**	1																
Fw2	0.08	0.11	0.08	0 15	0.17	**0.49**	1															
Fw2d	0.05	0.07	0.10	0.12	0.16	0.23	**0.30**	1														
FwSh	0.06	0.06	0.05	0.07	0.06	0.11	0.07	0.06	1													
Ant	0.06	0.13	0.04	0.07	0.07	0.15	0.07	0.06	0.04	1												
Pst	0.03	0.19	0.05	0.10	0.09	0.12	0.09	0.07	0.07	0.20	1											
FrC	0.05	0.09	0.06	0.07	0.08	0.09	0.08	0.08	0.09	0.06	0.08	1										
FrSh	0.09	0.08	0.07	0.08	0.08	0.13	0.06	0.07	0.13	0.05	0.05	**0.37**	1									
Tsk1	0.10	0.27	0.11	0.16	0.18	0.19	0.18	0.13	0.11	0.16	0.23	0.11	0.12	1								
Tsk2	0.07	0.14	0.09	0.12	0.11	0.19	0.11	0.06	0.05	0.11	0.12	0.08	0.07	**0.32**	1							
Tsk2d	0.06	0.14	0.09	0.13	0.09	0.13	0.08	0.07	0.06	0.09	0.11	0.06	0.06	0.28	**0.48**	1						
Tsh1	0.06	0.09	0.09	0.08	0.07	0.12	0.08	0.08	0.07	0.06	0.06	0.06	0.08	0.12	0.09	0.09	1					
Tshx	0.06	0.09	0.09	0.06	0.07	0.13	0.07	0.05	0.06	0.06	0.04	0.04	0.08	0.15	0.08	0.08	**0.31**	1				
Tey	0.06	0.06	0.13	0.09	0.08	0.13	0.11	0.09	0.04	0.05	0.07	0.07	0.12	0.13	0.09	0.07	0.20	**0.30**	1			
Tf1	0.07	0.06	0.06	0.06	0.06	0.10	0.07	0.08	0.04	0.09	0.05	0.06	0.05	0.18	0.09	0.07	0.08	0.10	0.26	1		
Tf2	0.08	0.13	0.05	0.07	0.08	0.19	0.09	0.06	0.05	0.18	0.12	0.06	0.03	0.24	0.13	0.09	0.06	0.09	0.05	**0.50**	1	
Tfd2	0.06	0.12	0.06	0.08	0.07	0.11	0.07	0.05	0.07	0.17	0.13	0.06	0.04	0.18	0.10	0.09	0.07	0.09	0.06	**0.40**	**0.56**	1

a Phb = plant habit, Stc = stem color, Stw = stem wing shape, Pdc=pedical color, Pln = pairs primary lateral leaflets (no.), Pin = primary interjected leaflets on rachis (no.), Sin = secondary interjected leaflets on petiolules (no.), Pdc = pedicel color, Klx = calyx color, Fw1 = predominant flower color, Fw2 = secondary flower color, Fw2d = distribution of secondary flower color, Fwsh = corolla shape, Ant = anther pigmentation, Pst = pistil pigmentation, FrC = fruit color, Fr Sh=fruit shape, Tsk1 = predominant tuber skin color, Tsk2 = secondary tuber skin color, Tsk2d = distribution of secondary tuber skin color, Tsh1 = tuber shape outline, Tshx = odd tuber shape, Tey = tuber eye depth, Tf1 = predominant tuber flesh color, Tf2 = secondary tuber flesh color, Tf2d = distribution of secondary tuber flesh color.

that comprised a high number of duplicate accessions in the collection.

The core collection of 306 accessions represents 12.9% of the whole. The analysis of means and frequency distributions based on data for morphological characters recorded in the whole collection and the core subset were statistically similar ($P > 0.05$ for 21 of 25 characters) (Table 2). The core collection was slightly biased to retain more cultivars with unusual flower shape (stellate) in cultivated potatoes, rare tuber shapes, or highly dissected leaves. The whole collection has low frequencies of cultivars with these characters. In the case of the predominant tuber skin color (Tsk1) character, the core also has a slightly higher proportion of red colors than in the whole collection.

The analysis of means and frequency distributions, based on data for resistance to diseases and pests and tuber dry matter content, revealed similar results for 4 out of 16 characters (Table 5). Compared with the whole collection, the core subset was biased only toward lower susceptibility for resistance to Potato Virus X; cyst nematode (*Globodera pallida*) race pa2 and pa3; and Andean potato weevil (*Premnotrypes* spp.)

Discussion

As the cultivated potato collection was assembled at CIP, the presence of numerous duplicate accessions of the same cultivar was quite evident. Therefore, duplicate identification was the first step to rationalize the size of collection to be maintained. That was also the only way to secure the clonal conservation of the most diverse sample of Andean potato cultivars. The maintenance costs of the field genebank and in vitro collection of *andigena* were reduced by about 78%, the same proportion as the number of duplicates identified. Earlier, efforts to minimize redundancy in the potato collection was one of the most important steps in selecting a core collection. With such a high level of duplication, it is highly unlikely that any random sample taken from the original collection would be representative of the total genetic diversity in this collection.

The procedure to choose accessions for the core collection was based on proportional sampling according to passport data and morphological clusters. The comparisons of means and frequency distributions for the morphological descriptors supported the sampling strategy. Furthermore, another independent assessment based on the different reactions to diseases and pests also validated this proportional sampling method. Insofar as possible, we attempted to include in the core subset those accessions that combine the most desirable traits for breeding.

The selection of a core collection of cultivated potatoes from Latin America offers many advantages. Since this collection is clonally conserved, only the core collection will be field planted. The reserve collection can be maintained in vitro. The assessment of new conservation methods, e.g., cryopreservation, could be made using just a few accessions representing a broad genetic base. Pathogen cleanup of clones for distribution should be a priority in the core collection. For security, core accessions could be duplicated in several countries. Most important of all is that the full breeding potential of these farmer-selected potato cultivars, which have been maintained for centuries in their center of diversity, remains unknown. A thorough evaluation of their disease and pest resistance and other desirable traits is now feasible because the core subset covers the broadest genetic base that is available in ex situ conservation.

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Table 5. Means (X), standard errors (SE), and X^2 tests of frequency distribution for reaction to diseases and pests of accessions in the whole and core collection of *andigena* potato cultivars. Descriptor states transformed into a 0 to 9 scale[a] except for tuber dry matter (%), CIP, Lima, Peru, 1998.

Resistance to	Whole			Core			Classes	X^2	$P > \chi^{2\,b}$
	N	*X*	SE	N	*X*	SE	(no.)	calculated	
Phytophthora blight in leaves	506	6.61	0.02	95	6.26	0.07	5	8.186	0.085
Phytophthora blight in tubers	304	5.09	0.03	55	4.76	1.32	5	5.193	0.268
Synchytrium wart	745	6.70	0.02	85	6.7	0.06	4	0.821	0.844
Macrophomina charcoal rot	37	5.32	0.03	10	5.5	0.10	3	1.289	0.525
Erwinia soft rot	361	7.75	0.03	42	7.52	0.09	4	2.732	0.435
Potato virus X	1739	5.52	0.03	206	5.31	0.09	3	6.86	0.032
Potato virus Y	1726	5.68	0.03	204	5.62	0.09	3	5.778	0.056
Potato leafroll virus	2505	6.74	0.02	289	6.71	0.05	3	4.551	0.103
Globodera pallida race pa2	1107	6.74	0.02	107	6.57	0.07	4	8.689	0.034
Globodera pallida race pa3	1096	6.62	0.02	107	6.14	0.10	4	25.558	0.001
Globodera pallida Cusco population	566	6.77	0.02	36	6.72	0.06	3	0.25	0.882
Globodera rostochiensis	480	6.60	0.02	54	6.74	0.06	3	1.248	0.536
Meloidogyne incognita acrita	1124	6.01	0.02	106	5.85	0.07	3	0.21	0.981
Phthorimaea tuber moth	1756	7.41	0.03	218	7.29	0.10	5	5.793	0.215
Premnotrypes Andean potato weevil	572	8.15	0.03	62	7.35	0.12	4	21.08	0.0001
Tuber dry matter content	785	24.14	0.06	114	24.06	0.16	4	0.944	0.815

[a] According to Huamán et al. (1977).

[b] $P > \chi^2$ means the probability of χ^2 greater than χ^2 calculated. If the value is greater or equal to 0.05, there is no significant difference between whole and core collections.

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Rustic Seedbeds: A Bridge Between Formal and Traditional Potato Seed Systems in Bolivia

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Potato (*Solanum tuberosum*) is a traditional staple crop produced by more than 200,000 families in Bolivia with total production estimated at 677,000 tons in 1993-94 (Zeballos, 1997). It is cultivated mainly in the highlands, above 3,000 m, with a low average yield of 5.6 t/ha. The severe poverty of the Bolivian highlands is partly due to the harsh climate that limits the options for agricultural production. Production risk for potato is high due to recurrent drought, frost, and hail. Yield losses of 40-60% are common. In addition farmers also face pests and diseases.

High production risk leads not only to direct yield losses, but also to low investments in agriculture. Adverse climate, high production risk, and poverty have led to a low-input/low-output system. Despite these conditions, there is potential for improvement of production systems as shown through on-farm research (Devaux and Gandarillas, 1998). There is a need for innovative strategies to promote an efficient use of appropriate technologies and to increase the income of farmers from agriculture.

Potato Seed Systems

In the highlands, most farms are small with an average of 5 ha of land and 1 ha of potato (Thiele, 1999). Data obtained from yield surveys by PROINPA[3] in the early 1990s showed the importance of seed tuber quality and seed sufficiency for improving potato productivity (Terrazas et al., 1998). Farmers are aware that their seed is of low quality after years of use and know they need to change it, but it is not easy for them to get good quality seed. Traditional seed systems supply about 98% of the seed potato demand in Bolivia (Thiele, 1999). Within these systems, farmers commonly save their own seed from one season to the next. Another option is to exchange seed within the family or with friends and neighbors (local seed flow). They may also buy seed from merchants and in local fairs (long distance seed flow). They base their choice on the reputation of the traders, but the quality is not always guaranteed and informal seed frequently is diseased or infested by pests (Thiele, 1999).

Bolivia is one of the few countries in Latin America that has a functioning formal potato seed system based on seed certification (Bentley and Vasques, 1998). The formal seed is produced mainly by a semiprivate company, the Potato Seed Production Unit (UPS/SEPA), which was developed with the support of the Swiss Development Cooperation (SDC). The healthy seed produced by this company is multiplied by nongovernmental organizations (NGOs) and seed producers through the formal system. In 1996, the 3,600 t of seed produced through the formal system represented about 2% of the seed volume used in the country (Programa Nacional de Semillas, 1996). Most highland farmers do not make use of the formal system seed because they live in areas with poor access away from sources of supply, they lack the

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3 PROINPA, formerly the national potato research program of Bolivia implemented through an agreement between the government of Bolivia, CIP, and the Swiss Development Cooperation (SDC), is now an autonomous Foundation dealing with Andean crops with its main emphasis on potatoes.

money or credit to buy certified seed, environment constraints make heavy seed investment risky, and most native cultivars are excluded from the commercial seed system.

Looking for ways to supply seed from the formal seed system to highland potato production systems, PROINPA began research to adapt rustic nurseries for potato seed production. NGOs developed the rustic nursery concept in the 1980s for vegetable production in the highlands of Bolivia. The technology was first adapted for seed potato tuber production in southern Peru by SEINPA, a national seed potato project implemented with the collaboration of CIP and SDC. Researchers in PROINPA adapted the idea to the highlands of Bolivia specifically for areas where risks for crop production are high due to adverse climatic conditions (Aguilera, 1995). This article describes the concept of rustic seedbeds as a strategy to bridge formal and informal systems and make good quality seed available to farmers. It also assesses progress made so far in validating the system at the farmer level.

The Rustic Seedbed

Based on the experiences mentioned above, and its own research, PROINPA developed a potato seedbed prototype with recommendations for its management (Aguilera, 1995). The rustic seedbed or nursery is a small hothouse (big box) made of local material, stones or adobes. It is about 1 m high with a surface area of from 15 to 20 m^2 (Figure 1). It can be covered and protected against frost and hail with a cover made of a wooden frame with a plastic sheet, and hand watered during drought. Its small size and protection from weather constraints means more intensive technology is applied to the nursery: pest free soil brought from non-cultivated areas, high planting density (22 plants/m^2), better fertilization using manure and limited amounts of chemicals fertilizers (mainly phosphorus), watering, and integrated pest management. When using small size tubers of 10 to 15 grams, 3 to 5 kg of seed are usually required for a rustic bed of around 17 m^2, which normally produces from 40 to 60 kg of high quality seed to be multiplied the next year in the field.

The theoretical advantages offered by rustic nurseries are:

- Decreased risks: protection against frost and hail.
- Better control of pests and diseases.
- Low construction and production costs.
- Optimization of local resources, including water, nutrients, soil, and labor.
- Higher efficiency: high rate of multiplication, may be used twice a year for potato or other crop, small seed tubers may be used with the possibility of using other planting material (e.g., sprout cuttings).

A project was begun in 1995 with SDC financial support, to evaluate and adapt the rustic seedbeds in pilot areas where PROINPA was already coordinating its research and technology transfer activities with other institutions. The objective was to test the seedbed system as a way to develop links between the formal and the informal systems for the production of healthy seed and new or inaccessible cultivars, and to disseminate this material in the highlands. The initial target of the project was for farmers to install and validate 500 seedbeds.

Materials and Methods

The seedbed system was tested and validated in collaboration with farmers' communities and NGOs. The pilot areas chosen for testing represented different agroecological zones of potato production in the highlands of Bolivia. Technical assistance was provided by PROINPA which also proposed a prototype design for the seedbeds as described above (Aguilera, 1995). PROINPA produced the seed for the non-commercial cultivars, normally basic seed, but for some cultivars prebasic seed was also used. In the case of commercial cultivars, certified seed from the commercial formal seed system was supplied to

Figure 1. Typical rustic seedbed in the highlands of Bolivia. Women and children take an active part in seedbed management.

farmers to plant their seedbeds. In this case, because of the bigger tubers, between 8 to 12 kg of seed was required. The PROINPA seedbed design and management were adapted by farmers according to local conditions in each area. Initially, the monitoring process emphasized seedbed management, i.e., recording data on cultivars used, quantity of seed, yield, production costs, and data for seedbed construction, and separating investment and labor costs.

Taking into consideration the production system and farmers' requirements, four categories of cultivar were multiplied.

Category 1. Commercial cultivars required by the market and included in the formal seed system. Basic or certified seed from seed organizations was used.

Category 2. Native and introduced cultivars of local commercial importance grown principally in the highlands and not included in the formal seed production system. At the request of farmers' communities and NGOs, PROINPA cleaned some of these cultivars of viruses through meristem tip culture to produce healthy seed.

Category 3. Native cultivars for subsistence use, which contribute to potato diversity and food security in local communities. There are still hundreds of native cultivars of different species cultivated by farmers in the highlands of Bolivia. Twenty-four native cultivars from different ecoregions were selected for their agro-economical and social characteristics. They were cleaned of viruses by PROINPA and returned to farmers.

Category 4. Selected clones from PROINPA breeding and selection program. The rustic beds allowed validation and multiplication of these cultivars in several potato-growing areas to determine their potential demand.

This analysis of seedbed management factors and yield is first reported for the northern Potosi Department of Bolivia. Situated at 3,500 m, this is one of the poorest and most isolated regions of the country. There PROINPA, UNICEF, and the local farmers' federation collaborated to install around 900 seedbeds. Complete data were collected in 1996 and 1997 on 630 of these seedbeds. Yield was measured in seedbeds with the help of extensionists working for the collaborative project implemented with UNICEF. Multiple regression analyses of factors such as site, cultivar, seed size, seed quality (basic and certified), and years vs. yields were run for all of these seedbeds. Similar analyses were carried out on 190 cases for the years 1995, 1996, and 1998 in more commercially oriented and accessible potato growing areas of central Potosi. Closer monitoring of seedbeds was possible through the collaboration with local development projects that introduced seedbeds in their rural development program.

In Central and Northern Potosi, the following cultivars were multiplied in the seedbeds:

Category 1. Waycha (*S. andigena*) and Desirée (*S. tuberosum*), commercial cultivars with seed from the formal system.

Category 2. Imilla Negra (*S. andigena*), Revolucion (*S. tuberosum*).

Category 3. Gendarme (*S. andigena*), a native cultivar selected for its resistance to the nematode Nacobbus aberrans and its relative tolerance to drought, and several native cultivars including Luky types, bitter potatoes (*S. juzepczukii*).

Category 4. Some promising selected clones.

A follow up of several multiplication cycles of the seed produced in the seedbeds was done with three case study farmers, each from different production systems: (1) a market-oriented system in Loyaza, La Paz, at 3,300 m, (2) a subsistence farmer with access to the market in Kollana, La Paz, at 3,700 m, and (3) a farmer growing native cultivars for his own consumption with limited access to the market in Tapacari, Cochabamba, at 3,500 m. In the first two cases, commercial native cultivars were multiplied; in the third, a local native cultivar that had been cleaned by PROINPA was used. A small quantity of basic seed, 3-5 kg, was initially given to the farmers for seedbed multiplication. Yields obtained for the successive multiplications were recorded and the use of the potatoes produced analyzed with the farmers.

In Loyaza, La Paz, the performance of seed produced in the seedbeds was compared to the informally produced seed of nine farmers. Each farmer planted the seed from the seedbeds near his own seed. At harvest, the yield of the plot planted with the seedbed seed was compared to yield samples taken in the farmer's seed plot.

A partial budget analysis was used considering the cost of the seedbed seed as the marginal cost. As, in most cases, farmers' seed had been multiplied for many years, no cost was attributed to the farmers' traditional seed. The marginal rate of return was calculated using the increase in net benefits obtained with the seedbed seed, compared to the existing technology, in this case farmers' seed, divided by the additional cost generated by the use of the seedbed seed, expressed as a percentage.

Farmers were fully involved in research and validation to obtain their ideas on how to adapt and improve the technology. In collaboration with UNICEF and the local farmers' federation, surveys were carried out through participatory meetings with 305 farmers to evaluate the acceptance of the seedbed system and factors limiting the adoption of the technology.

Results

After three years of validation, the initial target of installing and validating 500 seedbeds was almost tripled. More than 1,200 farmers working with PROINPA, helped by NGOs and other development institutions, have installed nearly 1,400 rustic seedbeds. It is estimated that in 1998 farmers produced about 45 t of healthy seed in seedbeds despite the shortage of irrigation water and high temperatures caused by el Niño.

Yield evaluation

Yield data for 1996 and 1997, in Northern Potosi, were analyzed by cultivar in the 630 seedbeds (Figure 2A). The highest yield of 5.6 kg/m² was obtained with the commercial cultivar Waycha. The 1996 average yield of 2.7 kg/m² was significantly higher than the 1.4 kg/m² obtained in 1997 because of El Niño. Multiple regression analysis of yield against site, cultivar, seed size, seed quality (basic and certified), and years showed significance only for a site that appears to be higher than the others (average of 3,958 m). The R^2 for the regression was low, $R^2 = 0.371$, which means that factors contributing to yield other than those included were more important, e.g., general management of the seedbeds by the farmers. The yield variability between farmers underscores the importance of seedbed management. These data show that by reducing climatic risks and improving crop management practices in the seedbeds, farmers can obtain a high production and much better seed multiplication rates than in open fields. Average seedbed production was more than 25 t/ha in 1996, and 14 t/ha in 1997. Field production in this area in normal years is between 5 and 7 t/ha, and is even lower in bad years.

In central Potosi, average seedbed yields were higher, 2.4 kg/m² in 1995, 3.6 kg/m² in 1996, and 3.1 kg/m² in 1997; highest yield was 6 kg/m² (Figure 2B). Multiple regression analyses of factors such as cultivar, seed size, site, and seed quality mainly showed the effect of cultivar and seed quality (prebasic seed) on yield. The R^2 for the regression was higher than in northern Potosi (R^2=0.602), partially because farmers received better technical support in seedbed management. On average the commercial cultivar Revolucion yielded 1 kg/m² more than other cultivars tested (Figure 2B). There was no significant yield difference between Revolucion and the promising selected clones from the PROINPA breeding program (Category 4). When farmers used their own seed in the seedbeds, their yield was 1.7 kg/m² lower than the prebasic seed.

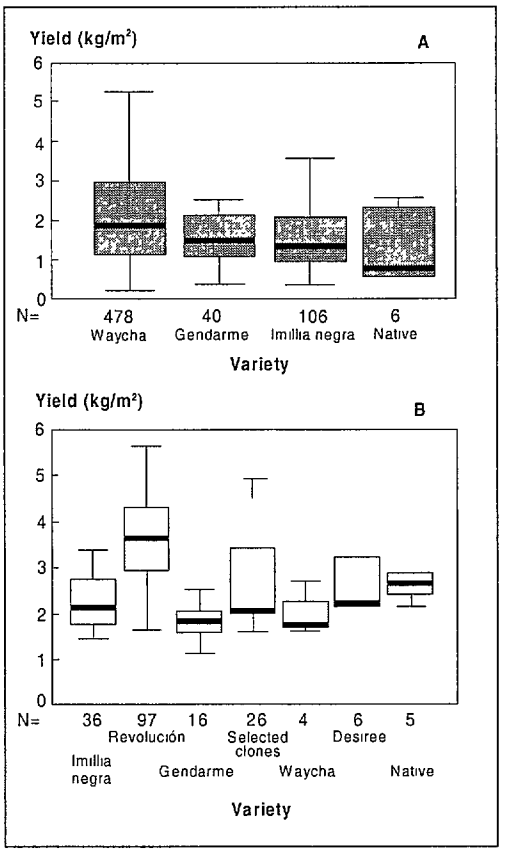

Figure 2. Seedbed yields in Bolivian highlands. (A) Average of 630 seedbeds by cultivar, northern Potosi, 1996 and 1997. (B) Average of 190 seedbeds by cultivar in central Potosi, 1995, 1996, and 1997.

It appeared from the follow up of several multiplication cycles of potatoes produced in seedbeds with the three case study farmers that small tubers from the first multiplication in the seedbed were kept to be planted in the seedbed the next season. Larger ones were set aside for field planting or for sale as seed to other farmers (Figure 3). The multiplication rate in the seedbeds varied from 1:6 to 1:41 with an average of around 1:15. In the field, the multiplication rate ranged from 1:5 to 1:14 with an average of 1:7. In Loyaza and Tapacari, farmers started to sell seed after one field multiplication. The farmer from Tapacari had the highest multiplication rates in seedbeds and in the field. He sold 300 kg of seed after one field multiplication and produced 3.5 t of potatoes after the second field multiplication. In Kollana, the farmer kept all his material until the third field multiplication and produced more than 7 t of potatoes from the initial 5 kg of seed planted in the seedbed.

Economic evaluation

The construction costs of the seedbeds varied between different areas and with the adaptations made by farmers. The labor costs to build the seedbeds varied from US$20 to US$31 by seedbed depending on the care taken in the construction and the distance farmers had to bring clean soil for the seedbeds. Cash costs for materials, mainly for the plastic cover, varied from US$25 to US$40 according to farmer's adaptation of the system. In some cases, farmers replaced the plastic sheets with empty fertilizer bags reducing the cash costs to around US$15. The effect of the type of cover on yield depends on the weather conditions, the plastic cover helps to maintain a higher average maximum temperature in the seedbeds which allows a faster development of the crop and also some protection against frost. But it was observed that the fertilizer bags were as efficient as the plastic cover and they also protect the crop from frost. With an external

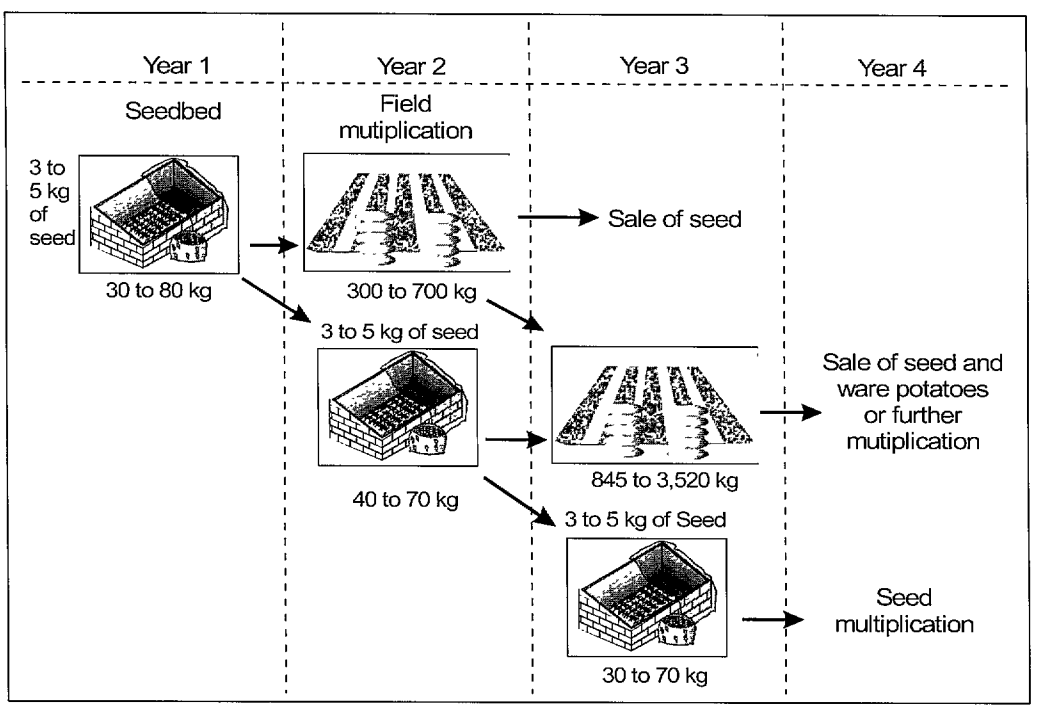

Figure 3. Seed flow from the seedbed combining multiplication in seedbeds and in open fields. Results from three case studies, 1994 to 1997.

temperature of -2.5°C, there was no significant difference in yield in the seedbeds between the two types of covers (Villalobos, 1998).

The production costs in the seedbeds varied between US$6.30 and US$23.90 per seedbed depending on the inputs used: seed, fertilizers and pesticides, and labor. Labor costs in some cases, are substantially increased because of the need for irrigation during periods of drought.

Considering the construction costs and the potato production costs in the seedbeds, the cost of the seed obtained in the seedbeds can be compared to the cost of the seed from the formal system. An opportunity cost was given to labor at the rural wage rate and construction costs were distributed over the four-year life of the seedbed and the cover (Table 1). A more realistic seed cost was calculated by valuing labor at an opportunity cost of 50% of the rural wage, reflecting the scarcity of local employment opportunities (Table 2). The price of the basic seed in 1996 was US$0.70/kg in the centers of supply. The real price to farmers is at least 10% more, because of transport and transaction costs associated with purchasing this seed in a distant location.

The analysis shows that even farmers with average productivity can produce seed in the seedbeds at a cost equivalent to or less than the price of basic seed. The most efficient farmers can produce seed much more cheaply than the basic seed price (Tables 1 and 2). In addition, the seedbeds make farmers less dependent on the formal seed system with all its uncertainties: it guarantees them access to seed of the cultivar they want when they need it. Compared to the formal seed system, in which most farmers buy more than 100 or 200 kg of seed at a time for field multiplication, the seedbed system means less financial risks. This is a great advantage for small farmers with limited financial resources.

Table 1. Seed production costs in the seedbeds (US$).

	Annualized construction costs		Production costs		Total Costs		Total
	Labor	Material	Labor	Inputs	Labor	Inputs + mat.	
Minimum	5.0	6.3	6.3	5.0	11.3	11.3	22.6
Maximum	7.8	10.0	23.9	8.0	31.7	18.0	49.7
Average	6.4	8.1	14.4	6.5	20.8	14.6	35.4

Table 2. Cost of seed at different productivity levels and based on two labor opportunity costs in 630 seedbeds, 1996 and 1997 (US$/kg).

Productivity kg/seedbed	Seed cost:opportunity cost (50% rural wage)			Seed cost: opportunity cost (0% rural wage)		
	Average	Minimum	Maximum	Average	Minimum	Maximum
8.75 (minimum)	2.9	1.9	3.9	1.7	1.3	2.1
98.3 (maximum)	0.3	0.2	0.3	0.1	0.1	0.2
34.5 (mean)	0.7	0.5	1.0	0.4	0.3	0.5

The evaluation carried out in Loyaza, La Paz, on the performance of seed produced in the seedbeds as compared to farmer's seed, showed that seed from the seedbeds was more productive than farmers' seed. It gave some farmers an acceptable return on the additional cash investment after just one field multiplication (Table 3). There is need to continue to monitor the performance of the seed from the seedbeds to determine with more precision the economic advantages of the system under different conditions.

Another advantage of the seedbeds is that farmers use them to grow other crops and protect them from frost when it is too late for these crops in open fields. The extra production means extra income and better food for the family.

Farmers' evaluation

Of the 305 farmers interviewed in northern Potosi, where more beds were installed, more than 95% accepted the seedbed technology, 74.5% are interested in building more seedbeds, and 27.5% have already installed a second one (Loredo and Choquehuanca, 1997). Eighty-four percent had set aside a specific plot in open fields to multiply the seed from the seedbeds. Some constraints were also mentioned. Access to healthy seed for the seedbeds was mentioned by 80% of the farmers. They want to be sure that in the future they will have access to good seed for their nurseries. Another aspect of concern for 70% of farmers is the replacement of the substrate of the seedbeds as fertility declines and pests build up after a number of years of use. The best technical option available to avoid contamination is to remove the substrate and replace it by a clean one. But that implies a lot of work and clean soil, which is not always available. The plastic covers, which deteriorate rapidly and are costly, concerned 69% of farmers. Some farmers have already found alternatives to the plastic covers as mentioned above. Farmers are generally enthusiastic about seedbeds, because their use gives them the opportunity to use improved seed, and they have a technical tool they can manage themselves.

Normally, men build the seedbeds, but they later often migrate in search of seasonal off farm work leaving the women in charge of seedbed management. Women play a significant role. In 1997, PROINPA oriented training activities to women; and out of 790 participants in training activities, 252 were women. They were very keen to learn new techniques or technologies for potato production and are requesting more training support.

Conclusions

The seedbed is a simple technology to renew farmer's seed and improve potato productivity that has been used by many farmers in the highlands where the technology was validated. Farmers adapted the

Table 3. Agroeconomical evaluation of seed produced in seedbeds of 9 farmers, compared with farmers' seed, after one field multiplication, Loyaza, Bolivia, 1995-97.

	Seedbed yield (kg/m^2)	Field production (t/ha) Seedbed seed	Farmer seed	Marginal rate of return (%)
Maximum	3.3	12.0	8.4	163
Minimum	1.7	4.7	3.1	73
Average	2.3	8.1	5.4	118

seedbed design to reduce construction costs and make them easier to manage. Farmers have also explored growing other crops in the seedbeds after potato such as flowers, vegetables, or fodder. Some of them have tried alternative propagation methods such as sprout cuttings to plant their nurseries. Others had their seedbeds certified by the Seed Certification System and began producing certified seed of native cultivars.

Seedbed technology is a vehicle for helping farmers to learn technical practices for more efficient crop management. Because women and children share responsibility for seedbed management, there is scope for working in closer collaboration with them and training them in potato and seed production techniques.

Based on the experience gained in validating the technology in this study, there are still some constraints to be resolved, including fertility of the substrate, control of soil pests (nematodes) and diseases, access to healthy seed to plant the seedbeds, and marketing of seed originated from the seedbeds after field multiplication. It will require more research to develop more efficient methods to control soil pests and maintain substrate fertility. Research is already underway to evaluate crop rotation and composting in the seedbeds.

A strategy needs to be developed with development institutions to supply healthy seed for the seedbeds and to reach the farmers of the informal system. Indigenous marketing channels should be taken into consideration and better used to link the formal to the traditional systems (Bentley and Vasques,1998). There is also a need to continue technical follow up in collaboration with NGOs and farmers' communities, emphasizing gender implications, postharvest activities, seed multiplication in open fields, and seed marketing for those who want to specialize in that area.

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Intensification of Potato Production in Rice-Based Cropping Systems: A Rapid Rural Appraisal in West Bengal

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Since the beginning of the green revolution in the mid-1960s, the growth in cereal production in South Asia has been spectacular. Recently, the longer-term sustainability of these productivity gains has been questioned. Emerging evidence on stagnating yields, declining factor productivity, and increasing intensification-induced land degradation is used to make a case for the importance of threats to sustainability (Pingali et al., 1997). The rice-wheat sequential cropping system, which is practiced on 12 million ha in South Asia, has been a focal point for diagnostic research on sustainability-related issues (Fujisaka et al., 1994).

The rapid expansion of potato production has also been impressive, if largely unnoticed, in the irrigated lowlands of South Asia. In 1997, India alone produced more than 20 million tons of potatoes. The bulk of this production takes place on the Indo-Gangetic Plain where potatoes often follow rainy-season rice. Rice-potato sequential cropping systems are increasingly common in Pakistan, Nepal, Bangladesh, China, and Vietnam.

This research is part of a new CIP project which aims to assess the scope for and enhance the possibilities of the sustainable intensification of potato production in cereal-based cropping systems in the subtropical lowlands of Asia. The project addresses the following issues: (1) the potential for intensifying potato production; (2) the extent of crop replacement or displacement effects when potato is introduced into diverse cropping systems; (3) interactions between potatoes and other crops in the system; (4) implications of intensifying potato production for natural resources management; and (5) the identification of research to overcome problems of location specificity.

We begin our inquiry with exploratory diagnostic research in the form of a rapid rural appraisal on the sustainability of the rice-potato sequential cropping systems in West Bengal. This is the most impressive example of the expansion of potato production in the subtropical irrigated lowlands of Asia. To set the stage for the rapid rural appraisal, we provide background information on the rationale for focussing on the rice-potato-rice cropping system, on production trends in West Bengal, and on the behavior of potato prices which were foremost in the minds of farmers at the time of the field work.

Rationale for Investigating the Sustainability of Rice-Potato-Rice

In May 1997, a "brainstorming session" was held in Shimla at the headquarters of the Central Potato Research Institute (CPRI) to obtain baseline information on potato-based diversification in the Indo-Gangetic plain. The meeting was well attended not only by potato scientists and directors from

1 Directorate of Agriculture, West Bengal, India.
2 CIP, Lima, Peru.
3 CIP, New Delhi, India.
4 CPRI, Patna, India.
5 AB-DLO, Netherlands.
6 IFDC/CIP, Lima, Peru.

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the Indian Council of Agricultural Research (ICAR) but also by several ICAR scientists from the rice and maize programs. Participants, who represented three broad regions of the Indo-Gangetic Plain, described common and emerging cropping systems. In total, more than 15 different cropping systems, featuring potato, were identified. For most of these, wet-season rice preceded potato. Potato had also found a home in other cereal-based systems. For example, an intercrop of maize/potato is growing in popularity in Eastern India.

No one cereal-based potato cropping system appears to account for more than 40 to 50% of potato production in the Indo-Gangetic Plains of India. In relative terms, no single cropping system incorporating potatoes is as common as rice-wheat. On the other hand, two rice-based cropping systems that include potato exhibited good potential for systems and natural resource management implications. One was rice-potato-sunflower, which is increasingly popular in northwestern India. The other was rice-potato-rice that was felt to be very productive, but was viewed as intensive in its demand for water. Hardpans from puddling rice were also thought to compromise the productivity of the system over time. Some anecdotal evidence suggested that potato yields were declining. For these reasons and because of its popularity across several countries, rice-potato-rice was singled out for our investigation, which began with a rapid rural appraisal (RRA) in West Bengal, where this system is most widely practiced.

Production and Price

Over the past 20 years, irrigation capacity has increased rapidly fueling the expansion of boro (summer) rice and opening up opportunities for triple cropping. In only one decade from 1985 to 1995, the area in boro rice has doubled from about 0.5 to 1.0 million ha (Directorate of Agriculture, 1994 and 1996).

Other rabi (post rainy season) and summer (non-rainy) crops have also benefited enormously from the increasing availability of irrigation. Wheat area increased fivefold in the Green Revolution Decade from 1966-1976 (Figure 1). Yields more than doubled in five years (Figure 2). Mustard acreage rose dramatically in the mid-1980s in response to a doubling in price. Mustard yield has increased slowly from a very low base. Steady expansion of potato area and progress in intensifying yield has resulted in sustained growth in production (Figures 1 and 2). Sesame, a summer oilseed crop, has also expanded rapidly.

This robust growth in potato production has been achieved in spite of strong price seasonality and cyclical price risk. The main harvest on the Plains occurs in February and March. Temperatures rise steadily until the onset of the southwest monsoon in June. Traditional storage is not an effective option from mid-April onwards, and cold storage is costly. Prices rise until the rainy season crop is harvested in October. Periodically, such as in 1992, this typical seasonal price movement, which makes cold storage profitable, is not manifested (see Figure 3). Supply substantially exceeds demand, and, in subsequent months, prices do not recover from their harvest season low. The depressing effect on prices of a very large increase in production was dramatic in 1997. Area planted to potatoes in West Bengal reached a record high of about 315,000 ha in 1996-97, up from the previous high of 255,000 ha the year before. With this background, it was not surprising that production problems were not foremost in the minds of farmers when we carried out the rapid rural appraisal in 1998. When asked about potato-related problems, the previous year's low prices and limited cold storage availability dominated the conversation.

The 1997-98 growing season was a return to normalcy. Indeed, potato prices have rebounded to set new highs for the

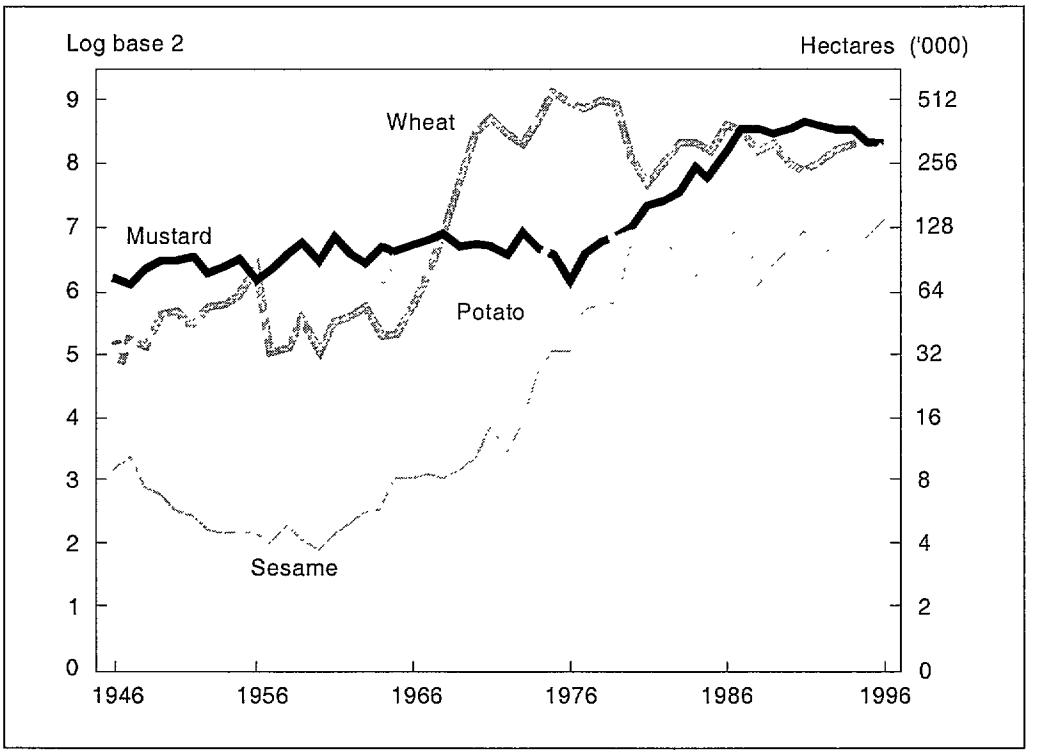

Figure 1. Area of selected post rainy season and summer crops in West Bengal, 1946-47 to 1995-96. (Source: Directorate of Agriculture (1994 and 1996).)

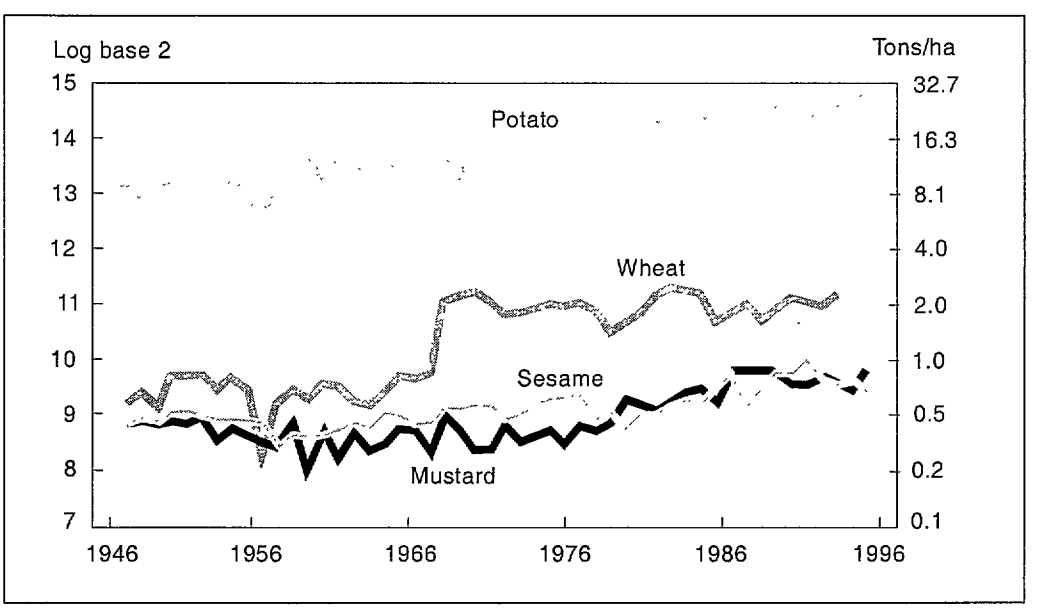

Figure 2. Yield of selected post rainy season and summer crops in West Bengal, 1946-47 to 1995-96. (Source: Directorate of Agriculture (1994 and 1996).)

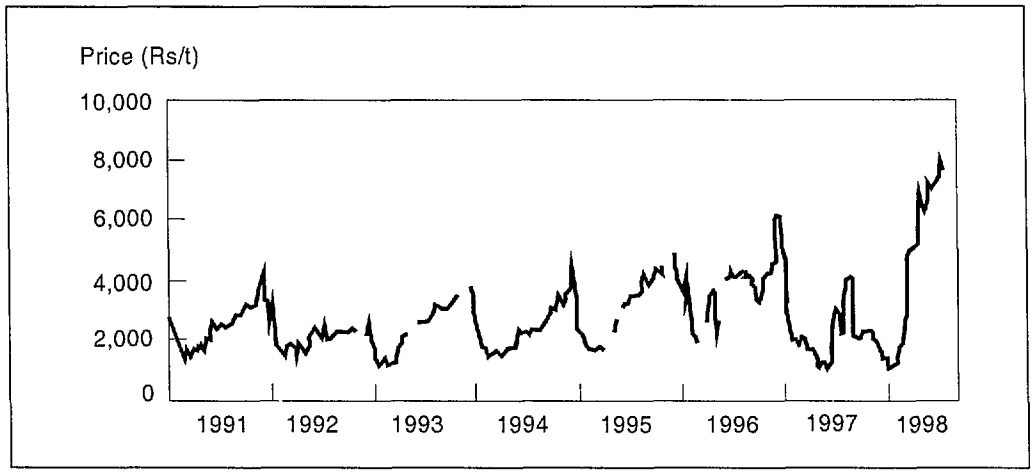

Figure 3. Real prices (1990 = 100) by week in the Calcutta wholesale potato market, January 1991 to July 1998. (Gaps indicate missing data.)

1990s (Figure 3). The 1996-97 experience will cause a major hiccup in the expansionary path of potato production in West Bengal, but it should not substantially affect the fundamentals responsible for the steady upward trend in production.

The Rapid Rural Appraisal

The rapid rural appraisal was patterned after similar diagnostic research on rice-wheat, particularly the Harrington et al. (1993) report on this cropping system in Karnal and Kurukshetra districts in Haryana. The diagnostic research featured two interdisciplinary research teams of NARS (national agricultural research system) and IARC (international agricultural research center) scientists.

Potato production in West Bengal is concentrated in Midnapore, Hooghly, and Burdwan districts. Villages in those districts were visited over a two-week period in late January and early February 1998 prior to the harvest. Group interviews were complemented by visits to potato fields in the village. Seventeen villages were visited with the assistance of staff of the Directorate of Agriculture of the State of West Bengal. The area planted to rice-potato-rice and proximity to a Block Development office were the criteria for village selection.

Findings and Prospects for Sustainable Diversification

The five cropping sequences described in Figure 4 are broadly representative for the surveyed villages. Pulses, jute, and vegetables can also figure in these rice-potato sequential cropping systems. Cropping patterns almost always start with a crop of aman (rainy season) rice. The aman rice-potato-sesame sequence is most popular, particularly in Midnapur where heavier clay soil is not as common as in Burdwan and Hooghly. Any serious limitation in water supply or in soil-available water capacity because of lighter, sandier soil confines summer cropping to sesame. If water is somewhat limiting, aman rice-potato-boro rice can still be taken, but an earlier maturing rice variety such as IR-36 is grown instead of Swarna Mahsuri. When water is non-limiting, farmers favor Swarna Mahsuri, which subsequently delays the production of boro rice by about 15 days. This cropping sequence is the farmer's preference for maximizing returns and productivity (Directorate of Agriculture, 1992). A few farmers who plant potatoes harvest them early at 75 to 90 days for sale on the fresh market. When potatoes are harvested early, boro rice is planted on time. Potatoes do not enter into the cropping sequence when soils are too

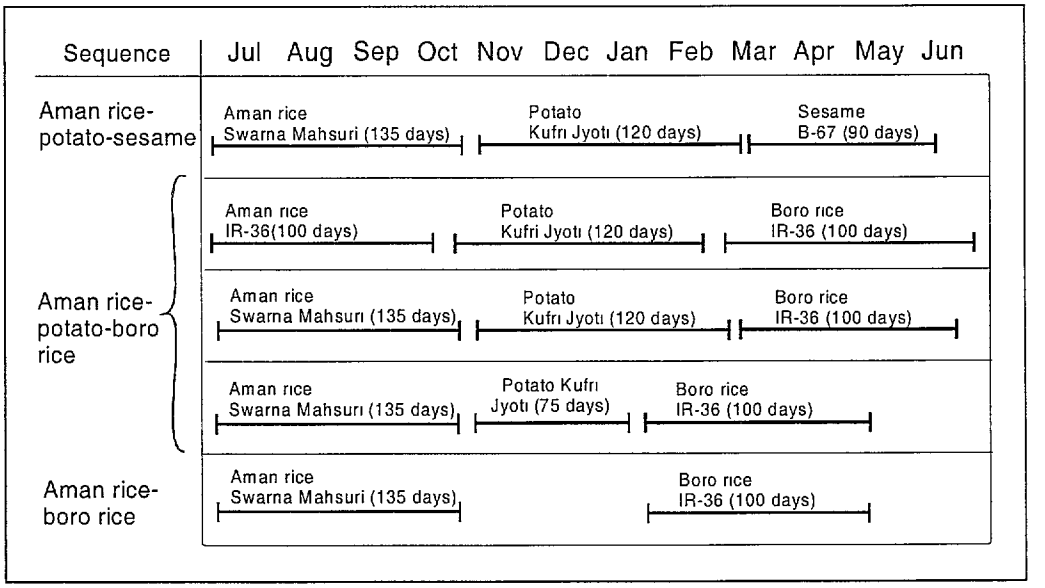

Figure 4. Typical rice and potato cropping sequences in the surveyed villages.

heavy or in areas where drainage is problematic. These areas are restricted to the double cropping of rice.

The most surprising feature of the sequential cropping systems depicted in Figure 4 is the dominance of a moderately long-duration rice variety to start the sequence. The cultivar of preference in the rainy aman season is still Swarna Mahsuri, a 135-to-140-day variety characterized by high yields, good cooking quality, and wide adaptability. Earlier maturing varieties, such as IR-36 are available, but farmers are willing to accept lower boro productivity if water for the summer season is readily available. This strong preference for a moderately long-duration rice variety to initiate a triple cropping sequence suggests that the conventional wisdom about the catalytic role of high yielding varieties of rice in facilitating the place of potatoes in the cropping system is somewhat misplaced.

The optimal planting time for potato is mid-November, and the turnaround time between aman rice and potato is 10-15 days depending on soil texture. Therefore, rice varieties of durations shorter than 120 days are not needed for the aman planting if irrigation is readily available in the summer season. Nonetheless, the preference for later maturing Swarna Mahsuri does increase the premium for reducing turnaround time in planting potato after aman rice.

Replacing a cool dry season fallow with potatoes to arrive at a triple cropping sequence is characterized by both positive and negative interactions for the following crop. Positive benefits take the form of cost savings in fertilizer use on boro rice and sesame. On a negative note, farmers believe that insect and disease infestation is higher on both rice and sesame when these summer crops are preceded by potatoes than when they are sown after seasonal fallows.

Over the past decade, potato yields have increased from about 15 to 25 t/ha. Farmers attribute this growth in potato productivity to more intensive use of inorganic fertilizer, better seed quality, and improved crop management. Fertilizer doses are high. During the last 3 or 4 years, fertilizer

intensity has hit a plateau, and farmers feel that gains from increasing fertilizer use are exhausted. In the majority of villages, use of farmyard manure is declining. To some extent, oilcake is purchased to substitute for manure.

Unlike the rice-wheat double crop, weeds are not a problem in the rice-potato-rice triple crop. Weed infestation was only readily visible in the village with the largest holding size. There was scant evidence of intensification-induced degradation.

Inserting potato before boro rice delays the planting of boro rice by about 15 days and substantially increases the demand for water with rapidly rising temperature in April and May. Groundwater is recharged during the rainy season, but is perceived to be seasonally declining during the warm summer months when boro rice is cultivated. A declining groundwater table appears to be less problematic in West Bengal than in the Punjab where seasonal recharge is considerably less. Nonetheless, water for irrigation is heavily subsidized, and the resource cost of delayed sowing of boro rice following potato is equivalent to about five irrigations.

The prospects are bright for planting more area to potato after wet season rice in the specialized potato-growing Midnapore, Burdwan, and Hooghly districts of West Bengal. As the 1997 slump in potato prices suggests, cyclical price risk can temporarily limit area response, but such periodic setbacks should not compromise the strong growth in area that has occurred in recent decades. Mustard is often grown rather than potato because of the government's protective policy on oilseed crops. This policy results in more area being planted to mustard than would otherwise be the case. Liberalization of oilseed imports should stimulate area response in potatoes. State and central government regulatory policies on cold storage and on the establishment of potato processing plants may also adversely affect the demand for potatoes. Adequate road infrastructure should also contribute to the strong growth in area response.

Increased area in potato will not be confined to the rice-potato-rice system. Declining seasonal groundwater availability will be an increasingly important constraint to the stability and expansion of that system. Prospects are brighter for the expansion of rice-potato-sesame which is less intensive in its use of water.

The expansion of potato area in West Bengal has not come at the expense of alternative crops. Increasing potato area has been contemporaneous with the expansion of irrigation. The rice-potato-rice sequence appears to be a more natural agronomic fit than rice-wheat. In contrast to wheat, crop stands of potato following puddled rice are definitely not a problem. The wet season rice crop does not unduly delay the planting of potato. Potato in the rice-potato-rice system resembles rice in the rice-wheat system in the sense that other crops in the seasonal rotation do not compromise its productivity. By the same token, boro rice takes on the role of wheat in the rice-wheat system. With potato, the sowing of the boro rice crop is delayed and pest and disease incidence is perceived by farmers to be higher than in a rice-rice double crop. Nonetheless, this rapid rural appraisal reinforced the impression that the negative productivity effects of potato on boro rice in the rice-potato-rice system are smaller than the adverse productivity consequences of puddled rice on wheat.

Longer-term threats to sustaining the expansion of potato production in these specialized potato-growing districts of West Bengal are not imminent. No farmers stated that potato productivity was declining over time. Evidence for intensification-induced land degradation is scanty. Hardpans were only cited as a problem in one village, and hardpans are desirable for irrigation efficiency in the production of puddled rice. Water for irrigation, particu-

larly seasonal groundwater availability, will become scarcer if over-utilization continues. But the casualty from the failure to price water according to its scarcity value will be boro rice and not potato. Farmers in several villages no longer produced boro rice when government authorities imposed seasonal irrigation restrictions. Nitrate leaching resulting in groundwater pollution could be a consequence of the relatively high doses of inorganic fertilizer applied in the intensification of potato production. However, no one said that nitrate leaching was a problem. (At the time of this rapid rural appraisal, arsenic poisoning was the main concern in the contamination of drinking water in some restricted areas in West Bengal.)

We observed that maintaining the historical growth rate in yield will be the most difficult proposition to sustain in the intensification of potato production in West Bengal. Average on-farm yields of 25 to 30 t/ha may be approaching the productivity potential of growing potatoes in short-day conditions. Biotic and abiotic stresses are not significant yield reducers. Seed quality is reasonably good and inorganic fertilizer is readily available. Improving irrigation and crop management and seed quality further could leverage some gains in productivity and there may be some scope for savings in fertilizer, but in general, we were hard pressed to identify production constraints whose solution would translate into substantial gains in productivity. With limited scope for irrigation expansion, an expected decline in the positive growth rate in yield is a cause for concern.

The productivity status of rice-potato-rice in West Bengal contrasts sharply with Bangladesh, Vietnam, and South China where the same cropping system is observed. In these areas, solving the seed quality and availability problem could easily result in yield increases of five tons or more.

Priority Research Areas and Future Directions

Following the implementation of the rapid rural appraisal, we arrived at a consensus on specific topics for future research. Three or four candidate topics were listed for each of the more general areas of productivity, sustainability, and demand. Most candidate topics related to the need for focused diagnostic research. This list of priorities has guided applied research that started in the 1998-99 cropping season.

Research and training in modeling some of the sustainability dimensions of growing potatoes in short-day irrigated conditions also began in 1998. Such modeling will figure more prominently in this project in the future as will a wider regional participation of countries of the subtropical lowlands of Asia where potatoes increasingly contribute to the cash income of small farm households and to the diversification of the diet of consumers.

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On-Farm Profitability of TPS Utilization Technologies

A. Chilver[1], T. Walker[2], V. Khatana[3], H. Fano[2], R. Suherman[4], and A. Rizk[5]

Poor tuber seed quality is often cited as the most important factor limiting potato productivity in developing countries (Rasco, 1994). Improving tuber seed quality and availability is institutionally complex in the tropics and sub-tropics. Progress of public-sector tuber seed programs has usually been slow and disappointing even in countries where sites for seed multiplication are agroecologically attractive (Crissman, 1987). True potato seed (TPS) is a captivating technological alternative that offers farmers an option to overcome the abovementioned weaknesses of clonally propagated tubers as a source of planting materials. Side-by-side comparisons of a jar of TPS with 20 100-kg bags of clonal planting material—the amounts needed to plant one hectare—are visually compelling about the potential of the technology.

Although the investment in agricultural research and extension of TPS technologies is small compared with the amount spent on clonal seed technologies and selection systems, sufficient experience has accumulated, largely over the past 20 years, to review achievements, shortcomings, and future prospects (Almekinders et al., 1996; Simmonds, 1997). "At present, there are few potato-producing countries in the developing world where TPS has not been tried, or suggested as a means to alleviate seed problems (p. 290, Almekinders et al., 1996)." One of the deficiencies in this experience has been the lack of documentation of on-farm performance with farmer management (Simmonds, 1997).

We address this large gap in the literature by reporting the results of on-farm research in Egypt, India, Indonesia, and Peru conducted in the mid-1990s. The research design is the same in the first three countries where farmers are experimenting with TPS technologies in the initial stages of acceptance or rejection. The Peruvian results are based on farmer-managed, on-farm trials.

Sampling and Data Collection

Sites in Egypt, India, and Indonesia were chosen based on farmers' experience with TPS utilization technologies. TPS farmers were stratified by wealth group based on asset holdings, mainly land, and a random stratified sample was taken.

The unit of observation was the field. One field planted using a TPS technology was monitored during the growing season. The point of reference for comparative inference was a neighboring or nearby field planted to conventional seed tuber technology. For those TPS farmers without a tuber-seed field available for comparison, a nearby field of another farmer was chosen.

An integrated production questionnaire combining survey responses and field measurements was canvassed. Field visits were made at planting, 45 days after planting, harvesting (twice), and postharvest marketing. Seed rate, yield, and tuber size were measured. Local market data were collected weekly on seed and ware prices.

The format of data collection in Peru was in the spirit but not to the letter of data collected in the other three countries. Data in Peru refer to more structured on-farm trials with two treatments in fields

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2 CIP, Lima, Peru.
3 CIP, New Delhi, India.
4 Lembang Horticultural Research Institute, Lembang, Indonesia.
5 Agricultural Economic Research Institute, Gharbia Govermorate, Egypt.

approaching one hectare in size. Fields in ten village locales were monitored.

Comparative evaluation was carried out in nine sites for TPS seedling tubers and in two of the three sites where there were sufficient observations to carry out an analysis of TPS transplants. Sites are described in Table 1. Almost all sites contained multiple locations comprising several or many villages. Although a minimum of 15 to 25 plots per site was the goal, the total number of TPS fields ranged from 13 to 99. Experience with and availability of TPS in the region significantly influenced sample size.

Results

The economic assessment shows that TPS has mixed prospects. Of the nine generalized locations, TPS seedling tuber technology was most profitable in Chacas, Peru, quite attractive in the northeastern hills of India and the Nile Delta of Egypt, and marginally profitable in the northeastern plains of India (Figure 1). In the other five sites, farmers lost the equivalent of more than US$100 per hectare (relative to clonally propagated material) by investing in seedling tubers. (Because of the small areas used to test TPS, no farmers lost a significant amount of money on the technology.)

The comparative profitability of TPS transplants hinges on whether or not the output is destined for ware or seed use. Production from TPS transplants was only competitive if the smaller-sized output was retained or sold for seed (see the hollow point estimates in Figure 1). Destining all output for ware consumption in the same year was a losing proposition (the solid point estimates for India NEH (TP) and NEP (TP) in Figure 1). Demand for TPS as transplants should be strong in India's northeastern hills. There, TPS technology has a clear economic advantage over clonally propagated material by about $500/ha. Transplants grown for tuber seed offer an attractive benefit. The fate of transplants on the northeastern plains is more problematic because the economic advantage of TPS seedling tubers was only about $60/ha. At this lower level of profitability, it is unlikely that the derived demand for transplants could be sustained.

Table 1. Description of recent on-farm research comparing TPS technologies with clonal seed tubers.

Country	Agroecology		Fields		
		Farmers	Clonal seed tubers	TPS seedling tubers	TPS transplants
India	Northeastern plains	119	99	99	34
India	Northeastern hills	24	20	15	8
India	Northcentral plains	22	17	17	0
India	Western arid zone	11	10	13	3
India	Deccan Plateau	14	11	14	0
Egypt	Desert	7	3	13	0
Egypt	Delta	40	26	42	0
Indonesia	Highlands	67	32	45	0
Peru	Highlands	11[a]	11	11	0
Total plots			229	269	53

[a] groups comprised of 197 farmers.
Source: Chilver (1997).

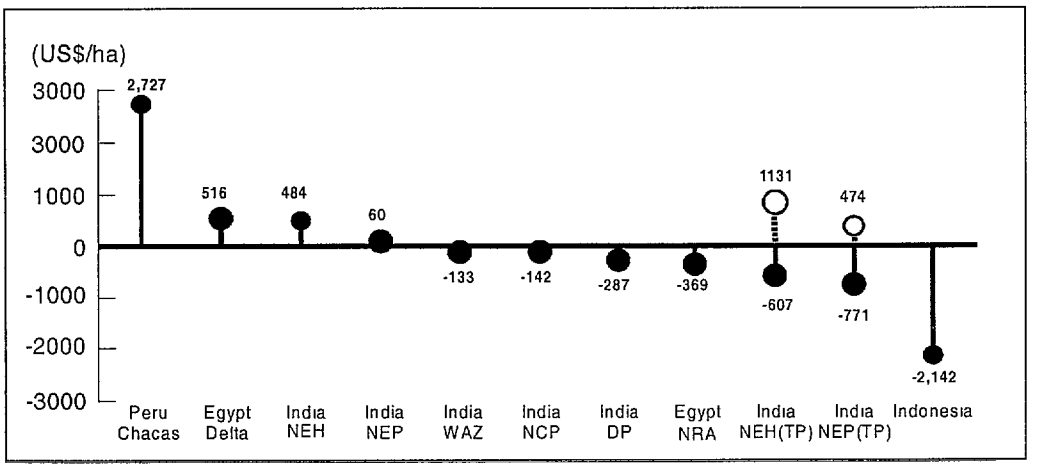

Figure 1. Difference in net economic benefit (US$/ha) of TPS technologies from clonal tuber seed. (Source: Chilver 1997.)

Yield

With a few notable exceptions, the conventional wisdom about the economic advantages and disadvantages of TPS relative to clonal tuber seed was confirmed. The symmetrical pattern in Figure 2 of yield differences between the two technologies suggests that productivity on aggregate was pretty much the same. Average seedling tuber yields were markedly higher in the Peru site, significantly lower in the highlands of Indonesia, and not significantly different from average yields of clonally propagated material in the other seven locations. The Indonesian results were driven by higher rates of yield deterioration over time for seedling tubers compared with the dominant clone Granola that demonstrated a slower rate of productivity decay. The large yield advantage of the variety Chacasina in Peru was attributed to loss of stand in clonally propagated material in a dry year. In 1997-98, these yield differences in Peru disappeared in a wet year in a more commercialized setting for production across 14 locations.

TPS transplants yielded fairly well at levels between 15 and 20 t/ha in both the northeastern plains and the northeastern

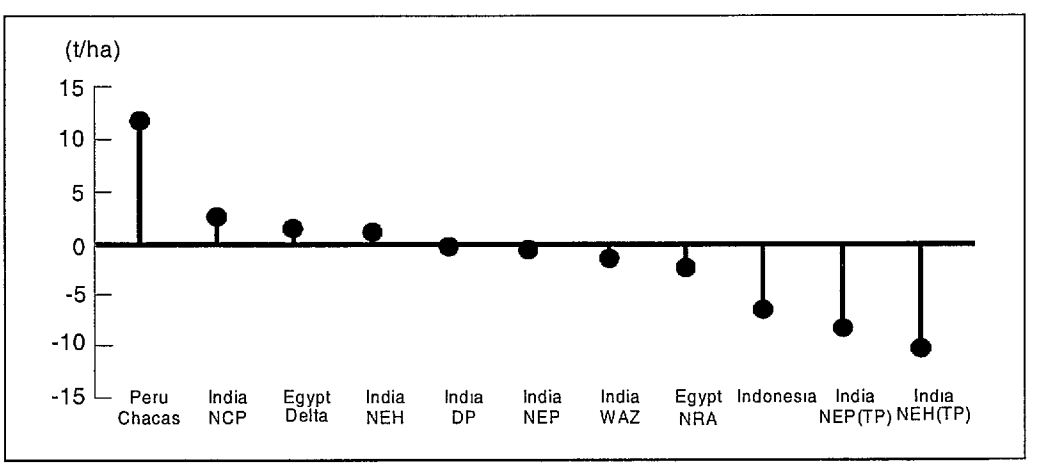

Figure 2. Difference in yields (t/ha) of TPS technologies from clonal tuber seed. (Source: Chilver 1997.)

hills of India. However, farmers in the same regions were producing 25-30 t/ha with clonally propagated material. Cost savings would have to be huge or output prices substantially higher to compensate for a relative loss of 10 tons of yield.

The results strongly confirm that seedling tubers of good hybrids are high yielding at levels exceeding 20 t/ha; but so are competing clones. The estimated high yields of competing clones are the most surprising finding in this study. The lowest average yield of clonal material across the nine locations was a respectable 12 t/ha.

Seed costs

As expected, the savings in seed costs were a marked advantage for the TPS seedling tuber technology. The average savings in seed cost ranged from about US$10/ha on the northcentral plains of India to about US$400/ha in the northeastern hills. The difference in these two regions largely reflects differences in seed prices. Tuber seed in western Uttar Pradesh on the northcentral plains is readily available. But to reach the northeastern hills, the material is trucked across the plains up into the mountains of Assam. The remoteness of the northeastern hills and transport difficulties makes good quality tuber seed a dear commodity.

Lower seed rates contributed proportionally more to the savings in seed costs than did lower seed prices. Using TPS technologies, less seed per ha was needed in all the locations. But lower per unit prices for TPS seedling tubers were notable only in three settings, the northeastern hills and the Deccan Plateau of India and the highlands of Indonesia. The commercialization of seedling tubers by large dealers in Egypt led to substantially higher prices per unit of material for propagation; so much so that the advantage of a 1.8 t/ha lower seed rate with seedling tubers did not translate into an economic reality. However, in three of the nine sites, the savings of using TPS seedling tubers over clonally propagated material approached 50%. In general, it appears that 50% is a realistic estimate for the cost saving potential of TPS seedling tubers.

Output price

Partial budgeting results also support the hypothesis that replacing clonal tuber seed with seedling tubers is accompanied by a fall in output price. But output price discrimination against seedling tubers was not as widespread as expected.

Two of the expected considerations pointing to lower prices for the output of TPS seedlings did not materialize. Except for Peru where the TPS progeny matured earlier than the clonal check, farmers harvested the production from seedling tuber and the conventional seed technology at the same time; therefore, price differences associated with seasonality were not a factor. Only in Indonesia did the later maturity of TPS progenies result in somewhat lower (4%) prices relative to the early maturing variety Granola. Nor did we find tangible differences in prices between TPS and clonal output in the same grade classification. This positive finding for TPS indicates that the progenies are sufficiently homogeneous to compete in the marketplace in these countries where fresh table consumption is the dominant form of utilization. Indeed, farmers commented that the shinier offspring of seedling tubers were even slightly preferred in some locations.

The cause of price disparities between TPS and clonal seed technologies centers on the potential for TPS to result in a smaller distribution of tuber size. This disadvantage was most salient in the Deccan Plateau in Karnataka where the output of seedling tubers fetched about US$15 per ton less than the production of clonally propagated material. The bulk (or 85%) of the production of the dominant clone Kufri Joyti belonged to the grade 2 category; while 75% of the output of seedling tubers was destined for the

smaller-sized grades 3 and 4. Farmers in Karnataka display a strong preference for fewer, but larger-sized, more marketable tubers. An inferior distribution of tuber size was also a disadvantage of seedling tuber technology in Gujarat in the western arid zone and in Uttar Pradesh in the northcentral plains of India. In these high-yielding regions, price differences of 8 to 12% may not seem that large, but they are equivalent to differences in net benefits of US$300 to US$400 per hectare.

Changes in other costs did not unduly affect the outcomes of the comparative profitability of the two types of potato propagation technologies. Only Indonesia realized large savings in fungicide cost. There, TPS progenies were more resistant to late blight than Granola, the dominant cultivar, but the longer duration of the TPS progenies increased the time of application; thus, the scope for cost savings was somewhat less than anticipated.

Sensitivity analysis

A simple sensitivity analysis was conducted to illustrate the most important variables in conditioning the comparative profitability of TPS seedling tuber technologies. Three possible improvements were tested: a reduction of 10% in the cost of seedling tubers; a 10% higher yield; and a 10% increase in the size distribution of output from the small to the large-sized categories. The analysis showed that proportional changes in yield and in the tuber size distribution are much more effective in increasing TPS benefits than proportional changes in seed costs.

Empirical Rules of Thumb

TPS utilization technologies presently are not sufficiently well developed to replace clonal propagation systems in large potato-growing regions of developing countries, although some places at some times would appear to be ripe for their deployment. Are there any empirical rules of thumb that would predict success so as to encourage more effective targeting of research and extension effort? In other words, can we find a good predictor of TPS profitability solely with information on the economic performance of clonal propagation systems? The response to this question appears to be yes: the cost of propagation material divided by the value of production is a reasonably good predictor of TPS performance when significant yield effects between the two types of technologies are absent.

This result is shown in Figure 3 for the seven locations where the yield differences in Figure 1 are not substantial. The scatter of the average values in Figure 3 suggests a linear association between the quotient of seed cost to value of production and change in net benefits between TPS and clonal propagation systems. The break-even point for the economic profitability of TPS utilization technologies is equivalent to seed cost comprising 19% of the value of clonal production. A value of 22% equates to an economic gain of US$200 per hectare.

Basing a decision rule on so few observations is risky, but the intuition behind the relationship depicted in Figure 3 is appealing. The quotient is comprised of two ratios: inverse of the multiplication ratio; and the seed:output price ratio. Clonal propagation systems with higher seed:output price ratios and lower multiplication ratios will generate higher values for seed costs to the value of production. Neither of these rules is as closely correlated with economic performance as is their combination in the suggested quotient.

As a point of reference, in the Red River Valley of North Dakota in the United States the value for this quotient is about 8 to 10% indicating a very effective seed system. Higher values signal more inefficiencies in the clonal seed system. Advances in TPS utilization technology will shift the relationship depicted in Figure 3 to the left; improvements in the clonal seed system is tantamount to observations sliding down the line.

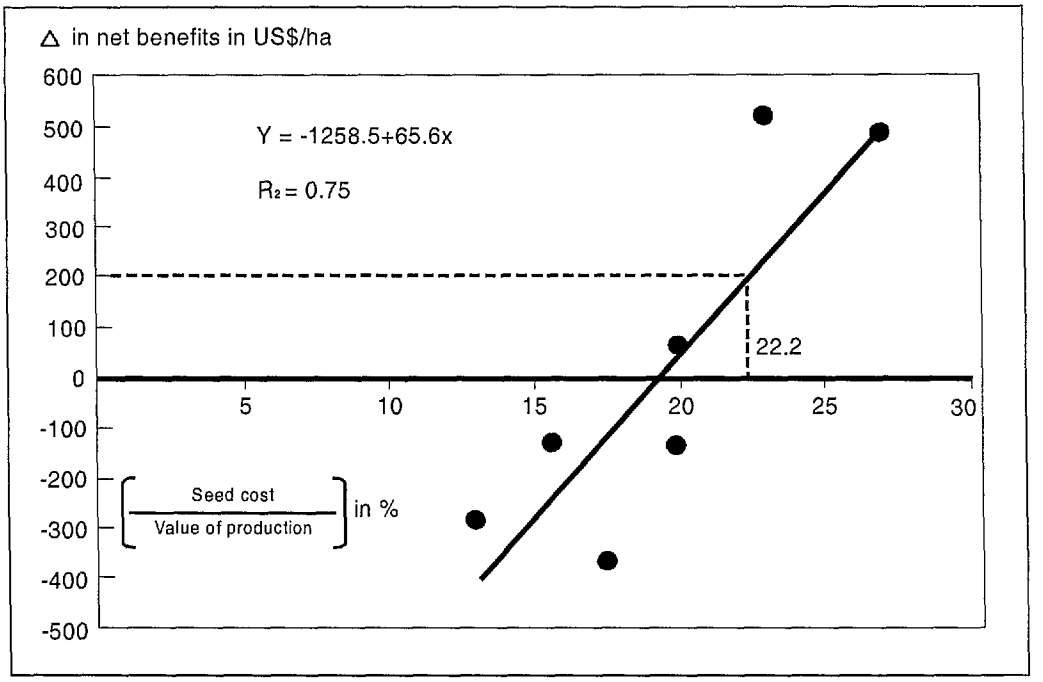

Figure 3. Association between comparative profitability of TPS utilization technologies and seed cost as percent of value of production in clonal tuber seed.

Applying even this very simple empirical rule is not without difficulty, but the problems are not insurmountable. Estimates are needed on farmers' yield, seed rate, price of tuber seed, and price of output at harvest. There is no substitute to investing in well focused, albeit limited, diagnostic research in farmers' fields and in local markets to obtain these estimates. The temptation to use national or FAO data on yield levels and import data on seed costs should be resisted. Yield sampling in farmers' fields show that officially published estimates often underreport per hectare potato productivity by 30% to 100% (Pakistan-Swiss Potato Development Project, 1991; Terrazas et al., 1998). Imported propagation material is usually multiplied several times before it becomes cost effective to produce potatoes destined for the fresh market.

The Indonesian highlands is an apt example where the use of the wrong data can give spurious results on the prospects for TPS-related technologies. Combining national yield levels at 15 t/ha with an imported seed price at US$2,000/ha gives an estimate of 46% for our empirical rule of thumb. The farm-level data show a "true" estimate of 18% which is less than our 20% threshold value indicating that TPS is not nearly as promising a venture as published data would suggest.

Concluding Comments

These evaluations bring out two positive developments in TPS technologies. First, for a given distribution of tuber size, price differences between TPS progenies and clones were not statistically different. Indeed, at times the shinier output of seedling tubers fetched more attractive prices than the output of clonal seed. Second, the fact that these evaluations could be carried out indicates that the supply of TPS is not a problem or should not be considered to be a constraint in technology assessment. Sufficient material

is available internationally for the technology to take off.

The immediate problems related to TPS utilization technologies are on the demand side. Cost savings are not sufficient to leverage adoption. TPS technologies have to produce as much or more than clonally propagated tuber seed. Seedling tubers more or less meet this production condition, but significantly lower yields of transplants from botanical seed are a binding constraint to technology acceptance. Moreover, the distribution of tuber size has been highlighted as a critical variable for improving the design of both transplants and seedling tuber technologies.

The results of these recent evaluations again confirm that utilization of seedling transplants and tubers will only be economically viable in regions such as the Red River Delta of Vietnam where clonal seed availability and quality is severely limiting. But even in these identified regions one has to remember that the potential for clonal propagation systems is also changing. For example, in our earlier example of the Red River Delta of Vietnam, liberalizing the imports of clonally propagated material from China or investing in cold storage could substantially erode the attractiveness of TPS technologies. Egypt is another case where the economic fundamentals have changed in favor of the importation of tuber seed (Chilver, El-Bedewy, and Rizk, 1997).

Of the nine multi-locational sites in Egypt, India, and Indonesia, TPS appears to have the brightest prospects in the northeastern hills of India. Thus far the experience with TPS is heavily concentrated in Tripura. Monitoring the extension of TPS technologies from Tripura to other states, particularly Assam, in the northeastern hills is a research priority.

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Globalization Takes Root: Potato Trade in Latin America

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Much of the recent debate about the implications of increased trade liberalization and globalization for developing-country agriculture has centered on cereals, livestock and dairy products, and fresh fruits and vegetables. Despite its current ranking among the ten most important food crops in developing countries, potato is rarely cited for its trade potential—as imports or exports. In fact, current potato trade is much more important than FAO statistics indicate. Such data only report trade in fresh potatoes for human consumption and seed, leaving out from published figures trade in processed products such as frozen french fries, potato chips, and starch.

After a brief review of global developments, this paper analyzes recent trends in the trade of potatoes and potato products in Latin America. Results presented and issues identified for this region are intended to promote a greater appreciation for and interest in similar trends elsewhere. The overall intent of the paper is to demonstrate that: (1) for a variety of reasons trade already has—and is likely to become—an even more important influence on the evolution of potato production in some Latin American countries than has heretofore been the case; (2) policymakers and potato researchers in those countries should take appropriate action now to remain competitive in the years ahead; and (3) measures required to improve competitiveness will, of necessity, involve seeking new partners beyond those traditionally engaged in activities aimed at improving potato production for purely domestic sale and use in fresh form.

Materials and Methods

Results presented in this paper synthesize information collected from a wide variety of sources. These include published and unpublished FAO trade data; USDA trade statistics; rapid appraisals carried out in collaboration with cooperators in a number of PRECODEPA[2] countries; thesis research in Peru; informal interviews with industry and National Agricultural Research Institute representatives in a number of Latin American countries; and figures and analysis gleaned from the "gray literature", e.g., newspaper articles, unpublished reports, and theses collected during visits to a series of Latin American countries over the last several years; and, proprietary information for reports commissioned by the private sector.

The method combines an historical analysis of time-series data on imports and exports with brief country or sub-regional case studies. The intent is to provide a clearer sense of the considerable differences that exist over time and by location as to the nature and likely trajectory of this commerce for Latin America in the decades ahead.

Results and Discussion

Global trends

World exports of ware potatoes and seed averaged 7.5 million tons during the period

1 CIP, Lima, Peru

2 The Programe Regional Cooperativo de Papa (PRECODEPA) is a regional network for potato research for Mexico, Central America, and the Caribbean and is comprised of scientists in the respective national potato programs with backstopping from CIP.

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1995-97, or about 2.4% of global production for these same years (FAOSTAT, June 1998). Recent estimates of potato exports, including processed products, place this total at about 4% of global production, or roughly double the percentage for fresh potato and seed alone (FAO, 1995). To put these figures in perspective, global rice exports represent an estimated 3% of the world's annual rice production (The Economist, 1993).

Exports of table and seed potatoes from developing countries averaged 1.2 million tons in 1995-97 or about one percent of production (FAOSTAT, June 1998). Imports were at the same level. The volume of this trade has tripled over the last three and a half decades. During 1995-97, major exporters were Egypt (321,000 t), Turkey (191,000 t), Indonesia (91,000 t), and Morocco (79,000 t). For the Mediterranean countries, these exports consist of early or winter table potatoes shipped to European Union markets under special trade arrangements. Many of these same countries also import seed potatoes from European seed producers because comparable growing conditions and similar consumer tastes and preferences are highly complementary. Egypt alone earns well over US$25 million from its annual potato exports, and policy reforms have spurred greater production for the local market and for export in recent years. As potato acreage steadily declined in Western Europe over the last three decades, Holland now ships four times the volume and roughly one quarter of its seed exports to African countries—mostly in North Africa—up from some 35,000 t and a 10% share in the early 1970s (Scott, 1994).

Latin America

Latin America is the only developing-country region with a trade deficit in potatoes—imports of table potatoes and seed exceeded exports by over 200,000 t during 1994-96 (FAOSTAT, March 1998) as total imports reached 363,000 t, or some 2.5% of regional production (Table 1). Though the statistics are sketchy and the figures not always available for the same time periods, recent information on imports of frozen french fries (Table 2), when added to the total for table potatoes and seed, suggests that this percentage total is at least double and growing at a remarkably fast rate. The bulk—but by no means all—of these imports came from industrialized countries: Canada, the Netherlands, and the U.S. The highly differentiated nature of regional import and export markets mean

Table 1. Import and export, in tons, of table and seed potatoes in Latin America, 1994–96.

	Imports (000 t)		Exports (000 t)
Brazil	95	Argentina	79
Venezuela	72	Colombia	36
Cuba	32	Guatemala	25
Mexico	31	Honduras	1
Trinidad and Tobago	27	Mexico	1
Uruguay	19	Ecuador	1
Nicaragua	13	Chile	1
Others	73	Others	3
Total[a]	**363**	**Total**	**145**

Source: *FAOSTAT*, March, 1998.

[a] Totals do not sum exactly due to rounding

Table 2. Imports of frozen french fries[a], in tons (t), into Latin America and the Caribbean from the USA, Canada, and the Netherlands, 1991–92 and 1994–95.

	1991-92				1994-95			
	USA	Netherlands	Canada	Total	USA	Netherlands	Canada	Total
Southern Cone	503	997	1,333	2,833	18,722	10,651	21,799	51,173
Brazil	218	987	575	1,780	12,159	5,986	13,874	32,019
Chile	134	10	108	252	3,726	612	2,192	6,529
Uruguay	-	10	149	159	930	3,483	1,016	5,429
Argentina	150	-	502	653	1,908	572	4,717	7,196
Andean Region	1,543	-	1,320	2,863	3,587	42	8,898	12,527
Ecuador	20	-	-	20	947	-	16	963
Colombia	7	-	16	24	191	42	495	729
Peru	-	-	83	83	220	-	1,608	1,828
Venezuela	1,516	1	1,221	2,737	2,229	-	6,778	9,007
Central America and the Caribbean	6,109	1,493	4,910	12,512	14,599	1,842	15,518	31,959
Guatemala	428	-	19	447	3,942	-	3,140	7,082
Dutch Antilles	359	-	1,317	1,676	1,543	-	2,715	4,258
El Salvador	227	-	-	227	1,492	-	-	1,492
Jamaica	480	-	-	480	1,399	-	1,715	3,114
Honduras	316	-	-	316	1,210	-	349	1,559
British Virgin Isles	36	-	-	36	302	-	-	302
Bahamas	2,317	-	435	2,752	801	-	577	1,378
Dominican Rep.	73	-	116	189	794	55	-	849
Costa Rica	314	-	-	314	609	-	-	609
Others[b]	1,560	1,493	3,139	6,192	2,506	1,787	7,022	11,315
Mexico	14,618	-	540	15,158	33,316	-	1,155	34,470
Total	**22,773**	**2,490**	**8,103**	**33,366**	**70,224**	**12,535**	**47,370**	**130,129**

Source: Pacific Vision (1996).

[a] Based on fresh weight, using one pound of frozen potato as equivalent to two pounds of fresh potato, and converted to metric tons

[b] In the case of the Netherlands, exports are mainly to Curaçao, Aruba, Martinique, Guadeloupe, Haiti, Anguilla, and the Bahamas. For Canada to Trinidad and Tobago, Jamaica, Bermuda, Barbados, and Cuba.

that such aggregate trends require greater scrutiny at the sub-regional and national level.

Multiple factors contribute to this expansion in imports of potatoes and potato products. On the demand side for processed products, large urban populations and rising per capita incomes have generated changes in diets—over 70% of all Latin American consumers now reside in urban areas and many households can afford to purchase more processed foods. Growing female participation in the formal workforce and the shift to shorter lunch hours have stimulated demand for easier-to-prepare foods. The explosion in tourism has brought new influences on local food demand both directly by non-residents and indirectly by the effect their eating habits has on local consumers. Rapid expansion of the fast food industry—both domestic

and foreign chains, with their associated aggressive advertising campaigns (Table 3) also merits mention as a factor influencing the demand for processed potato products. Similar factors have increased demand for fresh potatoes, albeit at a slower rate, in virtually all countries except Bolivia and Peru where per capita consumption is already quite high.

On the supply side, a combination of factors has made imported processed potato products more competitive. Imports are more affordable for the following reasons.

- Prices are falling due to tariff reductions.
- Economies of scale in large processing plants for french fries and starch in industrialized, exporter countries influence cost of production.
- There is an abundance, if not oversupply, of raw material in industrialized countries (New York Times, 1997) and selective export promotion schemes.
- Containerized shipping (The Economist, 1997) lowers long distance transport costs. At the same time, locally produced processed products have lost market share from high unit costs for domestically produced potatoes and poorly articulated linkages between producers, processors, and consumers. Seizing on these trends in neighboring countries as commercial opportunities, a number of Latin American countries have also entered the potato trade as exporters for many of the same reasons.

Imports vs. Importers. Only 6 of the 37 countries in Latin America that imported table and seed potatoes during 1994-96 accounted for 70% of all the imports: Brazil (95,000 t), Venezuela (72,000 t), Cuba (32,000 t), Mexico (31,000 t), Trinidad and Tobago (29,000 t), and Uruguay (19,000 t). Most (27 of 37) of the other countries import less than 5,000 t annually. They are found in the Caribbean; the Guyanas, e.g.,

Table 3. Distribution of McDonald's restaurants by region and country, 1987 vs. 1995.

Region/Country	1987	1995
Total Pacific	951	2,735
Total Europe/Africa	755	2,710
Total Latin America	99	665 (1,160)
Argentina	3	75
Brazil	37	243 (505)
Colombia	0	5
Costa Rica	4	14
Chile	0	21
Guatemala	3	15
Mexico	5	132
Panama	8	15
Puerto Rico	22	75
Uruguay	0	2
Venezuela	3	25
Others	14	286
U.S.A	7,567	11,368 (12,406)
Canada	539	902 (1,062)
Total	**9,911**	**18,380 (23,726)**

Source: McDonalds Corporation (1992, 1995) (Figures in parenthesis are for 1998 and are taken from the McDonald's web site)

Suriname; or in Central America, e.g., Belize, El Salvador, Nicaragua.

Imports of processed potato products are similarly diffuse in terms of numbers of countries and are equally concentrated in terms of volumes imported, with some overlap between the two. For example, Brazil, Mexico, and Venezuela import relatively high quantities of both fresh and processed potatoes. The run-up in the volume of imports of processed potato products is certainly noteworthy, as is the evolution of the combined totals. In recent years, Brazil's table, seed, and processed potato imports exceeded 214,000 t in 1994—nearly 8% of annual output, although imports of fresh potatoes in Brazil and elsewhere have fallen off since then (FAOSTAT, March 1998).

With continued growth in total population, urban area populations, tourism, and hopefully per capita incomes in the decades ahead, the questions that emerge are: What is the most likely scenario for the future evolution of the potato trade in Latin America? And perhaps of more importance, what can countries with limited resources available for research and development of the potato sector do about it? Given the wide range of participants, a typology of countries may help clarify the relevant options available to the different types.

Typology of Countries. For the purposes of this analysis, potato traders can be grouped into various categories: importers (big producers and small producers), exporters, and negligible traders.

Importers: Big producers. The foremost examples of this category are Mexico and Brazil. Each has a good-sized potato sector, although this commodity is not the principal crop. Each of the sectors is divided between a relatively few, large-scale, technically advanced potato farmers and a much larger number of small-scale, peasant potato households. Each country has a relatively large population, relatively high per capita incomes, and has witnessed a rapid expansion in the fast food trade in recent years (Table 3). Each has a sophisticated major potato producer as a neighbor that is responsible for nearly all its imports. Each has joined a regional trading bloc (i.e., NAFTA, MERCOSUR) and has seen imports of fresh and processed potatoes rise as tariffs have come down as a consequence of their trading bloc participation.

The Mexican case is particularly noteworthy because current tariffs on fresh potatoes are still above 200% but are scheduled to fall to zero by 2004. Although tariffs on processed potatoes are only a fraction of this level, quotas discourage unlimited imports. Imports in Mexico, like more recently in Brazil, have also temporarily stagnated for phytosanitary reasons and devaluations during the 1990s. Nonetheless, potato imports have continued to rise throughout the decade (Table 4). Recent studies suggest that, given current differences in the costs of production and

Table 4. Mexico: Potato imports from the U.S.A. by type of product, in 000 t, and % distribution of product, 1990–92 and 1994–96.

	1990-92	%	1994-96	%
Fresh	15	36	22	25
Frozen	11	29	34	39
Chips	9	23	16	18
Other	5	12	15	18
Total	**40**	**100**	**87**	**100**

Source: USDA (1991-97).

the growth in demand for potatoes, potato imports could rise considerably in the years ahead. At the same time, however, considerable improvements in productivity could be made to raise competitiveness in the fresh market, take advantage of local preferences for varieties not grown north of the border, and fully exploit year-round harvesting. Moreover, these initiatives could be linked to efforts to strengthen particular components of the processed potato industry (e.g., medium-scale chipping plants) so as to exploit emerging segments in the domestic regional market for processed potatoes, thereby satisfying growing demand with both imports and locally produced products.

Importers: Small-producers. These countries are largely those in the Caribbean, the Guyanas, Central America except Guatemala, and Venezuela. Potatoes are typically not a major part of the local diet and, with the exception of Cuba and Venezuela, are produced by relatively small numbers of local growers for sale on the fresh market as an expensive, luxury vegetable. Imports of processed potato products are on the rise in many instances simply because the local potato sector is typically too small and producer prices for fresh potatoes too high to economically justify processing on even a cottage-industry basis. Demand has mushroomed with rising incomes, the advent of more tourists, and fast food restaurants catering to local consumers and visitors. Lower tariffs and shipping costs have made imports cheaper in many instances.

Some countries—most notably Costa Rica, Panama, and Venezuela—have seen imports of table potatoes spike at particular times when a shortage of local supplies drive up prices on the domestic market. The response, in some instances, has been to reinstate high tariffs on a temporary basis to discourage flooding the local market with imports, but such ad hoc measures have been controversial because they provoke threats of retaliation by trading partners.

Seed represents a major share of potato imports in only a few instances, e.g., Cuba, Nicaragua, Venezuela.

In too many cases, local potato programs in these countries have responded to the rise in potato imports with a call for an indiscriminate expansion of the local processing industry for french fries, chips, starch, and even flakes. Or, they have issued appeals to government authorities to re-instate tariff barriers. An alternative approach would be to channel the limited, local resources available on improving performance of those producers engaged in table potato production. Their comparative advantage vis-à-vis imports is that some consumers will always prefer high quality, freshly produced local tubers and in many of these locations agro-climatic conditions allow continuous production throughout the year. This work might then be complemented with efforts focused on one segment of the processing industry such as potato chips where local spices, brand-name affiliation, and batch-style production techniques might be used as leverage to capture a significant, albeit not dominant, segment of the local market.

Exporters. This group of countries consists of Argentina, Colombia, and Guatemala. They export to Brazil, Venezuela and Ecuador, and El Salvador and Nicaragua, respectively.

Argentina's exports of table potatoes to Brazil topped 160,000 t in 1994 with the opening of MERCOSUR and the reduction in tariffs. Many of these potatoes are shipped from northern Argentina into southern Brazil when the early potato harvest on one side of the border coincides with high seasonal prices and scarcity in major markets such as Sao Paulo. With the opening of a large multi-national french fry processing plant in Balcarce in early 1995 and a second line to the same facility recently, Argentina's exports have also included frozen french fries. Large, irrigated, highly technically advanced

producers in Argentina will continue to put pressure on small, peasant producers in southern states like Parana who are dependent on rain-fed agriculture for their livelihoods. Brazil's recent 30% currency devaluation will give its growers breathing room, though perhaps only temporarily.

Colombia's exports of table potatoes and common seed to Ecuador and Venezuela are grounded in its:

- higher yields and lower unit costs of production, although this is exchange rate-sensitive;
- well-organized federation of growers, traders, and shippers; and,
- well-developed network of marketing infrastructure: roads, wholesale markets, and telecommunications (Scott et al., 1997).

Argentina and Colombia, in particular, have embarked on aggressive campaigns to capture a growing share of the sub-regional export market. These efforts have included:

- closer collaboration in research between the public and private sector (Revista Papa, 1992);
- policy measures to encourage expansion of infrastructure by processors, e.g., tax and investment incentives; and, perhaps most fundamentally,
- an approach that sees the search to develop or acquire improved potato varieties for processing as but a part of an integrated initiative intended to strengthen competitiveness in all aspects of the food system for potato: varieties; seed; raw material production; plant equipment and facilities; market infrastructure (e.g., ports, telecommunications); and trade and investment policy.

Negligible traders. This category includes Bolivia, Chile, Peru, and Paraguay. These countries traditionally have not imported (because they are self-sufficient) or exported (because they produce so few and what they ship abroad are simply transshipments from other countries) potatoes in any appreciable quantities. They have also explored export possibilities (Fano, et al., 1998; Muchnik and Tejo, 1997).

In recent years, however, these countries have witnessed a rise in potato imports of both fresh and processed potatoes. Though the quantities have remained small, they have attracted considerable attention in the press given their strategic presence in the fastest growing segment of the potato market as in Peru or due to Bolivia's recent ascension to associate member status of MERCOSUR. However, in both these cases, given the high levels of per capita consumption and the large numbers of low income urban consumers, the threat of much greater imports of processed or fresh potatoes that are much cheaper than locally produced material has to be taken seriously in the medium term. In that regard, a number of measures merit consideration.

In the production sphere, these countries can improve yields of locally preferred varieties and more effectively exploit year round harvesting of fresh potatoes. In the postharvest area, they can take fuller advantage of recent innovations in processing such as chilled, in lieu of frozen, potato products. As policy initiatives, they can promote up-grading of processing infrastructure by both domestic and foreign-based firms through tax and investment incentives. These various initiatives would provide strategic complements to long-standing work to develop improved varieties as well as more efficient and sustainable seed schemes.

Conclusions

Globalization has taken root in the Latin American potato trade. All indicators are that such trade is highly sustainable and is likely to expand rapidly in the decades ahead. Some Latin American countries have witnessed faster expansion in potato imports or exports than others have. From this collective experience the following action recommendations are suggested for Latin American governments.

- Become more informed about recent trends and trade commitments in terms of tariff reductions for different types of potato products so as to better ground local strategy.
- Target research and development efforts to focus on a particular segment of the domestic (import substitution) or export market for processed potatoes, rather than propose across-the-board initiatives involving several segments simultaneously or blanket proposals (e.g., reinstate tariffs).
- Seek out more information about how neighboring or other Latin American countries have addressed trade issues—including developments in industrialized countries with respect to such trends as the move toward chilled potatoes, the success and failure rate of such initiatives.
- Consider trade in particular product lines from the perspective of the whole system. This includes not just efforts aimed at raising productivity but also lowering processing and marketing costs, and improving quality. Inevitably, such an approach involves developing linkages that extend beyond the search for better varieties per se. It entails participation by all those engaged in improving system performance including private companies (e.g., input suppliers, potato wholesalers, and processors), growers' associations, and public policymakers outside agriculture, e.g., ministries of trade and industry.

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The Economics of Generating International Public Goods from Investing in Potato Plant Breeding

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The words "scarcity" and "fatigue" figure prominently in the recent literature on government-financed agriculture research (Alston, Norton, and Pardey, 1996; Anderson, 1998). After two decades of growth, the reality of tightening resources for public sector agricultural research became apparent in the mid-1980s for both developed and developing countries as well as for the CGIAR (Alston, Pardey, and Smith, 1998).

The economics of investing in crop improvement programs also have been known for some time (Binswanger, 1974). Relevant considerations include the potential for gains in well-defined environments, economies of scale, size, and scope in research, diminishing returns to search from the same distribution, and the scope for technology borrowing, i.e., spill-ins. In spite of a growing consensus about scarcity and of the existence of established economic knowledge, applications of economics to commodity crop improvement have been slow in coming.

In the 1990s, economists at the International Center for the Improvement of Maize and Wheat (CIMMYT) made several pioneering applications to bring economics to bear on decision-making in wheat breeding in developing countries (Brennan, 1992; Maredia and Byerlee, 1998). Those applications were motivated by two empirical facts that challenged the conventional wisdom on the location specificity of varietal transfer and on the reported underinvestment in plant breeding research. First, analysis of the CIMMYT/NARS (national agricultural research systems) international spring wheat data showed that wheat varieties are highly transferable within some mega-environments (Maredia, Ward, and Byerlee, 1998). This finding rings especially true in the important high rainfall and irrigated mega-environments where CIMMYT-bred materials yield as much as nationally bred materials. Second, many small wheat-producing countries have invested in plant breeding programs characterized by high research intensities in terms of investment per unit of production (or value) of the crop (Bohn, Byerlee, and Maredia, 1998). The results of economic modeling showed that 21 of 71 programs were investing too much in wheat breeding given the small size of their national production and ample potential for technology borrowing from abroad.

To what extent do the CIMMYT results for wheat breeding apply to potato breeding in developing countries? What is a "best-bet" spatial allocation of priorities by CIP to generate public goods in developing countries from potato breeding? We begin to answer these questions by comparing research intensities in potato and wheat improvement programs.

Research Intensities in Potato and Wheat Crop Improvement

In 1992, CIMMYT surveyed 71 wheat improvement programs in 37 developing countries. The results showed that average research intensity was inversely and strongly correlated with the size of NARS. The smallest systems were investing the equivalent of more than 100 full-time

1 CIP, Lima, Peru.
2 CIP, Bogor, Indonesia.

equivalent scientists per million metric tons of production. For the largest six NARS, each producing more than five million tons, the ratio fell to four full-time equivalent scientists per million tons.

About 1,200 full-time equivalent scientists with a B.S. or higher were working in the wheat breeding programs in countries which accounted for 97% of developing-country wheat production. Comparable estimates from similar surveys undertaken by CIP in 1993 indicated a total of about 350 scientists working in 21 countries accounting for about 70% of developing-country potato production.

We are assembling more complete data for potato so that a rigorous comparative analysis can be carried out for the two crops. But we can make four preliminary observations based on the 1993 survey and our knowledge of potato breeding in developing country agriculture. First, the weighted average research intensities across all developing countries between improvement programs for the two crops do not appear to be significantly different. Similar investments, in relative terms, in the largest NARS in China and India probably explain this finding. Second, the improvement programs are qualitatively different. Wheat research features a heavy concentration in breeding; potato research is more diverse with an emphasis on pathology, tissue culture, virology, and entomology. Third, more wheat-producing developing countries have invested in full adaptive breeding programs that not only test material from other programs but also make their own crosses. Sixty-one of the 71 programs had invested in breeding; only ten programs had restricted their activities to testing elite imported material. In potatoes, the majority of countries with a commitment to crop improvement have invested in testing programs that stop short of making their own crosses from parental material. And fourth, very high research intensities in small NARS seem to be more of a source of inefficiency in the genetic improvement of wheat than in potatoes. Urban consumer subsidies probably explain the interest of small NARS, particularly those in Sub-Saharan Africa, in investing in agricultural research to increase their domestic wheat production. Potatoes have not benefited from such urban biases nor are they as traded internationally as is wheat.

Threshold Levels of Production

The economic modeling of wheat breeding by CIMMYT focuses on the size of country production that warrants a given level and type of investment. Based on costs, three mutually exclusive outcomes are possible: (1) production is insufficient to justify an investment in testing, (2) production is sufficient to make testing profitable but insufficient to establish the economic superiority of breeding, and (3) production is sufficient to justify an investment in breeding the most expensive alternative. Note, however, the profitability of a breeding program cannot be considered without quantifying the opportunity cost of investing in a testing program. The structure of the model is given as equations (1), (2), and (3) in Figure 1. An equation identical to (3) can also be written for the breeding alternative.

Applying the CIMMYT model to potatoes requires one major modification on the assumptions about the parameters (see Table 1). Patterns of varietal change are very different in potatoes and wheat (Walker, 1994). Maredia's and Byerlee's adoption scenario in their base model features a rapid rate of varietal turnover. Annually, a new variety is released that reaches peak adoption in five years. After 20 years, the mean age of varieties in farmers' fields approaches five years. An average varietal age of five years may be a reasonable target for wheat, but it is not for potatoes (even if one wants to err on the side of optimism). The incidence of successful released varieties is also substantially lower in potatoes than in wheat, although the odds for success (contrary to intuition) favor developing countries over

(1) $Q^{*T} : NVP^T = O$

(2) $Q^{*B} : NVP^B - NPV^T = O$

(3) $$NVP^T = \sum_{t=1}^{n} \left[\frac{P_t Q \sum_{i=1}^{j} v_{it} g_i - Y_s \; C_t}{(1+r)^t} \right]$$

Where

Q^{*T} = Minimum size of production for which testing is profitable;

Q^{*B} = Minimum size of production for which breeding is more profitable than testing;

NVP^T = Net present value;

P_t = Price of output in year t;

Q = Size of production;

Y_S = Number of full-time equivalent scientist for program s;

C_t = Cost per scientist in year t;

r = Discount rate;

v_{it} = Proportion of area sown to variety i in year t;

g_i = productivity gain attributed to variety i.

Figure 1. Equations (1), (2), and (3).

developed countries that have mature production and processing sectors. For these reasons, a mean varietal age of 15 years for potatoes is used to anchor the analysis in a realistic setting for potatoes.

The estimated threshold levels of production and incidence of inefficient programs are compared for the two crops in Table 2. These results are generated from a best-bet set of assumptions. Threshold levels of 25,000 and 200,000 tons in potatoes are about twice as large as the amounts needed for wheat.

Using these threshold levels, we make the following country breakdown for the 94 developing nations producing potatoes from 1995 to 1997 (FAOSTAT, 1998). Thirty-three countries produce less than 25,000 tons annually. Of these, only five have invested in testing programs, and three have released varieties that were selected from CIP material. Four have been

Table 1. Comparing parameter assumptions on the economic feasibility of wheat and potato breeding programs.

Parameter assumptions	Wheat	Potato
Benefits		
Rate of genetic gain		
Testing	6.35/kg/yr	0.635%/yr
Crossing	10/kg/yr	1%/yr
Price (US$1/t)	Real price trend	150
Adoption		
Varietal success	Annually	Once in a decade
Average varietal age (years)	5	15
Research lags (years)		
Testing	5	5
Crossing	12	12
Costs		
Number of scientists per year		
Testing	1	1
Crossing	3	3
Cost per scientist (US$)	35,000	50,000
Other		
Discount rates	12%	12%
Time horizon of the project (years)	70	50

partners in larger regional networks. Overall, the economic loss attributed to investing too much in testing in very small producing countries does not appear to be sizeable.

Twenty-four countries have levels of production between 25,000 and 200,000 tons which economically warrants a testing program but does not justify the additional investment in a breeding program. Several of these countries do have active testing programs, but only one, Uruguay, has a full adaptive potato-breeding program.

The remaining 37 developing countries produce more than 200,000 tons annually. Only 11 of these invested in full potato breeding programs in the 1990s. The two smallest of these countries are Cuba with about 350,000 tons and Ecuador with around 500,000 tons. These levels are considerably above the threshold justifying a breeding program. About half of the remaining 26 countries have testing programs. A sizable number of countries, mainly those in North Africa and the Middle East, do not even invest in testing and selecting imported material. In summary, the picture emerging in Table 2 is markedly different from Maredia's and Byerlee's analysis of wheat. Only a handful of countries can be described as overinvesting in potato breeding on a size-of-production criterion.

Table 2. Size of threshold production to justify investing in a testing or a more expensive crossing program and the number of national programs that have over-invested relative to this economic criterion for wheat and potato.

	Threshold production (t)		Inefficient programs (number of programs)	
Program capacity	Wheat	Potato	Wheat	Potato
Testing only	14,800	25,000	2	5
Crossing	111,400	200,000	19	1

International Public Sector Investment in Potato Crop Improvement in Developing Countries

Finding an absence of overinvestment makes the efficient allocation of international resources destined for potato plant breeding all the more imperative. Walker and Fuglie (1999) set forth some economic cornerstones for establishing a strategy to generate international public goods from collective action in potato plant breeding. Spill-in benefits from varietal change are well documented in North America and elsewhere. It is clear that alternative sources of supply are important from NARS in other developing countries, as well as from NARS in developed countries. Typical of the experience with varietal change in North America, economic returns to potato breeding are likely to fall as the production and consumption environments improve. Over time demand for disease resistance decreases and demand for traits related to market quality increases. Higher market quality begets economic rigidities that favor varieties already in the market. Lastly, as we saw in the previous section, national production below 25,000 tons does not warrant an investment in potato plant breeding.

Armed with these facts, we now tackle our decision-making problem: What is a "best-bet" spatial allocation of priorities by an international agricultural research center (IARC) to generate international public goods in potato crop improvement? Rather than use a mathematical model to solve the problem, we employ a more intuitive approach drawing on our earlier findings and on additional information related to technological change in potatoes in specific regions.

Our population of interest is the 94 developing countries that produce potatoes. We break our decision-making problem down into its parts by specifying criteria in the form of questions that facilitate the sorting of countries into groups for differential treatment (Figure 2).

The production threshold of 25,000 tons is our first criterion. About one-third of the countries fall below this economic threshold for investing in a genetic improvement program for potatoes. In these very small producing countries, potatoes are neither a staple food crop nor a crop that is important to the rural and urban poor. Countries close to the 25,000-ton threshold warrant a watching brief, but overall, the priority for investing in plant breeding is negligible.

The next criterion gives priority to countries that have stable breeding programs and do not appear to have reached the point of diminishing returns to investment as exemplified by constant or even rising varietal age. Only one country fits that bill: China. China is the largest potato

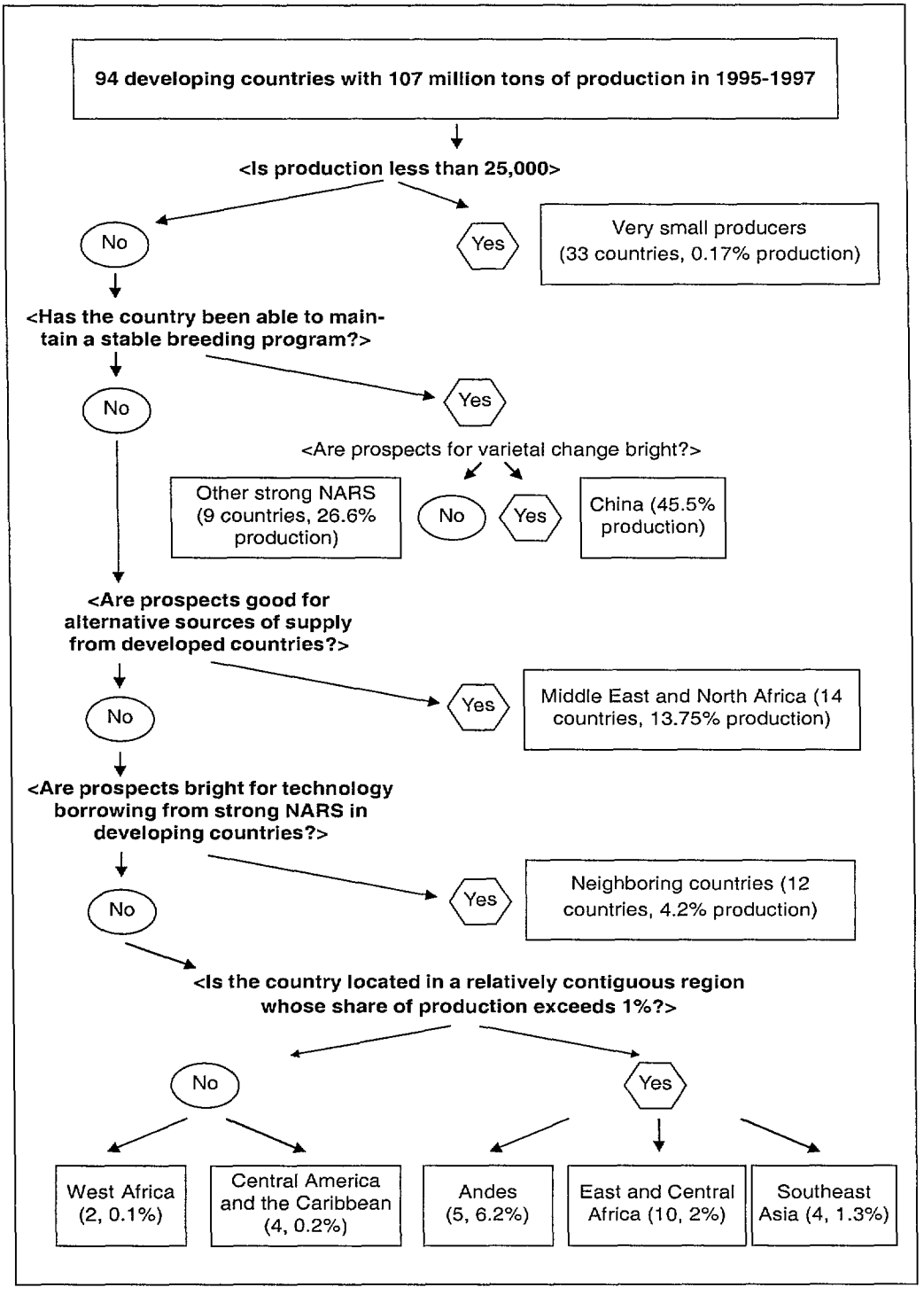

Figure 2. Spatial and institutional priorities for generating international public goods from potato breeding.

producer in the world accounting for 40% of developing country output.

Demand for varietal resistance to disease is strong in China. Provincial seed programs are improving, but on average, they are not as developed as those in other strong NARS. Several old cultivars, such as Mira, are still cultivated in China. There appears to be ample scope for varietal change, however, and China is still likely to be a major recipient of spillover benefits from other strong NARS. Therefore, input of CIP to China should span the gamut of material from elite clones for testing to parents for crossing.

The other strong NARS that have mature plant breeding programs have for the most part suffered from a slowing in the pace of varietal change. For these strong NARS, the role of an IARC such as CIP should focus on the provision of appropriate parental material for crossing. Strong NARS may still benefit from selection of outstanding individuals from progeny of crosses made by CIP, but a more upstream, strategic research role should enhance the prospects for the attainment of genetic progress by strong NARS. Equally important, CIP needs to find ways to maximize the chances that strong NARS will generate spillover effects in neighboring regions or in kindred agroecologies.

Many of the conditions that give rise to strong NARS may also stimulate the development and enforcement of intellectual property rights which will enhance greater private sector participation particularly in the area of transgenic varietal change. Development of intellectual property rights has not been sufficient to engender much private sector participation in potato crop improvement in developing countries. But transgenic varietal change could result in more private sector participation. More needs to be learned about the prospects for and implications of transgenic varietal change in strong NARS in developing countries.

Our next criterion focuses on alternative sources of supply from developed countries. The countries of the Middle East and North Africa (MENA) region, are characterized by some unique opportunities for potato production (particularly in North Africa and to a lesser extent in the Middle East). They export potatoes to Europe in the winter season and rely on imports of tuber seed from Europe. The seasonal export market influences local consumer preferences. European varieties, particularly Dutch varieties, do well in this setting, and seed companies aggressively promote them. Ten countries in this region are large enough to warrant a national potato-breeding program, but none have invested in one on a sustained basis. In this relatively homogeneous region where a handful of clones account for the bulk of production, transgenic varieties will likely have a greater role to play than conventionally bred varieties. Private sector biotechnology companies, most likely in collaboration with public sector institutes in Europe, are well placed to provide transgenic varieties for the MENA region.

We are not saying that investing in potato crop improvement in a wider sense will not pay in the MENA region. Indeed, success stories of applied research on integrated pest management and on seed production and supply to farmers are well documented. We are saying, however, that internationally assisted breeding will not be productive.

This brings us to countries bordering strong NARS. Developing country alternative suppliers is our next filter (Figure 2). Does the country border a strong NARS or is it located in a proximate and shared agroclimatic environment? An affirmative response to this question applies to 12 countries that account for about 5% of developing country production. At times, receiving spill-in benefits from neighboring countries may not be politically popular, but it is economically correct particularly in times of scarcity. These countries should

invest in testing programs targeted on adaptation of elite clonal material and not wait for farmer seed from the donor country to spill across the border. The role of an IARC is to provide an alternative source of material.

The above four criteria allow us to sort 70 of the 94 countries into five groups. The remaining countries produce more than 25,000 tons, have not been able to establish a stable potato breeding program without donor assistance, do not border a strong NARS, and do not have production characteristics which allow for the transfer of developed country material without the need for considerable adaptation. From the perspective of potato breeding, the optimal configuration is centralized breeding with decentralized selection (Simmonds, 1997). This observation suggests a final filter: Are there contiguous countries that account for a sizeable share of developing country production? Finding such groupings could warrant a direct investment by CIP in a regional breeding program. We find three such groupings: the Andes, the East and Central African Highlands, and Southeast Asia.

Regional groupings of the remaining countries account for less than one percent of global production in our population of interest. These countries come from two sources: large pockets of potato production in West Africa, specifically northwest Cameroon and the Jos Plateau of Nigeria, and in the highest elevations of Central America and the Caribbean. Traditionally, CIP has serviced the needs of these countries through donor-assisted special projects, and this would appear to be the most effective modus operandi in the future.

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Research on Sweetpotato

Impact on a Changing World

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The Causes and Control of Virus Diseases of Sweetpotato in Developing Countries: Is Sweetpotato Virus Disease the Main Problem?

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Virus diseases can pose a significant constraint to sweetpotato production (Mukibii, 1977; Hahn 1979). As a result of the historical neglect of sweetpotato research in most developing countries, our knowledge of sweetpotato viruses, their importance, distribution, and control are still rather limited. However, recent studies on the occurrence of sweetpotato viruses in a number of countries are helping to clarify our understanding of the global importance of sweetpotato viruses, and to define control strategies. An array of complementary techniques are being used. They include diagnostic methods for the detection of specific viruses, pathogen-tested planting materials for the assessment of yield loss due to viruses, and host plant resistance to virus diseases.

More than 14 virus diseases of sweetpotato have been reported (Moyer and Salazar, 1990; Brunt, et al., 1996 onward). Study of several of these diseases has been hampered by the lack of simple detection techniques. Antisera are now available against a number of sweetpotato viruses including sweetpotato chlorotic fleck virus (SPCFV), sweetpotato latent virus (SPLV), sweetpotato mild mottle virus (SPMMV), C-6, sweetpotato mild speckling virus (SPMSV), sweetpotato feathery mottle virus (SPFMV), and sweetpotato chlorotic stunt virus (SPCSV) previously known as sweetpotato sunken vein virus (SPSVV).

Antisera for all but SPCSV are produced at CIP and are routinely used for nitrocellulose membrane-enzyme-linked immunosorbent assay (NCM-ELISA). Antisera (monoclonal antibodies) specific to SPCSV are produced by J. Vetten at the Institute for Biochemistry and Plant Virology, Braunschweig, Germany (Hoyer et al., 1996). These antisera have been used to survey the incidence of sweetpotato virus diseases at a number of sites.

Sweetpotato virus disease (SPVD) is the name that has become associated with a serious disease of sweetpotato, symptoms of which typically include leaf distortion, chlorosis, discoloration, and stunting. Work initially in West Africa and later in East Africa showed it to be caused by combined infection with aphid-borne SPFMV and whitefly-borne SPCSV (Schaefers and Terry, 1976; Winter et al., 1992; Hoyer et al., 1996; Gibson et al., 1998a) Despite the apparent broad meaning of the name SPVD, the symptoms are so characteristic that the name has become restricted to the disease with these symptoms and caused by these viruses.

The first report of SPVD may have been in eastern Belgian Congo (now DR Congo)

1 CIP, Nairobi, Kenya.
2 Natural Resources Institute, UK.
3 CIP, Lima, Peru.
4 Research Institute for Food Crops Biotechnology, Bogor, Indonesia.
5 Namulonge Agricultural and Animal Production Research Institute, Uganda.
6 Shangdong Academy of Agricultural Sciences, China.
7 Xuzhou Sweetpotato Research Center, China.
8 University of Ainshams, Egypt.

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in 1939. SPVD was first described in East Africa by Sheffield (1953).

SPVD can reduce yields of infected plants by up to 80% (Hahn, 1979; Mukiibi, 1977). It has recently been shown to be the principal virus disease of sweetpotato in East Africa where high disease incidences are often recorded in farmers' fields (Gibson et al., 1998b; Aritua et al., 1998a). In Uganda, disease incidence and severity in farmers' fields have been shown to be closely associated with prevalence of whiteflies (Aritua et al., 1998a, b, c). There are large varietal differences in susceptibility to SPVD. Good sources of resistance are present in local germplasm, but often are associated with later-maturing, lower-yielding genotypes (Aritua et al., 1998b, Carey et al., 1997). SPCSV isolates from eastern and southern Africa have been shown to be serologically different from those from West Africa, Brazil, USA, and Israel (Hoyer et al., 1996; Gibson et al., 1998a). These different isolates may have biological significance inasmuch as cultivars resistant to SPVD in Nigeria were susceptible to SPVD in Uganda (Mwanga et al., 1991).

This paper presents a brief overview of recent collaborative sweetpotato virus research conducted by our project. We start with evidence from surveys conducted in a number of countries using antisera available against sweetpotato viruses, including SPFVM and SPCSV, the components of SPVD. We then assess the effectiveness of the use of planting material free of known pathogens (pathogen-tested) as a virus control measure in China and Uganda. The implications of these results for virus control strategies are discussed.

Materials and Methods

Surveys of sweetpotato viruses were conducted in China, Egypt, Indonesia, Peru, and Uganda. Viruses assayed using antisera and NCM-ELISA kits from CIP were SPCFV, SPLV, SPMMV, C-6, SPMSV and SPFMV. SPCSV was assayed by different means at different sites. In Uganda, triple antibody sandwich-ELISA was used as described by Gibson et al. (1998b). This method used two sets of monoclonal antibodies to discriminate between the East African and West African serotypes of SPCSV. In Indonesia and Peru, SPCSV was detected using NCM-ELISA. In Egypt, SPCSV was detected using polymerase chain reaction (PCR) assay and tests were conducted by Dr. S. Winter, Braunschweig, Germany. Details of sampling procedures at each survey location are given in the references cited in Table 1. In Kenya and Egypt, both symptomless and symptom-expressing plants were sampled. At other sites, only symptom-expressing plants were sampled.

Pathogen-tested planting material for trials in China and Uganda was obtained using standard techniques of thermotherapy and meristem tip culture, followed by indexing to assure virus-free status (Love et al, 1989). Field trials were conducted to compare yields of the pathogen-tested planting material with farm-derived planting material of the same cultivars. In China, trials were conducted during the spring cropping season of 1997 at Xuzhou, Jiangsu Province, and Jinan, Shangdong Province. Five cultivars were used. Trials consisted of 100-plant plots (5 rows of 20 cuttings each) planted in a randomized complete block design (RCBD) with three replications. Trials were harvested 170 d after planting.

In Uganda, three cultivars were used and trials were conducted at three sites: Kachwekano in the southwestern highlands, and Namulonge and Nakabango in the tall grasslands agoecological zone in the south-central part of the country. Trials were conducted at Kachwekano in 1995, and at Namulonge and Nakabango in 1996. Planting material from the 1995 trials was used to plant the 1996 trials. Each trial was planted using a RCBD with three replications. Harvest plot sizes were 16 plants for trials conducted in 1995 and 54 plants for the trials conducted in 1996.

Table 1. Frequencies of detection of sweetpotato viruses from surveys conducted at various sites.

Location	SPCFV	SPLV	SPMMV	C-6	SPMSV	SPFMV	SPCSV	SPFMV+SPCSV	Reference
Uganda (six sites sampled)	5/106	0/106	6/106	na[a]	na	58/106	105/106[b]	57/106	Gibson et al. 1998a
Kenya (four sites sampled)	0/182	6/182	13/182	0/182	na	40/182	na	—	Carey et al., 1998
Cañete, Peru	0/183	13/183	4/183	0/183	12/183	43/183	59/183[b]	34/183	Salazar, 1998
San Ramon, Peru	2/87	0/87	0/87	0/87	2/87	72/87	61/87[b]	59/87	Salazar, 1998
W., C. and E. Java, Indonesia (20 villages)	na	na	na	na	na	256/890	237/890[c]	155/890	Prain et al., 1998
Irian Jaya germplasm collection, Lembang, Indonesia	11/381	8/381	5/381	7/381	5/381	18/381	na	—	Prain et al., 1998
Kafr El Zayat, Egypt (6 cultivars from the Egyptian seed program)	4/382	5/382	6/106	na	na	67/382	+[d]	yes	Abo El-Abbas et al., 1998
Shangdong, China (5 infected farmers' cultivars)	0/115	15/115	0/115	0/115	0/115	93/115	na	—	Zhang and Ma, 1998

[a] na = not assayed.
[b] E. African strain detected by use of monoclonal antibodies.
[c] NCM-ELISA test, SPCSV strain not yet identified.
[d] + signifies detected by PCR, but frequency not quantified.

Results

Results of virus surveys conducted in China, Egypt, Indonesia, Kenya, Peru, and Uganda are presented in Table 1. SPFMV was assayed at all sites and was detected with high frequency. SPCSV was not assayed at all sites, but where assayed, it was detected at high frequencies, similar to SPFMV. In Uganda, 54% of the plants sampled had SPVD, being infected by both SPFMV and SPCSV. At sites in Java, Indonesia, about 65% of the SPCSV-infected samples were also infected with SPFMV. In Egypt, there was also combined infection, but the frequency of SPCSV was not quantified. In Peru, the frequency of combined infection by SPFMV and SPCSV was 34% of the sampled plants. The serotype of SPCSV was only determined during surveys in Uganda and Peru. In both countries, the so-called East African serotype was detected, not the West African serotype. The remaining viruses, except for C-6, which was only detected in the Irian Jaya germplasm collection at Lembang, Indonesia, were generally detected at a low frequency but on each of the continents surveyed.

Yield loss assessment trials in China (Table 2) demonstrated a significant benefit to using pathogen-tested planting material at both Jinan and Xuzhou. The effect of using pathogen-tested planting material was greater at Jinan, with a significantly higher yield from pathogen-tested planting material than from farm-derived material for each cultivar. At Xuzhou the pathogen-tested planting material only yielded significantly more for two of the cultivars evaluated. However, the mean yield from pathogen-tested planting material was consistently higher than from farm-derived material.

In the Ugandan trials (Table 3), no significant effect of using pathogen-tested planting material was detected. The mean yield of pathogen-tested planting material was not consistently higher. However, in three of four trials, the mean yield from pathogen-tested cultivar Tanzania was higher than the yield from farm-derived planting material. Tanzania was also the highest yielding cultivar in three out of four trials.

Discussion

The finding that SPFMV was predominant at each site sampled is in line with previous information about the cosmopolitan distribution of this virus. In the countries where it was assessed—Egypt, Indonesia, Peru, and Uganda—SPCSV was present in as high a proportion of virus symptom-expressing plants as SPFMV, often in association with the latter. This appears to indicate a broader distribution and importance of SPVD than has previously been reported. The detection of the East African strain of SPCSV as the predominant form in Peru also indicates a wider distribution of this serotype than was previously reported (Hoyer et al., 1996). Preliminary results have indicated the presence of SPCSV in China (L. Salazar, CIP, Lima, Peru, 1999, pers. comm.).

The results of the present study indicate that SPVD may be the most important virus disease of sweetpotato globally. Until now, its global impact has been overlooked. That is largely because diagnostic tools have not been readily available for SPCSV, so only SPFMV was ubiquitously detected. Further survey work is required to confirm the occurrence and prevalence of SPVD and its causal agents (SPFMV and SPCSV) around the world. Further work is also required to clarify the biological significance of different serotypes of SPCSV. Because of a lack of antisera against a number of additional sweetpotato viruses reported in the literature, these have not yet been widely surveyed. One or more of them could also be important.

Results from China of yield comparisons of sweetpotato varieties using pathogen-tested and farm-derived planting materials (Table 2) indicate the large yield gains that can be made using this technique. Indeed,

Table 2. Fresh storage root yields (t/ha) of five major sweetpotato cultivars grown from pathogen-tested and farm-derived planting materials at two sites in China in 1997.

Cultivar	Planting material source[a]	Yield and difference (%) between planting material sources for each cultivar[b]	
		Jinan	Xuzhou
Xushu 18	PT	43.1 (36%**)	41.5 (22% ns)
	F	31.6	34.0
Lashu No. 7	PT	46.4 (35%**)	39.0 (17% ns)
	F	34.6	33.3
Lushu No. 8	PT	39.9 (23%**)	41.6 (48% ns)
	F	32.4	28.0
Beijing 553	PT	39.4 (47%**)	39.0 (64%*)
	F	26.9	23.8
Fenghsoubai	PT	37.7 (75%**)	45.7 (92%*)
	F	21.5	23.8

[a] PT = Pathogen-tested, F = Farm-derived.
[b] Significant according to LSD (0.01) = ** or LSD (0.05) = *, not significant = ns.

Table 3. Fresh storage root yields (t/ha) of three sweetpotato cultivars grown from pathogen-tested and farm-derived planting materials at three sites in Uganda during two seasons.

Cultivar	Planting material source[a]	Yield and difference (%) between planting material sources for each cultivar[b]			
		Kachwekano	Nakabango		Namulonge
		(1995)	(1995)	(1996)	(1995)
Tanzania	PT	15.0 (19%)	39.8 (39%)	11.5 (-14%)	13.8 (50%)
	F	12.6	28.7	13.4	9.2
Bwanjule	PT	5.9 (-40%)	28.2 (28%)	19.3 (7%)	11.0 (29%)
	F	9.9	22.1	18.0	8.5
Wagabolige	PT	6.3 (-40%)	20.8 (-13%)	20.4 (16%)	9.4 (-8%)
	F	10.5	23.8	17.6	10.2

[a] PT = Pathogen-tested; F = Farm-derived, symptomless.
[b] No significant effect of planting material source was detected.

in Shangdong, the use of pathogen-tested planting material has been widely adopted in the past few years and extended to all parts of the Province (Fuglie et al., 1999). There has been a very high payoff to this research and extension effort. Increased production has supplied the increasing demand for sweetpotato as an industrial and feed source, while farmers' production costs have actually been reduced due to improved seed health. Following initial investment of public money in the clean-seed system, the costs of operation of the seed system are borne by the farmers who

purchase the planting material, resulting in an economically viable business. The experience in Shangdong is being extended to other provinces in China, and may continue to have a large impact on sweetpotato production there. A successful clean planting material program has also been established in Egypt, made highly effective by the high virus pressure there and the susceptibility to viruses of the major commercial cultivars (Abo EL-Abbas et al., 1998).

Results of our assessment of the potential for using pathogen-tested planting material in Uganda were in marked contrast to the results from China. In Uganda, no benefit to using pathogen-tested planting material was demonstrated. That was probably due to the relatively high levels of virus resistance in the landrace cultivars that we used for our test in Uganda. Also, we followed the normal farming practice of using only symptomless (essentially healthy) plants as sources of planting material (Gibson et al., 1997).

Had we chosen more susceptible genotypes for our comparison in Uganda, or had we chosen to use symptom-expressing farm-derived planting material for our experiments, it is likely that we would have detected differences. Indeed, for cultivar Tanzania, the most virus-susceptible of the genotypes evaluated (rated moderately resistant by Mwanga et al. (1995)), there was a tendency for pathogen-tested planting material to yield higher than farm-derived planting material. We will continue to investigate the potential for using pathogen-tested planting material in Uganda and elsewhere in eastern and southern Africa, particularly for more virus-susceptible but high yielding cultivars. It should be noted, however, that sweetpotato production systems in Sub-Saharan Africa are less commercially oriented than systems in China and elsewhere, with sweetpotato primarily a food security crop for low-income farmers. That might pose a constraint to the widespread implementation of pathogen-tested planting material schemes as viable enterprises.

Given the relatively unpromising prospects for pathogen-tested seed schemes in Uganda, and the high levels of resistance to SPVD that exist in the African germplasm (Carey et al., 1997), breeding resistant varieties will continue to be a principal component of SPVD control here. As already mentioned, there is a tendency for local farmers' cultivars with high levels of resistance to be rather low yielding and late maturing compared with earlier maturing, high yielding, yet susceptible local cultivars or exotic introductions (Aritua et al., 1998b; Carey et al., 1997). The higher mean yield of the more virus susceptible cultivar Tanzania compared with the other two cultivars in our trial is in line with this observation.

A principal aim of the sweetpotato breeding program at Namulonge, Uganda, where the Ugandan program and CIP are concentrating breeding efforts, is to combine SPVD resistance with desirable agronomic traits such as yield, earliness, and acceptable culinary quality. Considerable progress has already been made, and the program has released 12 cultivars combining good levels of field resistance with high yields and other desirable traits (Mwanga et al., 1995; Turyamureeba et al., 1998). However, improvements in breeding efficiency are required, including the development of screening techniques to rapidly identify resistant genotypes. Currently, very large progeny populations (as many as 100,000 seedlings) are required to identify a handful of resistant, agronomically superior genotypes. The inheritance of host plant resistance is under study. It is anticipated that considerable progress will soon be made in breeding for resistance.

The international value of resistance breeding will depend on the degree to which resistant genotypes from one site maintain their resistance at other sites. Recent evidence of the widespread global

occurrence of SPVD leads us to anticipate that resistance from Africa may hold up in other environments where viruses are a problem. However, differences in viruses or virus strains between sites could cause resistant genotypes from one site to be susceptible in others. International studies are underway to investigate this, using standard sets of genotypes with various levels of resistance to SPVD.

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Economic Impact of Virus-Free Sweetpotato Planting Material in Shandong Province, China

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In many developing countries, yields of root and tuber crops are significantly reduced due to diseases and pests in the planting material. (In sweetpotato, the sources of planting material [which are either vine cuttings or roots] are equivalent to clonal seed for vegetative propagation.) The development and transfer of new methods and technologies for producing disease-free clonal seed can overcome this constraint and help unlock the significant yield potential of these crops. In potato, the use of virus detection and tissue culture techniques in tuber seed programs is common especially in developed countries. In sweetpotato, such techniques have not been used even in the United States where propagation material is periodically renewed to maintain clonal purity. Virus elimination is not an objective or consequence of these programs.

In the late 1980s, the International Potato Center (CIP) in collaboration with Chinese agricultural scientists began a project to develop and transfer new methods for propagating virus-free roots and vines for sweetpotato production in China. Such systems are now being developed in the main sweetpotato growing areas of China. The most advanced program can be found in Shandong Province, where virus-free roots were first distributed to farmers in 1994. This paper briefly describes the sweetpotato propagation program, its impact on yield, and its economic consequences.

1 CIP, Bogor, Indonesia.
2 SAAS, Jinan, China.
3 CIP, Lima, Peru.

Development of the Virus-Free Sweetpotato Multiplication System

Sweetpotato is the third ranking crop in Shandong Province after maize and wheat. In the farmers' traditional system, sweetpotato roots are stored from the fall harvest to the following spring planting. Sweetpotatoes are typically grown on poorer-quality rainfed land in rotation with maize or groundnuts, or in a winter wheat-sweetpotato-maize rotation that produces three crops every two years. The spring sweetpotato crop is planted in late March or April and harvested in September or October. When following winter wheat, sweetpotato is planted as a summer crop in July and then harvested in October after the spring crop is harvested. The spring crop accounts for about 60% of the total sweetpotato area in Shandong and exhibits a higher average yield than the summer crop because of its longer growing season. Planting material for the summer crop comes from vines cut from the previously established spring crop.

In the late 1980s, propagation of virus-free roots was identified by international and national sweetpotato scientists as a possible means of improving farm yields of existing sweetpotato varieties in China. Field observations together with laboratory testing indicated high levels of virus infection in sweetpotato plants in farmer's fields, especially the sweetpotato feathery mottle virus (Zhang, 1996). In 1988 with technical assistance from CIP, training courses were organized to demonstrate how to produce and multiply virus-free sweetpotato roots. The technique involves taking meristem tips from selected plants

and then regenerating the entire plant using a culture medium (Salazar, 1996). Heat treatment is used to reduce virus concentration in the plant's growing tips up to a point where some are freed of viruses. ELISA tests are conducted to confirm that plantlets are free of virus infection. Virus-free plantlets are then grown out in heated greenhouses and used as mother plants for multiplication.

Following the CIP training courses, scientists from the Shandong Academy of Agricultural Science (SAAS) conducted applied research in tissue culture and multiplication techniques to establish the most appropriate medium for the cultures, the best timing for transplanting, and other multiplication methods. Beginning in 1992, SAAS conducted field trials in different locations of the province to compare yields of virus-free roots with yields from farmers' roots. These trials showed an average yield increase of around 40% in plots using virus-free roots of popular new varieties and even larger increases with virus-free roots of older varieties (Zhang, 1995). The success of the trials led to substantial financial support from provincial and local governments for extension and multiplication of virus-free material for propagation. In 1993 and 1994, large-scale extension and demonstration trials were carried out in all of the major sweetpotato producing counties of the province. The first virus-free roots were extended to farmers in 1994 and extension activities were intensified in 1995.

The organization of the virus-free sweetpotato multiplication system in Shandong is depicted in Figure 1. Because of the possibility of getting two multiplications of propagation material per year (the spring and summer crops), the Shandong program has achieved exceptionally high rates of multiplication: one ha planted the first year can provide sufficient clean roots to plant 250-400 ha the following year. In 1998, net houses in the province had a capacity to produce 10,000 plant cuttings per year, enough to produce first generation production roots for more than 500,000 ha two years later.

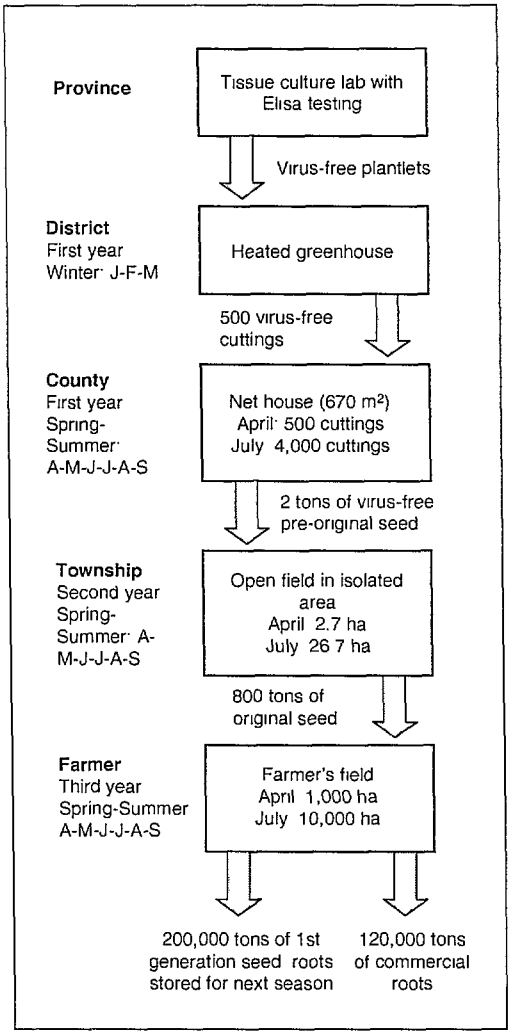

Figure 1. The virus-free seed propagation system in Shandong Province.

Data and Methods for Impact Assessment

Two main sources of information were used to examine the impact of virus-free sweetpotato plant material on farm yields, production, and income: (1) a survey of sweetpotato farmers in 30 villages conducted in 1998; and (2) data on yield demonstration trials, plant material production, and costs of research, extension, and plant multiplication provided by SAAS.

The village survey was designed and conducted by a multidisciplinary team of researchers from SAAS and CIP in August and September 1998. Thirty villages in Shandong Province were selected from the seven districts with the greatest area planted to sweetpotato.

Results and Discussion

Market structure

Responses from the surveys suggest that demand is highly elastic. Not only is production impact regional, but more than 80% of the sweetpotatoes produced in the province are either fed to livestock (where they compete with locally grown and imported maize-based feed) or are processed into starch and/or noodles for export to other provinces or countries. In the survey, farmers were asked whether the sweetpotato market prices had been affected in recent years by the increase in production attributed to virus-free planting material. In all cases, farmers responded that market prices for sweetpotatoes had been stable over the past several years and that demand from the processing industry was strong and could absorb whatever they produced.

Survey responses also provide evidence of an inelastic supply, at least with respect to the adoption of virus-free planting material. Inelastic supply coupled with elastic demand is our preferred "baseline characterization" of market structure for estimating the economic impact of virus-free planting material in Shandong Province.

Estimation of benefits

According to the sweetpotato multiplication program, virus-free plants were estimated to have reached 84% of the sweetpotato area in Shandong Province by 1998. This estimate includes areas planted to new and first and second generation planting material. Among the 30 villages surveyed, virus-free roots were first used in 1995 and by 1998 had spread to 78% of the sweetpotato area in the villages (Figure 2).

The rapid diffusion of virus-free roots can probably best be explained by its significant and noticeable effect on yield. Both large-scale demonstration plots conducted by the Shandong agricultural extension service during 1993-1994 and the village survey show similar levels of average yield improvement from virus-free roots. For the most widely grown variety, Xushu 18, virus-free roots are estimated to have increased yield of the spring crop by 11 t/ha, or by more than 30% over the yield obtained from farmers' own roots. Yield gains from other important varieties (Lushu 7, Lushu 8, Beijing 553) for the spring crop ranged from 6.7 to 10 t/ha according to the village survey and by between 13 and 16 t/ha in the demonstration plots.

For the summer crop, yield of Xushu 18 was estimated by farmers to have increased by an average of 10.6 t/ha, or by 41%. Summer crop yields of other varieties were estimated to have increased by from 8.5 to 10 t/ha.

Gross benefits are estimated by multiplying the estimated area planted with virus-free roots by the average production increase per ha by age of the planting material. For new roots, the production increase is estimated to be 10.35 t/ha, for first generation roots the production increase is estimated to be 9.6 t/ha, and for

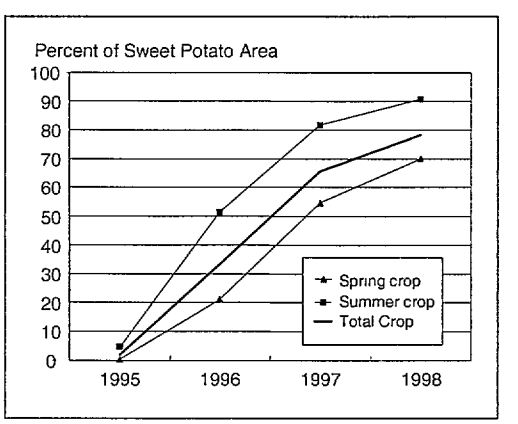

Figure 2. Diffusion of virus-free sweetpotato seed in the 30-village survey.

second generation roots it is estimated to be 6.9 t/ha. These figures are derived from the village survey. Area planted to virus-free roots is derived from data on virus-free planting material production that was provided by the provincial seed program and assumes a seeding rate of 750 kg/ha. The benefit estimation also assumes that the total area planted to sweetpotatoes will remain at about 533,000 ha in the future and that the diffusion of virus-free roots reaches an upper limit of 78% of the total sweetpotato area. Both assumptions are probably conservative.

The program is estimated to increase sweetpotato production in the province by 3.965 million metric tons annually equivalent to a value of gross benefits of US$167 million/yr. Benefits are assumed to remain at this level until the end of the activity in 2020. The diffusion of virus-free roots between 1994 and 1998 resulted in a 22% increase in sweetpotato production in the province, equivalent to a 2.6% increase in global production.

Costs of research, extension and seed multiplication

Research and extension costs were incurred early in the project and were soon dwarfed by expenses for the multiplication of planting material. Research was the principal activity for the first four years of the program. As virus-free roots were being tested and provided to farmers, government subsidies—especially for technical training, construction, and materials—played an important role in getting the multiplication system established and providing farmers with relatively low-cost material. Once farmers were convinced of the benefits of virus-free roots and adopted them, revenues from sales of virus-free roots soon supported most of the costs of the program. By the eighth year of the program, about 90% of the annual US$19.6 million cost of the program was derived from seed sales.

The initial subsidies provided to the program helped keep the price of improved planting material low, and thus promoted its rapid diffusion. One factor that furthered rapid diffusion was that virus-free roots were relatively cheap compared with the benefits of higher yield. Partial budgeting shows that adoption of first generation virus-free roots for the spring sweetpotato crop produced on average nearly 7 Yuan in additional value of yield for each 1 Yuan of added costs. Although it may have been possible to fund a larger share of the program from root sales, it would have required charging farmers higher prices for improved seed and could have dampened diffusion. After large-scale adoption has occurred, it should be possible to recover the initial subsidies through a small, temporary tax on virus-free root sales. Such a tax could provide revenues for funding the development and diffusion of improved planting material in other regions.

Benefit-cost measures and sensitivity analysis

Under the baseline assumptions described above, benefit-cost analysis shows that the virus-free roots program in Shandong Province had an internal rate of return of 202%, and, assuming a 10% discount rate, yielded a net present value of $550 million. Once the program was fully established (1998 and beyond), virus-free roots provided net benefits of $145 million per year.

Other scenarios in Table 1 show the sensitivity of the results to the estimates of yield gains and project costs. Even under grossly conservative assumptions, the virus-free roots project appears to have resulted in impressively high returns.

Poverty and the distribution of benefits to producers

Villages located in the more industrialized parts of Shandong Province, such as those in Yantai and Weifang districts, are noticeably better off than villages in other parts of the province. Villages in the mountainous central and southern districts (including RiZhao, LinYi, and Jinzing districts) are significantly poorer. In the poorer districts, sweetpotato area per

Table 1. Benefit-cost analysis of virus-free sweetpotato seed in Shandong Province, China.

Assumptions	Internal rate of return (%)	Net present value[a] (million US$)	Annual net benefits at full diffusion (million US$)[b]
1. Baseline assumptions	202	550	145
2. Adoption peaks at 90%	202	620	168
3. Costs of research, extension, and seed multiplication doubled	170	467	124
4. Yield improvement estimate halved	170	234	62
5. Costs doubled and yield improvement halved	132	151	40

[a] Net present value is calculated assuming a real discount rate of 10%.

[b] Figures in 1998 US dollars.

household is larger and sweetpotatoes make up a larger component of household income. Survey responses from the 12 villages in Yantai and Weifang indicated an average total income for 1997 of 3,064 Yuan/capita (or 9,817 Yuan/household), and an average agricultural income of 1,798 Yuan/capita. In these villages, average area planted to sweetpotatoes was 0.07 ha/household, and sweetpotatoes contributed 15% of agricultural income. Among the 18 other villages in the survey that were located in poorer areas, average income was reported to be 2,091 Yuan/capita (or 7,316 Yuan/household), with 1,394 Yuan/capita from agriculture. Sweetpotato area per household was 0.14 ha, and sweetpotatoes contributed 25% of agricultural income. The virus-free roots diffused equally well in poor villages as in relatively rich villages and yield effects were not significantly different between rich and poor villages.

First generation virus-free roots gave a net benefit of 3,500 Yuan/ha for the spring crop and about 1,600 Yuan/ha for the summer crop. Multiplying these figures by the average sweetpotato area planted to virus-free roots suggests that in the Yantai and Weifang area, improved sweetpotato planting material increased household incomes by an average of 160 Yuan/household/yr. In the poorer villages of the hilly regions in the center and south of the province, adoption of virus-free roots increased household incomes by an average of 265 Yuan/household/year because of the larger area planted to virus-free roots per household. In the richer areas, virus-free roots only increased average household income by around 1.6%/yr, and in the poorer regions the increase in total household income from virus-free roots was 3.6%/yr. The income effects were thus progressive, with a larger share going to households in relatively poor regions. The effects on household income do not appear to be large because the benefits are so widely distributed among seven million small farmers of the province, each of which, on average, plants about 0.10 ha to sweetpotatoes annually.

Summary and Conclusions

The rapid diffusion of virus-free sweetpotato planting material in Shandong Province, reaching 80% of the province's small growers in only 4 years, can be explained

by several factors. Most importantly, users of the new roots saw yields increase by 10 t/ha, or 30%. Further, the technical package was simple and required only one small change in the farmers production system: the replacement of the source of planting material. Strong demand for sweetpotatoes from the food processing industry also contributed to rapid diffusion by keeping prices from falling in the face of increased supply. This enabled farmers, including late adopters, to continue to capture the gains from technical change. Finally, government subsidies for the establishment of the multiplication program made large-scale production possible in a short time and helped keep the price of improved planting material low.

Shandong Province represents only about 9% of the total area planted to sweetpotatoes in China, and it would seem that virus-free roots would have considerable potential for increasing yield in other provinces as well. In fact, virus-free roots programs are currently under development in all of the major sweetpotato-producing provinces in the country. A straight-line extrapolation of the net value of productivity increases achieved in Shandong in 1998 (when 80% of the sweetpotato area was estimated to have been planted to virus-free roots) would imply potential benefits to all of China of around US$1.5 billion per year.

It is not yet known whether China's success with virus-free sweetpotato planting material can be extended to other countries. Experiments with virus-free seed in East Africa, for example, have not resulted in much yield gain. The reasons for this are not yet well understood, but they may imply that the success of the multiplication program in Shandong Province might not be replicable in some other important sweetpotato-growing areas, such as those found in Sub-Saharan Africa.

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Biological and Selective Control of the Sweetpotato Whitefly, *Bemisia tabaci* (Gennadius) (Hom.: Aleyrodidae)

F. Cisneros and N. Mujica[1]

Sweetpotato (*Ipomoea batatas*) whitefly (SPWF), *Bemisia tabaci* (Gennadius) is widely spread throughout the tropics and subtropics. The pest infests many food crops, ornamentals, and weeds. In temperate countries, whitefly infestations often occur in greenhouse crops.

For the most part, infestations have been trivial. Then, in the 1970s and 1980s, extraordinary whitefly outbreaks occurred in such diverse areas as Sudan, the Middle East, and California and Florida in the United States.

In most cases, whitefly outbreaks have been associated with the intensive use of insecticides, greater tolerance of the pest for insecticides and destruction of natural enemies. Insecticides have been reported to stimulate whitefly fertility (Castle, 1998). There are cases, however, of outbreaks before the appearance of modern insecticides.

A new whitefly species

In the 1990s, widespread whitefly infestations occurred in the tropics and subtropics, including Central and South America and the Caribbean. This new aggressive whitefly was initially thought to be a new strain of *B. tabaci* (strain B). It now has been described as a new species, *B. argentifolii* Bellows & Perring. It is commonly called silverleaf whitefly (SLWF), an apparent reference to the symptoms produced in cucurbit plant leaves (Cohen et al., 1992).

Compared with SPWF, SLWF is becoming one of the most important crop pests because of its higher rate of increase (Bethke et al., 1991), wider range of thermotolerance (Salvucci et al., 1998), efficient transmission of a group of geminiviruses (Gilbertson et al., 1998), high levels of resistance to insecticides (Byrne et al., 1998), more honeydew production (Byrne and Miller, 1990), and a wider range of host plants (Byrne et al., 1990).

Occurrence of SPWF in Peru

The occurrence of SPWF in Peru was overlooked until 1982 when it was reported for the first time in a review of sweetpotato insect pests (Cetraro and Ortiz, 1982). Rodriguez and Redolfi (1993) reported the first evaluations of SPWF population densities in cotton, string beans, and sweetpotato. Population densities were low (av 1.0 nymph/leaf for Rimac Valley and 3 nymphs/leaf for Cañete Valley). According to Gerling (1985), whitefly infestations are considered low when nymph/leaf is < 5.

This situation changed dramatically in 1997 and part of 1998 with climatic changes brought about by El Niño. Heavy infestations were even higher in areas where insecticides were applied. That could be interpreted as a result of the destruction of the whitefly's natural enemies.

These heavy infestation coincided with reports of SLWF in the Cañete Valley. High infestations are seen on sweetpotato, cucurbits, and cotton, leading to specula-

1 CIP, Lima, Peru.

tion that the pest may be replacing SPWF as a sweetpotato pest.

Natural enemies of SPWF

Numerous predators, parasitoids, and some entomopathogenic fungi attack whiteflies. They are usually able to effectively regulate whitefly populations. That was so much the case that for years outbreaks were linked to mismanagement of the agroecosystem, particularly the destruction of natural enemies. General surveys in sweetpotato fields conducted from 1987 to 1991 indicated 65 species of natural enemies that prey upon or parasitize sweetpotato pests. For decades, entomologists considered sweetpotato fields that had not been sprayed with insecticides as natural refuges for biological control agents.

Effects of nonselective compounds on the upsurge of SPWF

More than 50 conventional insecticides are registered for use against *Bemisia* whiteflies, in some cases for reducing virus transmission. All kinds of products are involved including organophosphates, carbamates, and pyrethroids. Most treatments are directed toward controlling adults, because immature life stages are usually less susceptible and more difficult to reach. Whiteflies at those stages are immobile and located on the underside of leaves.

Additional applications are required as new adults emerge from undamaged puparia. Nine to 15 applications may be necessary to keep adult populations low. Under these conditions whitefly readily develops resistance to insecticides.

In 1997, under the influence of high temperatures brought on by El Niño, most affected farmers applied insecticide 2-4 times, some up to 6 times, against the West Indian sweetpotato weevil (*Euscepes postfasciatus*), whiteflies, and white grubs. As many as 30 commercial insecticide formulations were used. One of the most commonly used against the West Indian sweetpotato weevil was carbofuran. Fields treated with carbofuran showed the highest populations of whiteflies. This effect was not only due to the destruction of natural enemies, but to the trophobiotic effect of the insecticide on the whitefly.

Effects of bioinsecticides and other selective compounds on whiteflies

A search for alternative compounds led to the use of rotenone, pyrethrum, a chitin inhibitor, and entomopathogenic fungi against the whitefly pest.

Plant-derived insecticides and mineral oil. Plant-derived insecticides, particularly rotenone and pyrethrins, are coming back into use to control crop pests in response to the need for safer products. Mineral oils act as a suffocating agent for immature stages of whiteflies.

Selective compounds. Several chitin inhibitors have been introduced in recent years (buprofezin, pyriproxyfen, diafenthiuron, and imidacloprid) to control *Bemisia* whiteflies on cotton and other crops. Most of them have low toxicity to mammals and to biological control agents. Buprofezin shows low toxicity to *Encarsia formosa* Gehan and *Cales noacki* Howard, parasitoids of whiteflies (Mendel et al., 1994; Garrido et al., 1984). It affects embryogenesis in adults and moulting in immature stages.

Entomopathogens. Pathogens most commonly recorded infecting *Bemisia* whiteflies in nature are *Paecilomyces fumosoroseus*, *Verticillium lecanii*, and *Aschersonia* sp. Occasional pathogens infecting *Bemisia* whiteflies, also under natural conditions, are *Beauveria bassiana* and *Entomophthora* sp.

There is not much information on the occurrence of epizootic diseases caused by pathogenic fungi. But under high humidity, and if sufficient numbers of pathogenic spores are present, disease should develop. Experiences with the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), and the citrus woolly whitefly, *Aleurothrixus*

floccosus, have shown that pathogenic fungi can be effective (Fransen, 1990; van der Shaaf et al., 1991).

Project goal

A strategy has been developed for an integrated pest management (IPM) program for the management of *Bemisia* whiteflies in sweetpotato. The activities reported here were aimed at evaluating the occurrence of natural enemies and the effectiveness of selective compounds, including bioinsecticides, plant-derived products, and a chitin inhibitor to identify an alternative to chemical insecticide use.

These studies were undertaken before the incidence of SLWF in the Cañete Valley. It is hoped that the methods reported here will have similar efficacy in the management of SLWF.

Materials and methods

Natural enemies of the whitefly

CIP, in collaboration with the Department of Entomology of the Agrarian University, La Molina, Peru, has studied sweetpotato pests and their natural enemies along the central coast of Peru since 1986. In 1997 and 1998, the research emphasis was on studying the natural enemies of whitefly.

Soil-inhabiting predators. Pitfall traps, 1-L plastic cups containing 500-cc formaldehyde (5% concentration), were placed in sweetpotato fields. Traps were collected weekly and the number of predators recorded.

Foliage-inhabiting predators. Predators were collected directly from the canopy of sweetpotato plants and their presence and numbers recorded. Samples (25 plants/field) were taken weekly.

Parasitoids. Whitefly-infested leaves of sweetpotato were gathered at 15-day intervals during the sweetpotato-growing season. Collected leaves were placed in plastic containers and covered with a fine mesh until the emergence of parasitoids.

Selective compounds

Several compounds from different groups (plant-derived insecticides, entomopathogens, a chitin inhibitor, and mineral oil) were tested for their effectiveness against whitefly (Table 1).

Preliminary trial. A preliminary study was conducted in a commercial sweetpotato field, 30 d after planting, with sweetpotato cultivar INA-100, at San Luis, Cañete, Peru, May 1998. Five compounds were evaluated (rotenone, buprofezin, *Verticillium lecanii, Entomophthora virulenta*, and detergent). Carbofuran was used as a farmers' check. The field was set up in a randomized complete block design (RCBD), with seven treatments and four replicates, in plots 30 rows (l m between rows) wide and 50 m long (1,500 m^2). Dosages are presented in Table 1. The plots were sprayed on 27 May with a motorized, backpack sprayer at a rate of 300 L/ha.

Trials with bioinsecticides and other selective compounds. Four trials were conducted to evaluate the effectiveness of the five compounds listed in the preliminary experiment. The compounds were tested individually and in mixtures. Trials were carried out in a sweetpotato field 60 d after planting with sweetpotato cultivar INA-100 in San Luis, Cañete, Peru, May-July 1998.

Trial 1 - Plant-derived insecticides. Plant-derived insecticides selected were three commercial formulations of rotenone, an emulsifiable concentrate (EC), a wettable powder (WP), and a commercial mixture of rotenone and pyrethrin (EC).

Trial 2 - Chitin inhibitor. The chitin inhibitor, buprofezin, was tested in a mixture with plant-derived insecticides.

Trial 3 - Entomopathogens. Three fungi pathogens were selected and tested in the

Table 1. Treatments used in 5 different trials with selective compounds (entomopathogens, plant-derived insecticides, mineral oil, and a chitin inhibitor) against sweetpotato whitefly. Checks included are absolute checks and insecticide-treated checks. Cañete Valley, Peru, 1998.

		Technical name	Trade name[a]	Concentration/ dosage
Preliminary experiment	T1	Buprofezin	Aquitin	0.1%
	T2	Rotenone	Extracto 50 WP	0.1%
	T3	*Verticillium lecanii*	Vertisol	$1x10^9$ conidias/bottle
	T4	*Entomophthora virulenta*	Vektor	$1x10^9$ conidias/bottle
	T5	Detergent	Ace	
	T6	Treated check: carbofuran	Carbofor 75 WP	0.2%
	T7	Absolute check		
Experiment 1	T1	Rotenone + buprofezin	Rhotenox 10 EC + Aquitin	0.4% + 0.1%
	T2	(Rotenone and pyrethrum)+buprofezin	Rhotenox-SP + Aquitin	0.4% + 0.1%
	T3	Rotenone + buprofezin	Extracto 50 WP + Aquitin	0.1% + 0.1%
	T4	Check		
Experiment 2	T1	Rotenone	Rhotenox 10 EC	0.4%
	T2	Rotenone and pyrethrum	Rhotenox-SP	0.4%
	T3	Rotenone	Extracto 50 WP	0.1%
	T4	Check		
Experiment 3	T1	Oil mineral	Triona-5	1%
	T2	Oil mineral + rotenone	Triona-5 + Extracto 50 WP	1% + 0.1%
	T3	Treated check: endosulfan	Thiodan 35 EC	0.15%
	T4	Treated check: carbofuran	Carbofor 75 WP	0.2%
	T5	Check		
Experiment 4	T1	*Verticillium lecanii*	Vertisol	$1x10^9$ conidias/bottle
	T2	*Entomophthora virulenta*	Vektor	$1x10^9$ conidias/bottle
	T3	*Beauveria bassiana*	Bauveril	$5x10^{11}$ conidias/bottle
	T4	Check		

[a] WP= wettable powder; ED=emulsifiable concentrate, SP=supension powder.

field: *Verticillium lecanii, Entomophthora virulenta,* and *Beauveria bassiana*. Formulations of the fungi (dehydrated conidia) were commercially-produced. Dosages used were those recommended by the manufacturer.

Trial 4 - Other products. Selective products were an emulsifiable mineral oil and mineral oil mixed with rotenone. Two nonselective products were used as farmers' check (endosulfan and carbofuran).

Each trial was an RCBD with four replicates. Experimental plots were 14 rows

wide and 25 m long (350 m^2). Plots were treated twice at 14-d intervals (24 June and 10 July) using a motorized, backpack and sprayed at a rate of 400 L/ha. Sprayers used special nozzles to ensure wetting of the underside of leaves where whiteflies live.

Sampling methods

At weekly intervals, 20 leaves/plot were collected from among the most heavily infested leaves on the bottom or middle part of the plant. Nymphs and pupae were counted under a stereoscope in the laboratory. Mortality of nymphs and pupae was determined when they were dry. Population density was expressed as number of immature stages/cm^2 due to the differences in leaf size.

Estimates of the whitefly populations were done 0, 7, and 14 d after application in the preliminary trial. In the four other trials, estimates of the whitefly population were done 0, 7, and 14 d after the first application; and 7, 14, and 21 d after the second application. Adult populations were not evaluated because of the high migratory movement of whiteflies from highly infested surrounding fields.

Statistical analysis

Data were transformed (square root) before statistical analysis and were analyzed using 1-way ANOVA. Means were separated by LSD (P = 0.05). To separate the effects of pesticide treatment from those caused by natural factors, the percent of population reduction was corrected using a modified Abbott's formula (Fleming and Retnakaran, 1985).

Results and Discussion

Natural enemies of the whitefly

Predators. Predators collected in the canopy of sweetpotato plants (Table 2) were as varied as the groups reported worldwide by Nordlund and Legaspi (1995), except for mites, which were not sampled. The most abundant predators were spiders of two genera, *Anyphaena* and *Pardosa,* and the fly, *Condylostylus similis.* The predatory

Table 2. Ocurrence of canopy inhabitant predators[a] in sweetpotato infested with white fly *Bemisia tabaci* in the Cañete valley, Peru.

Predators	1994		1995		1996	
	No	%	No	%	No	%
Spiders	101	57.4	93	45.5	113	38.4
Chrysoperla externa	3	1.7	15	7.3	9	3.1
Orius sp.	-	-	-	-	7	2.1
Hyaloides sp.	-	-	-	-	5	1.4
Nabis punctipennis	5	2.8	8	3.9	7	2.4
Rhinacloa sp.	18	10.2	24	11.7	7	2.4
Aknisus sp.	4	2.3	9	9.4	3	0.3
Scymmus sp.	-	-	-	-	13	4.3
Coccinelids	18	10.2	18	8.8	30	10.1
Condylostylus similis	26	14.8	30	14.6	93	32.1
Syrphidae	-	-	-	-	8	1.3
Geocoris sp.	1	0.6	8	3.9	8	3.2
Total	**176**	**100**	**205**	**100.0**	**292**	**100.0**

[a] Number of predators in 1.25 m^2

activity of nonwebbing spiders on whiteflies is not well known, but *Anyphaena* spp. efficiently trapped whitefly adults in their webs. The coccinellids (*Cycloneda sanguinea, Scymnus* sp., *Hippodamia convergens, Eriopis connexa,* and *Coleomegilla maculata*) were fairly abundant and preyed upon whitefly immature stages. Other, less abundant species, that also preyed upon the immature stages were *Chrysoperla* spp. *Hyaliodes* sp., *Rhinacloa* spp., *Nabis punctipennis,* and *Geocoris punctipes.*

The most abundant soil inhabiting predators were a carabid beetle (*Pterostichus* sp.) and one species of earwig (*Labiduria riparia)* (Table 3).

Parasitoids. Three genera of parasitoids were recorded in the Cañete Valley (Table 4). As in other parts of South America and the world, *Encarsia* species were the most abundant, with *E. portieri* being the most frequently found. Parasitism used to be the most important mortality factor of whiteflies in the Cañete Valley. In 1987, an average of 41% parasitism was recorded, ranging from 4% in fields with insecticide treatments to 70% in untreated fields (Table 5).

Parasitism has been reduced with increased insecticide use. At the same time, infestations of whitefly have steadily increased to present levels. Donet and Vergara (1994) recorded the destruction of spider populations in sweetpotato fields treated with insecticides against the West Indian sweetpotato weevil. Velapatiño and Sanchez (1996) recorded low populations of predators in Cañete fields commonly treated with insecticides.

Table 3. Soil inhabitant predators captured by pitfall traps in sweetpotato fields in Cañete Valley, Peru, 1998.

Year	Predators /trap/season (No)	
	Pterostichus sp. (Coleoptera: Carabidae)	*Labiduria riparia* (Dermaptera:Labiduridae)
1994	306.4	94.8
1996	100.0	44.9
1998	26.0	350.7

Table 4. Parasitoids[a] of sweetpotato whitefly nymphs, central coast of Peru.

Parasitoids	Locality	
	La Molina	Cañete
Platygasteridae		
Amitus sp.	VS	-
Encarsia sp. prob. *bicolor* De Santis	S	VS
Encarsia porteri (Mercet)	A	S
Encarsia (Prospaltella) sp. (A)	VS	VS
Encarsia sp. (B)	VS	-
Eretmocerus sp.	-	VS

[a] VS= very scarce; S= scarce; A=abundant.
(A) and (B) non-identified species.

Table 5. Variation in the level of parasitism of the sweetpotato whitefly *Bemisia tabaci*, on sweetpotato during the last 11 years, Cañete Valley, Peru, 1987-1988.

Year	Nymph/leaf	Parasitism (%)		
		Minimum	Maximum	Average
1987	1.9	4.0	70.0	41.2
1989	2.4	5.0	27.0	28.0
1994	20.5		(few, not quantified)	
1995	39.8	0.0	2.6	0.3
1996	46.4	0.0	0.0	0.0
1998	853.5		(few, not quantified)	

Selective compounds

Preliminary trial. Buprofezin was very effective against nymphs, reducing the whitefly population of 32.1 nymph/cm^2 to 0.9 nymph/cm^2 in 14 d (98% mortality). No significant differences in nymph number were observed between other treatments (rotenone, entomopathogens, and detergent) and the check, but a decrease in the adult population in the field was observed. Plots treated with carbofuran had an increase in whitefly populations from 62.7 nymphs/cm^2 to 102.9 nymphs/cm^2 in 14 d. In the trials discussed below, rotenone and buprofezin were mixed for better whitefly control.

Identification of nymphs affected by the different treatments was one of the main difficulties faced during the experiments. Because nymphs and pupae are immobile and fixed to the underside of the leaf surface, movement could not be used as a sign of life. In addition, most products (entomopathogens, rotenone, mineral oil, and buprofezin) are intrinsically slow acting. Mortality does not occur as fast as with conventional insecticides. It was also difficult to spray the underside of the leaf surface even with the special nozzles used.

Trial 1 – Plant-derived insecticides. No significant differences (P = 0.05) in nymph number were observed until 2 wk after the second application (Table 6). Rotenone + pyrethrin resulted in an average of 1.2 nymph/cm^2 compared with 5.2 nymph/cm^2 in the check, representing 73% mortality (Table 6). These formulations can be used under moderate levels of whitefly infestation.

Trial 2 – Chitin inhibitor. Buprofezin mixed with other compounds (rotenone or pyrethrin) did not increase control of immature stages (Table 6). The effect of buprofezin was evident (more than 90% mortality) 7 d after the second application when the av was 0.6-0.8 nymph/cm^2 compared with 13.3 nymphs/cm^2 in the check. The residual effect of buprofezin in the field resulted in nymph mortality of 76-88.5% over 21 d.

Trial 3 – Entomopathogens. To separate healthy immature stages from those infected by the entomopathogens was difficult, particularly during the first 10 d after the first application when no external changes in nymphs and pupae were evident. After the second application, only *B. bassiana* was effective, with 69% of nymph population dead (dried) after 21 d (Table 6). We were unable, however, to detect the fungus before dehydration.

Trial 4 – Other products. Mineral oil acts as a suffocating agent for immature

Table 6. Leaf average nymph population per square cm at the indicated days after application per treatment, Cañete, Peru, 1998.

		Before		Days after application									
		treatment		First application				Second application					
	Treatment			7		14		7		14		21	
Exp. 1	Rotenone	15.5	a	5.8	a	5	a	2.7	b	2.4	ab	2.03	a
	Rotenone and pyrethrum	23.6	a	5.1	a	11.2	a	3.7	b	1.2	b	1.2	a
	Rotenone	34.6	a	7.5	a	11.7	a	12.3	a	4.7	ab	3.2	a
	Check	27.6	a	7.3	a	11.7	a	9.3	ab	5.2	a	2.73	a
Exp. 2	Rotenone + buprofezin	21.9	a	7.5	a	4.9	a	0.7	b	0.3	b	0.26	a
	(Rotenone and pyrethrum) + buprofezin	36.5	a	6.4	a	5.7	a	0.6	b	0.1	b	0.5	a
	Rotenone + buprofezin	33.4	a	7.5	a	7.2	a	0.8	b	0.4	b	0.83	a
	Check	35.7	a	8.5	a	9.1	a	13.3	a	3.5	a	3.7	a
Exp. 3	*Verticillium lecanii*	34.9	a	13.9	a	8.9	a	6.6	a	2.8	a	0.85	a
	Entomophthora virulenta	30.6	a	11.7	a	8.2	a	4.4	a	2.3	b	0.83	a
	Beauveria bassiana	34.6	a	13.3	a	11.8	a	6.9	a	1.8	ab	0.4	a
	Check	20.9	a	14.3	a	10.2	a	5.7	a	2.1	ab	0.78	a
Exp. 4	Oil mineral	16.2	a	6.1	b	4.6	a	2.2	c	3.8	b	3.48	ab
	Oil mineral + rotenone	21.3	a	5.6	b	6.4	a	2.3	bc	3.1	b	2.6	ab
	Treated check : endosulfan	24.2	a	9.9	ab	6.7	a	2	c	2.7	b	2.45	ab
	Treated check : carbofuran	15.1	a	6.6	b	9.7	a	7.6	a	7.8	a	5.35	a
	Check	20.9	a	14.3	a	9.8	a	4.5	ab	4.2	ab	3.6	ab

Within a column, means followed by a common letter do not differ significantly at P=0.05 by DMRT.

stages of whitefly. Its effect was noticeable 7 d after the first application. The number of nymphs was reduced by 45% compared to the check (6.1 nymph/cm^2 compared to 14.3 in the check) (Table 6). No residual effect was observed. When rotenone was added to the mineral oil treatment, no significant increase in the effect (P = 0.05) was observed throughout the evaluation dates (Table 6).

Mineral oil treatment was as good as the farmers' check (endosulfan) or better in the cases where farmers used carbofuran. Plots treated with carbofuran showed the highest whitefly population when, 14 d after the second application, the population increased 157% compared with the check. This illustrates the trophobiotic effect of carbofuran on the whitefly nymph population.

Conclusions

All treatments—entomopathogens, rotenone, mineral oil, and buprofezin—contributed to controlling whitefly by killing nymphs. Mortality probably was higher than the level recorded due to their slow action. The compounds tested are consid-

ered fairly safe for natural enemies (except carbofuran and endosulfan, used as treated checks).

Unfortunately, under the experimental conditions, it was not possible to verify the reaction of natural enemies. The area had been under such intensive chemical control for several seasons that no parasitoids were recovered. Under other conditions we might have expected the action of natural enemies to complement treatments.

The whitefly outbreak in Cañete Valley, which coincided with the identification of SLWF, a new species of whitefly displacing SPWF in Cañete, is a repeat of what has happened in other parts of the world. Conditions were similar, in particular the intensive use of insecticides. The effects were also similar: higher populations, wider range of crops affected, more severe damage, and resistance to insecticides.

The use of rotenone, chitin inhibitors, mineral oils, and entomopathogenic fungi were fairly effective in our experiments. These products can be integrated with other IPM components to manage SPWF. Also, these treatments are expected to allow the recovery of parasitoids and predators decimated by the use of conventional insecticides.

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An Efficient System of Embryogenic Suspension Cultures and Plant Regeneration in Sweetpotato

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Genetic transformation offers great potential for improving the disease or pest resistance and nutrition quality of sweetpotato [*Ipomoea batatas* (L.) Lam.]. On-going research in these areas includes developing transgenic sweetpotato with resistance to sweetpotato virus diseases (Beachy et al., 1992; Murata et al., 1998), sweetpotato weevil and other insect pests (Newell et al., 1995; Zhang et al., 1997), and enhanced protein content in the storage root and leaves (Prakash et al., 1998). In spite of the various successful cases in sweetpotato transformation, the lack of an efficient system for regeneration has been a bottleneck for the application of transgenic technology in sweetpotato. The regeneration frequency in sweetpotato is often genotype dependent, ranging from 0 to 85% in tested cultivars (Gosukonda et al., 1995, Zhang et al., 1997). So far only a small number of genotypes have been regenerated, based on the information gathered from the related publications.

In sweetpotato, shoot apices of many genotypes can produce embryogenic callus with somatic embryos on the medium supplemented with 2,4-D. Somatic embryos can also develop into whole plants on the basal medium (Liu and Cantliffe, 1984; Jarret et al., 1984; Liu et al., 1992, 1993, 1997; Tan et al., 1993; Desamero et al., 1994; Otani and Shimada, 1996). However, in most cases the frequencies of somatic embryogenesis were low.

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The development of a system of embryogenic suspension cultures has been a focal point for improving the regeneration frequency in sweetpotato. Chee and Cantliffe (1988, 1989), Chee et al. (1990), and Bieniek et al. (1995) succeeded in establishing embryogenic suspension cultures of sweetpotato cultivar White Star. Liu et al. (1997) investigated embryogenic suspension cultures of a Japanese cultivar Kokei No.14 and a Chinese cultivar Xindazi. An improved frequency of plant regeneration from the embryogenic suspension cultures was obtained.

The objective of this research is to develop an efficient system of embryogenic suspension cultures for a wide range of sweetpotato genotypes, which will eventually lead to a universal regeneration protocol for sweetpotato.

Materials and Methods

Plant materials

Eight cultivars of sweetpotato, Gaozi No.1, Koganesengan, Kokei No.14, Lizixiang, Nongdahong, Tamayutaka, Xindazi, and Xushu 18 were used in this study. They are important cultivars in China or Japan. The storage roots were grown in pots in a greenhouse. The young sprouts obtained were used for the isolation of shoot apices.

Induction of embryogenic callus

Young shoots about 30 mm-long were excised, washed with tap water, and sterilized with 70% ethanol for 20 sec and 2% sodium hypochlorite solution for 5 min. The sterilized materials were fully rinsed

with sterile distilled water. Shoot apices of about 0.5 mm in length were isolated with the aid of a dissecting microscope and cultured on MS medium supplemented with 2.0 mg/L 2,4-D, 3.0% sucrose (w/v), and 0.8% (w/v) agar, pH 5.8, at 28°C in the dark. The cultures were examined periodically under a dissecting microscope.

Initiation and maintenance of embryogenic suspension cultures

Embryogenic calli were obtained from shoot apices of 8 cultivars. Six- to eight-week-old embryogenic calli were used for the initiation of embryogenic suspension cultures. Embryogenic calli were crushed into cell-aggregates and free cells through a stainless steel microsieve with mesh size of 0.46 mm. The cells were then placed into a 100 mL Erlenmeyer flask containing 20 mL liquid MS medium with 2.0 mg/L 2,4-D and 3% sucrose (pH=5.8). The cultures were incubated on a reciprocal shaker (100 strokes/min) at 28°C under 13 h of cool-white fluorescent light at 500 lux. Embryogenic suspension cultures were maintained by subculture at a 2-week interval. At each subculture, cell-aggregates over 0.5 mm in size were crushed through a stainless steel microsieve with mesh size of 0.46 mm and then transferred to the fresh medium.

Regeneration of plants from embryogenic suspension cultures

Twenty weeks after the initiation protocol and at 4-week intevals cell-aggregates about 1.0 mm in size were transferred to solid MS medium supplemented with 2,4-D (2.0 mg/L). This condition is suitable for the proliferation of cell-aggregates and the formation of somatic embryos at 28°C in the dark. Four to six weeks after transfer, the embryogenic calli obtained with somatic embryos were further cultured on MS medium supplemented with 1.0 mg/L ABA for 4 to 5 weeks to induce the germination of somatic embryos at 28°C under 13 h of cool-white fluorescent light at 3000 lux. Plantlets from somatic embryos developed into whole plants on the basal medium.

Results

Formation of embryogenic callus

The incubated shoot apices responded actively to the culture conditions. After 3 to 4 days, most of them started to produce white, friable callus. This callus was non-embryogenic and grew rapidly. A few of shoot apices directly formed embryogenic callus. This type of embryogenic callus grew much slower than the non-embryogenic callus. Four to five weeks after incubation, embryogenic calli were formed on the surface of the non-embryogenic calli (Figure 1). These two kinds of embryogenic calli (the one directly formed from the shoot apices and the one formed on the surface of the non-embryogenic calli) were easily distinguishable from the non-embryogenic calli because of their bright-yellow and compact appearance. Both embryogenic calli were used to initiate embryogenic suspension cultures. All of the eight tested cultivars successfully formed an embryogenic callus, although there is variation in the frequency of embryogenic callus formation (Table 1).

Establishment of embryogenic suspension cultures

Using embryogenic calli derived from shoot apices of eight cultivars, we have developed a system of embryogenic suspension cultures, which has high potential for regeneration. When maintained in liquid MS medium containing 2.0-mg/L 2,4-D, the cells proliferated rapidly and dispersed well (Figure 2). The embryogenic suspension cultures consisted of bright-yellow and compact embryogenic cell-aggregates and free cells. After 20 weeks of initiation, approximately 20,000 embryogenic cell-aggregates about 1.0 mm in size were obtained from a single embryogenic callus derived from a shoot apex in all eight cultivars.

Regeneration of plants from embryogenic suspension cultures

After 20 weeks of the initiation protocol, the regeneration ability of embryogenic

Table 1. Formation of embryogenic callus from shoot apices in eight sweetpotato cultivars.

Cultivar	Origin	Shoot apices Incubated	Shoot apices forming embryogenic callus	
		No.	No.	%
Gaozi No.1	China	57	16	28.1
Koganesengan	Japan	27	5	18.5
Kokei No.14	Japan	115	98	85.2
Lizixiang	China	89	61	68.5
Nongdahong	China	56	29	51.8
Tamayutaka	Japan	53	14	26.4
Xindazi	China	30	5	16.7
Xushu 18	China	32	7	21.9

suspension cultures was tested every 4 weeks. By the transfer of cell-aggregates (about 1.0 mm in size) to solid MS medium supplemented with 2.0 mg/L 2,4-D, the cell-aggregates proliferated rapidly into typical embryogenic calli with large numbers of somatic embryos (Figure 3). When the obtained embryogenic calli with somatic embryos were further cultured on MS medium supplemented with 1.0 mg/L ABA, somatic embryos germinated and formed plantlets (Figure 4).

The regeneration frequency peaked at about 24 weeks after initiation when 100% of the cell-aggregates regenerated into plants in all eight cultivars. After that, the regeneration frequency gradually decreased, as some of the cell-aggregates became non-embryogenic. However, there is cultivar difference in this regard. For example, Xindazi still maintained a frequency of up to 100% as long as 36 weeks after initiation.

Discussion

The structure, color, and pattern of the embryogenic calli formation from shoot apices of the eight cultivars were very similar to those reported by Liu et al. (1992 and 1993). The formed embryogenic calli were used to initiate embryogenic suspension cultures. The embryogenic suspension cultures proliferated rapidly and dispersed well in MS medium containing 2.0 mg/L 2,4-D. By using the suspension culture for 20 weeks, approximately 20,000 embryogenic cell-aggregates about 1.0 mm in size can be produced per embryogenic callus derived from shoot apices. The suspension cultures can maintain their embryogenic ability for at least 24 weeks.

The long-term maintenance of embryogenic suspension cultures can be achieved by the re-cultivation of embryogenic cell-aggregates isolated from the suspension cultures. Additionally, several factors are important for successfully maintaining an embryogenic culture.

First, the embryogenic culture needs to be subcultured in a timely fashion. Our previous study shows that delaying the subculture diminished the embryogenic ability of the cell-aggregates. Liu et al. (1997) reported that at 21 weeks after initiation, only 61.1% of cell-aggregates of Kokei No.14 were still embryogenic if the suspension cultures were not subcultured in a timely way.

Second, the proliferation of cell-aggregates on solid MS medium with 2.0 mg/L 2,4-D is of critical importance for achieving a high frequency of somatic embryo formation and plant regeneration.

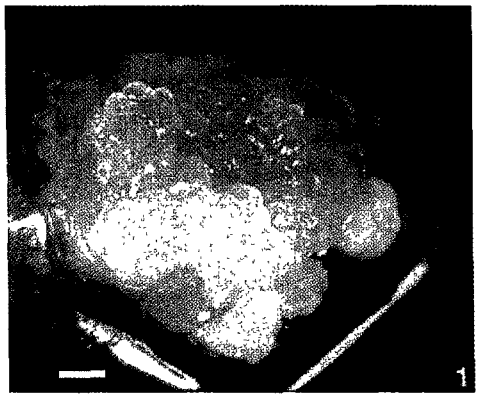

Figure 1. Embryogenic callus derived from a shoot apex of sweetpotato cultivar Lizixiang on MS medium supplemented with 2.0 mg/L 2,4-D (scale bar = 1.0 mm).

Figure 2. Embryogenic suspension cultures of sweetpotato cultivar Lizixiang proliferating in MS medium containing 2.0 mg/L 2,4-D.

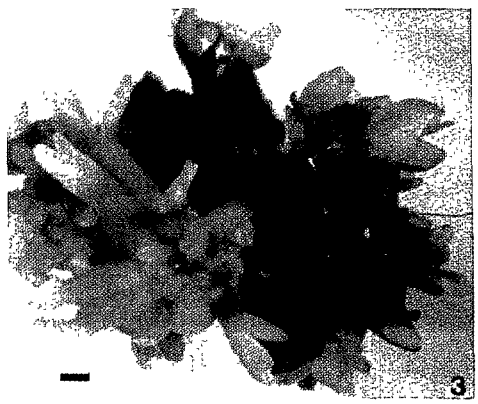

Figure 3. Somatic embryos formed on embryogenic callus derived from a cell aggregate of sweetpotato cultivar Lizixiang on MS medium supplemented with 2.0 mg/L 2,4-D (scale bar = 1.0 mm).

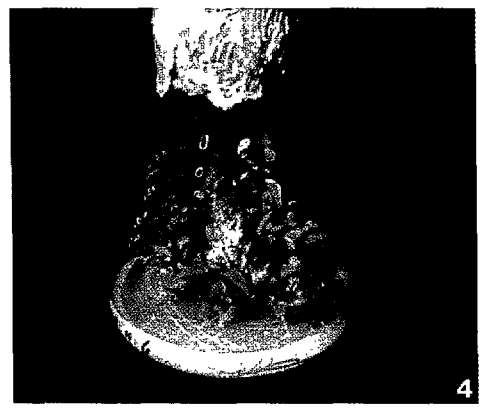

Figure 4. Germination of somatic embryos and formation of plantlets of sweetpotato cultivar Lizixiang on MS medium supplemented with 1.0 mg/L ABA.

Third, the size of cell-aggregates, which were transferred to 2,4-D solid medium, is also important to obtain a high regeneration frequency. Chee and Cantliffe (1989) reported that the percentage of somatic embryo formation decreased as the size of the cell-aggregates decreased. They found that sweetpotato somatic embryos only formed on cell-aggregates at least 0.18 mm in size and cell-aggregates 0.71-1.0 mm in size gave the maximum percentage of somatic embryo formation (up to 70%). Our results indicated that 100% of cell-aggregates about 1.0 mm in size produced somatic embryos and plants in all 8 tested cultivars.

We have succeeded in the development of an efficient system of embryogenic suspension cultures and plant regeneration in eight sweetpotato cultivars. This system of embryogenic suspension cultures has an excellent application potential in genetic transformation for cultivar improvement, as

well as in cryopreservation of sweetpotato germplasm.

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Expression of Soybean Proteinase Inhibitor in Sweetpotato

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Transformation of sweetpotato (*Ipomoea batatas*) with serine-type proteinase inhibitors (PIs) offer a new strategy for developing host resistance against sweetpotato weevil (*Cylas* spp.), the major threat to sweetpotato worldwide. Foreign genes encoding PIs have been introduced into tobacco, tomato, strawberry, potato, and many other crops for control of a range of insect pests. These proteins bind to proteinases in the midgut of the insect thus interfering with the insect's metabolism. Transgenic tobacco plants expressing recombined serine PIs have demonstrated enhanced resistance to Heliothis *virescens* (Hilder et al., 1987), *Manduca sexta* (Johnson et al., 1989), and *Spodoptera litura* (Yeh et al., 1997).

The predominance of serine-type proteases in the midgut of three *Cylas* spp. was confirmed by inhibition assays. Serine-type inhibitors, regardless of the species or developmental stage of the insect, inhibited the proteinases detected (Rety et al., 1998). The inhibitory spectrum of soybean (*Glycine max*) trypsin inhibitor (SBTI) against the midgut proteases was apparently larger than that of endogenous inhibitors in sweetpotato. It was apparently stable in the presence of insect insensitive proteinases, suggesting the potential usefulness of this inhibitor in controlling weevil larvae and adults (Zhang et al., 1997).

Newell et al. (1995) developed the first transgenic lines of PI-expressing sweetpotato with a cDNA sequence encoding a cowpea (*Vigna unguiculata*) trypsin inhibitor (CpTI). Feeding tests with the West Indian sweetpotato weevil (*Euscepes postfasciatus*) were carried out recently at CIP by performing a no-choice test in a screenhouse-based bioassay. Two transformed clones were found moderately resistant in consecutive tests over 2 years, suggesting the actual usefulness of the trypsin inhibitor in weevil control.

This paper describes the Agrobacterium-mediated transformation of sweetpotato with a soybean kunitz trypsin inhibitor (SKTI-4) cDNA clone and the analysis of recombinant SBTI produced in sweetpotato cells against trypsin and sweetpotato leaf proteinases.

Materials and Methods

Sweetpotato transformation with SKTI-4 gene

Complete leaves with petioles of in vitro plants of sweetpotato cv. Jewel, PI-318846-3, and Jonathan, and leaf segments of cv. Maria Angola were used as explants. Explants were inoculated and co-cultivated with *Agrobacterium tumefaciens* LBA4404 carrying plasmid pKTI-4. The T-DNA region of this plasmid harbors the SKTI-4 gene, the b-glucuronidase (GUS) reporter gene, and the NPTII marker gene (Figure 1).

The first three explants went through two successive transfers: First to F15 medium (Murashige-Skoog (MS) salts, 0.2 mg/L 2, 4-D; 0.2 mg/L zeatin; 50 ppm kanamycin-sulfate; 200 ppm cefotaxime; 30g/L sucrose; and 3.6 g/L phytagel) for 3 d; and second to F9 medium (same as F15 but without 2, 4-D). All calli formed were analyzed for GUS activity, and positive calli were transferred to G24D medium (basal medium supplemented with 0.2 mg/L 2,4-D

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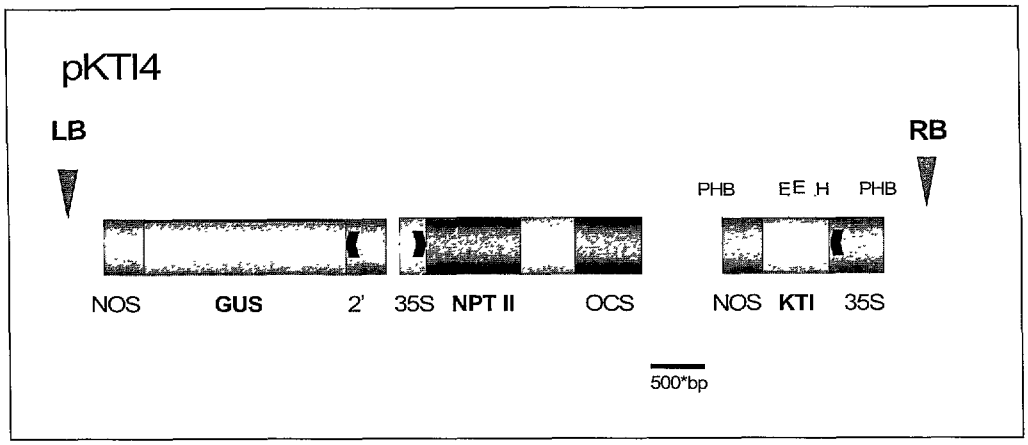

Figure 1. Diagram of T-DNA region of plasmid pKTI-4. Coding regions for ß-glucuronidase (GUS), neomycin phosphotransferase II (NPTII), and Kunitz trypsin inhibitor (KTI) genes are transcribed between TR 2' (2') or Cauliflower mosaic virus 35S (35S) promoter sequeneces and nopaline synthase (NOS) or octopine synthase (OCS) terminator sequences. The direction of transcription is shown by the arrowhead. Relevant restriction enzyme sites are indicated: Pac I (P), Hind III (H), Bam HI (B), Eco RI (E). Left border (LB), right border (RB), base pairs (bp).

and 0.05 mg/L gibberellic acid) for multiplication. After 2 mo they were transferred to auxin-free media for regeneration.

Leaf segments of Maria Angola, following inoculation and co-culture, were cultivated in medium G24D for 2 mo for embryogenic calli induction. These calli were evaluated for GUS activity and positive calli were transferred to MS30-Vit medium for embryo development.

GUS test of SKTI-4 transgenic lines

GUS expression in transformed plants was evaluated by histochemical assay as described by Jefferson (1987). Leaves, roots, and stem segments were incubated in phosphate buffer pH 7 with X-gluc (5-bromo-4-chloro-3-indolyl-beta-D-glucuronic acid) substrate. Blue staining of the tissue denoted positive reaction.

Kanamycin resistance evaluation of SKTI-4 transgenic lines

Three petridishes with five leaf segments (each segment corresponding to a different leaf) were cultivated for each putative transgenic line. Included in each petridish were two leaf segments of a known transformed line as a positive control. In addition, 2-4 leaf segments of an untransformed plant of the same cultivar were included as a negative control. Medium used for calli induction was 303-64 (MS salts, 1 mg/L zeatin, 0.1 mg/L naftalen-acetic acid, 30 g/L sucrose, and 3.6 g/L phytagel) containing a high concentration (100 mg/L) of the antibiotic kanamycin sulfate. As a control for the effect of the physiological status of the plants, or the effect of the medium, the same experiment was repeated with each line without kanamycin, and also with the untransformed cultivars with the same concentration of kanamycin. Calli development was evaluated after 1 mo in culture.

Southern blot test of transgenic lines

The presence of SKTI-4 sequence was confirmed by Southern blot analysis. DNA was isolated from 4 g of frozen leaf tissue from in vitro plantlets (Dellaporta et al., 1983). Ten micrograms of DNA were digested with restriction enzyme BamHI (the SKTI-4 gene has BamHI restriction sites at left and right borders as shown in plasmid pKTI-4, Figure 1), and separated by electrophoresis in a 0.9% agarose gel. The gel was treated for 10 min with a solution

containing 0.25N HCl, twice for 15 min in 0.5N NaOH, 1.5M NaCl, and twice for 30 min in 1M tris pH 7.4, 20 mM NaOH and was blotted to a nylon filter (Amersham) by capillarity.

One hundred nanograms DNA of SKTI-4 gene isolated by restriction of the plasmid pKTI-2 was radiolabeled with ^{32}P (dATP) and used as a probe for filter hybridization. After hybridization, the membrane was washed twice, for 5 and 15 min in a buffer solution containing 2X SSC, 0.5% sodium dodecyl sulfate (SDS) at room temperature. The membrane was washed twice more for 30 min each in 0.1 X SSC and 0.5% SDS, once at 37°C and once at 65°C. Filters were exposed for autoradiography with an intensifying screen at -70°C for up to 2 d.

PCR analysis of transgenic lines

The SKTI-4 gene was targeted with specific primers and amplified by polymerase chain reaction (PCR) from DNA of in vitro transgenic plants. These 18 base pairs (bp) forward and reverse primers where specially synthesized to flank the 653 bp of the SKTI-4 gene according to the complete PUC-derived pKTI-2 plasmid's sequence provided by C. Newell of Pestax Ltd., UK (Table 1).

The PCR amplification condition was as follows:

1 cycle:	94°C for 1'
35 cycles:	94°C for 1'
	52°C for 2'
	72°C for 3'
1 cycle:	72°C for 7'

For the amplification of each transgenic line, 40 ng of DNA extracted from in vitro plants were used. One nanogram of plasmid pKTI-2 (PUC-derived plasmid harboring the SKTI-4 gene) was used as a positive control. DNA of untransformed plants (C-) and the amplification mixture without DNA (M) were used as negative controls.

Protease and protease inhibitor assays

The protease assay was adapted from Michaud et al. (1993). Thirty-five µL of leaf protein extracts from 8 transgenic lines or from an untransformed control of genotype PI-318846-3 (1 µg protein/µL extract) were incubated with 5 mL of 0.5mg/mL (w/v) trypsin dissolved in 50 mM tris, pH 8.0. The samples were incubated for 15 min at 37°C to allow protease inhibition, and 80 µL of 2% (w/v) azocasein dissolved in the same buffer was added as substrate to each sample. After a 180-min incubation, 300 µL of 10% (w/v) trichloroacetic acid (TCA) was added to the mixture, and residual azocasein was removed by centrifugation for 5 min at 14,000 rpm. The supernatant (350 µL) was then added to 400 µL of 1N NaOH, and the absorbance was measured at 440 nm using a Spectronic spectrophotometer (Milton Roy, Rochester, NY, USA). The absorbance of blanks, which consisted of complete mixtures without trypsin or plant extract submitted to the same treatment, was subtracted from each value. One unit of protease activity was defined as the amount of enzyme required to produce an absorbance change of 1.0 h^{-1} in a 1 cm-cuvette, under the conditions of the assay. The results obtained were compared with controls consisting of (1) trypsin without plant extract (maximum hydrolysis), and (2) trypsin plus extract from an untransformed plant.

Electrophoretic analyses

Expression of proteinase inhibitors in the leaf tissues was visualized by polyacryla-

Table 1. Primer's sequence for PCR reaction.

Primer name	Corresponding sequence	Sequence	Melting temperature (°C)
SKTI2.1 (forward)	SKTI leader sequence	ATGAAGAGCACCATCTTC	52
SKTI2.2 (reverse)	C terminal peptide	TCACACACTGCGAGAAAG	54

mide gel electrophoresis (PAGE) on gels treated with SDS, a mildly denaturing agent. Plant extracts from transgenic lines or from untransformed (control) plants were first incubated with trypsin for 15 min at 37°C to allow protease inhibition by recombinant SBTI. The samples were then fractionated into 10% (w/v) polyacrylamide gel slabs containing 0.1% (w/v) gelatin. The SDS-PAGE procedure is more fully described in Michaud et al. (1996). After electrophoretic migration at 4°C using the MiniProtean II electrophoretic unit (Bio-Rad, Richmond, CA, USA), the gels were transferred into a 2.5% aqueous solution of Triton X-100™ for 30 min at room temperature to allow proteinase (trypsin) renaturation. The gels were then placed in an activation or proteolysis buffer (50 mM tris, pH 8.0) at 37°C for 3 h and finally transferred into a protein staining solution [0.1% (w/v) Coomassie Brilliant Blue in 25% (v/v)/ 10% (v/v) acetic acid]. For storage, the gels were dried using Gel Drying Film (Promega, Madison, WI, USA). Trypsin activity was visualized as a clear (lysis) band against the blue gelatin background; trypsin inhibition was visualized as a weaker band compared with noninhibited controls, i.e., those with no plant extract and/or with extracts from nontransformed plants.

Results

Transformation

Calli were obtained in different parts of the explants, mainly at the cut edge of the petiole. Most positive calli were small, green, and round. After 2 mo in G24D medium, all calli proliferated. All established calli lines were confirmed GUS positive. Most developed calli were light green or yellowish, friable calli. Embryogenic orange calli were also obtained in Jonathan and Jewel. In regeneration media without auxins, a total of 50 transgenic lines have been obtained. Through somatic embryogenic regeneration of leaf segments, 22 transgenic lines of Maria Angola have been obtained.

GUS test of SKTI-4 transgenic lines

Good expression was observed in the 72 SKTI-4 lines of the 4 cultivars. Because GUS and SKTI-4 genes are driven by CaMV35S, it was possible to obtain positive reaction in different parts of the transgenic plants.

Kanamycin resistance evaluation of SKTI-4 transgenic lines

Eighteen lines of Jewel, PI-318846-3, Maria Angola, and Jonathan have been tested. All lines had the same performance in the medium with 100-mg/L kanamycin and without kanamycin, showing good calli formation. Untransformed leaf segments were necrotic in the presence of kanamycin in all cases. Figure 2 shows the response of Maria Angola's transgenic line and the negative control to the presence of kanamycin antibiotic in the medium.

The resistance to the antibiotic is due to the expression of the NPTII gene, which correlates with the expression of the inserted foreign gene. These lines are in propagation for bioassay (Table 2).

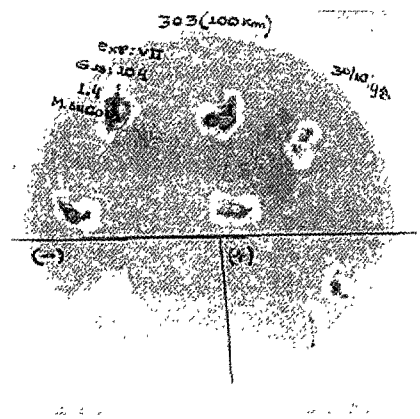

Figure 2. Kanamycin test. Calli formation on leaf segments of in vitro plant of transgenic line of cultivar Maria Angola in presence of high concentration of the antibiotic kanamycin (100 mg/L). Note dried segments and no calli formation of untransformed leaf segments of the same cultivar (negative control).

Table 2. List of transgenic clones with SKTI-4 gene ready for bioassay.

Name of transgenic lines ready for bioassay	
PI-318846-3 41 (1.1)	PI-318846-3 92 (1.3)
PI-318846-3 73 (1.1)	Jewel 6 (1.1)
PI-318846-3 89 (1.1)	Jonathan 3R (1.1)
PI-318846-3 89 (1.2)	Jonathan 21 (1.7)
PI-318846-3 89 (1.3)	M. Angola 63 (1.1)
PI-318846-3 89 (1.4)	M. Angola 104 (1.2)
PI-318846-3 89 (1.5)	M. Angola 104 (1.4)
PI-318846-3 89 (1.7)	M. Angola 104 (1.7)
PI-318846-3 92 (1.1)	M. Angola 106 (1.1)

Southern blot

To date eight transgenic lines of PI-318846-3 have been confirmed through Southern blot. Total DNA of transformed and untransformed control was digested with BamHI to release the internal fragment (653 bp) corresponding to the SKTI-4 cDNA. The SKTI-4 probe did not hybridize with DNA of the control plant (nontransgenic) but did with DNA of all PI-318846-3 transgenic lines tested, showing the insertion of the SKTI-4 gene in the transformants.

PCR analysis

The SKTI-4 gene was targeted with specific primers and amplified by PCR from DNA of in vitro transgenic plants. Twenty-four transgenic lines of Jewel, PI-318846-3, Maria Angola, and Jonathan have been confirmed for the insertion of SKTI-4 gene. The amplification band is shown for 16 samples (Figure 3).

Activity of recombinant SBTI

The inhibitory effect of recombinant SBTI on trypsin activity was analyzed in vitro with protein extracts from upper (youngest), middle, and bottom (oldest, nonsenescent) leaves of sweetpotato greenhouse plants (Figure 4). For each assay, the data were analyzed by comparing protease activities measured in the modified extracts with those measured in extracts from untransformed plants. That took into account the age-dependent activity of plant leaf endogenous protease and trypsin inhibitor activities (data not shown). Because the parental leaf material was identical for all clones analyzed, it could be assumed that the variations observed for a given stage of leaf development resulted

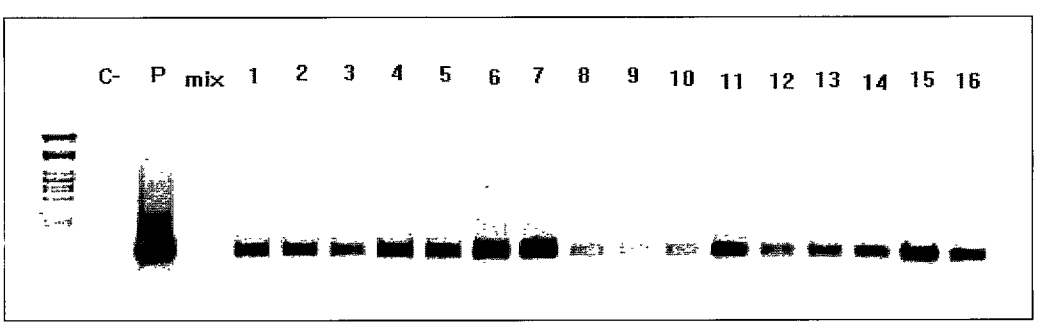

Figure 3. PCR amplification of 16 putative transgenic plants with SKTI-4 gene. The absence of the band in negative control (C-) and the band of the same weight (653 bp) in the positive control (P).

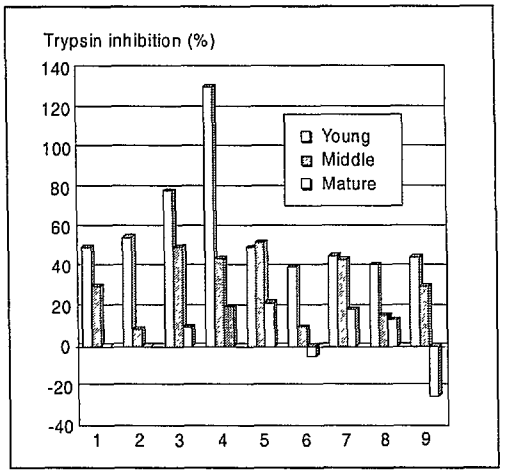

Figure 4. Differential expression of SBTI inhibitor in transgenic sweetpotato lines divided by young, middle, and mature leaves. Clones 1-8 are lines of transgenic PI-318846-3; Clone 9 (NT) is the nontransgenic control.

from various expression levels of the inserted DNA. As shown in Figure 4, a net increase in antitrypsin activity was noted for some clones regardless of leaf age (e.g., clones 3 and 4), when compared to the activity measured in the corresponding extracts obtained from nontransgenic clone 9. Collectively, these observations indicate the presence of *added* antitrypsin activity in the transgenic lines, due to the insertion and expression of the SBTI-encoding cDNA sequence into the sweetpotato genome.

Electrophoretic analysis

In parallel, mildly denaturing gelatin/SDS-PAGE allowed the occurrence of SBTI activity in extracts of transgenic plants expressing SKTI-4 to be seen. Because SBTI is a strong inhibitor of trypsin, the complex formed between the enzyme and the recombinant inhibitor may remain stable in the presence of SDS. That prevents restoration of trypsin activity during migration and allows the identification of transgenic lines expressing SBTI under an active form (Michaud et al., 1996). In the present case, noninhibited trypsin activities appeared as clear (lysis) bands against the blue gelatin background following electrophoresis.

Conversely, under the electrophoretic conditions used, the enzyme was *irreversibly* inactivated when mixed with an extract from a transgenic plant expressing active SBTI, resulting in no or only a weak lysis zone in the gel following gelatin/SDS-PAGE. Figure 5 shows the difference between the lysis bands obtained with extracts from the untransformed control and from two samples of transgenic lines with different levels of trypsin activity. Compared with the bands observed when trypsin was previously mixed with leaf extracts from the untransformed line, the bands observed with extracts from the transformed lines were weaker. The resulting intensities (and inhibitory levels) varied with the expression of the recombinant inhibitor.

Discussion

The present study was aimed at assessing the potential of an SBTI cDNA clone for the production of weevil-resistant sweetpotato plants. It is clear from both in vitro and electrophoretic assays that the transgenic lines possess increased antitrypsin activities compared with the parental control (nontransgenic) line. The most obvious increase in antitrypsin activity in the transgenic lines was noted for the upper

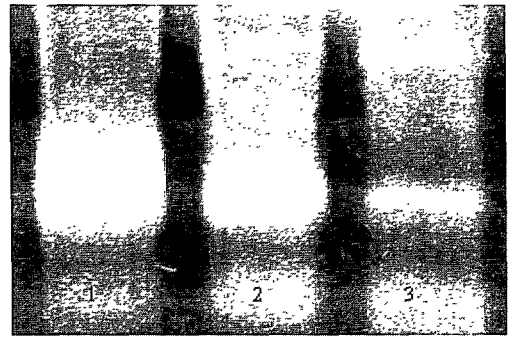

Figure 5. Electropherogram showing the gelatinolytic activity of trypsin preincubated with sweetpotato leaf extracts. Wells were loaded with 5 mg sweetpotato leaf proteins. Lane 1: untransformed control extract; lanes 2-3 PI-318836-3 transgenic lines extract.

(young) leaves (Figure 4, clone 4). Increased inhibitory activity was also noted for older leaves, suggesting the presence of recombinant SBTI in most of the leaves. Given the occurrence of SBTI-sensitive trypsin activity in sweetpotato weevils (Zhang et al., 1997), clones 3 and 4 (Figure 4) may represent interesting candidate lines for the development of sweetpotato weevil management strategies.

These two PI-318846-3 lines (89 1.3 and 89 1.4) are part of a group of transgenic lines expressing active SBTI that are in the multiplication process for bioassay. Continued efforts are needed to find the most appropriate combination of protease inhibitors, for enhancing the expression of plant defense proteins in sweetpotato, and for designing strategies to introduce protease inhibitor-expressing plants into integrated pest management systems.

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Starch Content and Properties of 106 Sweetpotato Clones from the World Germplasm Collection Held at CIP, Peru

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Poverty alleviation through increased postharvest crop use is the major thrust of CIP's research on sweetpotato (*Ipomoea batatas*) in Asia. Much of the effort has focused on China, which produces roughly 85% of the world's sweetpotato (CIP, 1998). A series of collaborative diagnostic studies, and technology and market assessments identified sweetpotato starch production, especially for noodle processing, as an important income-generating activity in poorer areas of China (Scott and Wheatley, 1997; Scott et al., 1992).

Realizing the full income-generating potential of this activity depends on an integrated approach that includes better raw material and improved procurement, processing, and packaging (Wheatley et al., 1997; Zhang, 1999). From a varietal perspective, increasing starch content in fresh roots, extraction rate, and quality are critical components. A better knowledge and understanding of sweetpotato starch properties, and how they compare with those of other starch sources, is necessary to enhance the potential value of sweetpotato starch in existing and novel uses. Latex, the resin produced by sweetpotato latificers, is another important trait to be considered by the starch industry as the latex may contaminate the starch and adhere to equipment (Woolfe, 1992).

There is significant cultivar difference in the content and properties of sweetpotato starch (Tian et al., 1991; Woolfe, 1992), which suggests that genetic improvement of these traits may be achieved. However, the variability of starch content and properties in accessions from the sweetpotato gene bank held at CIP has not been comprehensively evaluated. The gene bank maintains a collection of about 5,500 cultivated accessions from 57 countries.

The objectives of this study were to (1) evaluate the variability of starch content and properties (amylose content and pasting properties) in advanced sweetpotato clones selected from the gene bank held at CIP, (2) estimate the most relevant correlation between the evaluated variables, (3) identify clones with potential for incorporation into CIP's breeding programs for starch production and use, and (4) provide recommendations for future evaluation and use of the sweetpotato gene bank.

Materials and Methods

Plant material

One hundred and six sweetpotato clones were evaluated in this study (Table 1). The set was chosen to represent diverse geographical origin, high variation in predominant root flesh color, and high dry matter (DM) content (> 25% for orange-fleshed clones and > 30% for others). Clones were also selected for adaptation to the agroecological conditions at the trial site based on CIP's root yield data. In addition, performance (high root yields) and relative importance of the clones in CIP's regions (widely grown) were considered.

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Table 1. Origin and predominant root flesh color of 106 sweetpotato clones selected from the gene bank held at CIP, Lima, Peru.

Origin	Clones (N°)	Predominant root flesh color[a]		
		White/cream	Yellow	Orange[b]
North America	**(10)**	**(1)**	**-**	**(9)**
Mexico[c]	1	-	-	1
United States	9	1	-	8
Central America and Caribbean	**(8)**	**(7)**	**(1)**	**-**
Cuba	1	1	-	-
Puerto Rico	7	6	1	-
South America	**(18)**	**(6)**	**(4)**	**(8)**
Brazil	3	1	2	-
Peru	15	5[d]	2	8
Sub-Saharan Africa	**(11)**	**(5)**	**(3)**	**(3)**
Burundi	1	1	-	-
Kenya	1	-	1	-
Nigeria	7	3	1	3
Rwanda	1	1	-	-
Uganda	1	-	1	-
Middle East and North Africa	**-**	**-**	**-**	**-**
East and Southeast Asia and the Pacific	**(57)**	**(27)**	**(11)**	**(19)**
China	5	4	-	1
Japan	5	1	4	-
Korea	2	1	-	1
Papua New Guinea	9	7	1	1
Philippines	5	1	1	3
Taiwan, China	15	2	3	10
Thailand	15	10	2	3
Tonga	1	1	-	-
South and West Asia	**(2)**	**-**	**(1)**	**(1)**
Bangladesh	1	-	-	1
Sri Lanka	1	-	1	-
Oceania	**-**	**-**	**-**	**-**
Total	**106**	**46[d]**	**20**	**40**

[a] Assessed visually after cross sectioning fresh roots according to the method described by Huaman (1991).
[b] Including yellow/orange- to orange-fleshed clones.
[c] Including bred lines developed at CIP.
[d] One clone was strongly pigmented with anthocyanins.

Sweetpotato clones were grown under standard cultural practices during the dry season (av temperature range 18.9-32.5°C, total rainfall 437 mm) at CIP's experiment station in San Ramon, Peru (tropical midland located at lat. 11°06' S, long. 75°18' W, and 800 m above sea level). Nitrogen fertilizer was applied at the rate of 80 kg/ha and sprinkler irrigation was supplied as needed. Clones were planted on 26 May 1997 and harvested after 164 d. Two-row plots were used with 10 plants per row spaced 0.25 m within rows and 0.90 m between rows. Plots were separated by one unplanted row and not replicated. Ten to 20 healthy roots (> 125 g each) per clone were sampled and immediately placed in paper bags under shade. They were then taken to CIP-Lima and stored at 13°C until processing. Because of the large number of clones and the long distance between field and laboratory, the time between harvest and processing was about 15 d.

Sample preparation

Washed and unpeeled sweetpotato roots were cut longitudinally in one half and two quarters after removing the extremities. One half was used for starch extraction, one quarter for flour preparation, and the other quarter for determining DM content.

Starch. Root halves were sliced and thoroughly mixed. A subsample of approximately 1 kg was macerated in a kitchen blender with tap water (1:1 v/v) for 2 min at maximum speed and filtered through a muslin cloth. The residue was resuspended in tap water (1:2 v/v), macerated, and filtered in the same way. The two filtrates were pooled, passed through a 250 µm sieve and adjusted to 4 L with tap water. Starch was allowed to settle for 3 h at room temperature (20-24°C) and the supernatant was discarded. The starch was resuspended in 2 L of tap water, filtered through a 75 µm sieve and left to settle in a tray for 2 h. This last step was repeated three times without the sieving step, and using deionized water instead of tap water for the last two washings. The recovered starch was dried in a forced-air oven at 40-45°C for 24 h, ground with a mortar and pestle to pass through a 250 µm sieve, and stored in sealed polyethylene bags at 6°C.

Flour. Root quarters were cut into 1 mm thick slices and mixed. A subsample of approximately 400 g was freeze-dried, then ground in a mill to pass through a 425 µm sieve. The resulting flour was stored in sealed polyethylene bags at -20°C.

Root analysis

Dry matter. Root quarters were cut into about 0.5 cm^2 cubes and mixed. Three subsamples of approximately 200 g were dried in a forced-air oven at 90°C for 48 h (i.e., until constant weight).

Extractable starch. Extractable starch was calculated as the ratio of g starch at standard 14% moisture content (MC)/100 g fresh roots.

Total starch. Total starch in flour was determined using a Total Starch Assay Kit (Cat. No. K-TSTA, Megazyme, Ireland). The method consisted of hydrolyzing starch to glucose by an enzymic procedure. Glucose was measured colorimetrically with glucose oxidase-peroxidase reagent. Flour MC was determined using the AOAC Official Method 925.10 (AOAC, 1995). Both analyses were done in duplicate.

Latex. Latex production was assessed visually after cross sectioning five fresh roots using the ratings 0 = latex not discernible, 3 = little latex, 5 = some latex, and 7 = abundant latex.

Starch properties

Moisture. MC was determined by oven drying two representative starch samples of about 4 g each at 105°C for 24 h.

pH. 5 g of starch on a dry weight basis (dwb) were dispersed and stirred in 50 ml of distilled water at room temperature for 30 min. After filtering, the pH of the

solution was measured. The analysis was done in duplicate.

Amylose. Amylose content was determined using the differential scanning calorimetry method described by Mestres et al. (1996).

Pasting properties. Viscosity profiles of starch suspensions of 9% (dwb/w) in distilled water through a heating and cooling cycle were obtained using a Rapid Visco-Analyzer (RVA) model 3D (Newport Scientific, Australia) as described by Collado and Corke (1997). Pasting temperature (Tp) at which viscosity started to increase, maximum or peak viscosity (PV), viscosity at the end of the hold time at 95°C or hot-paste viscosity (HPV), and viscosity at the end of the hold time at 50°C or cool-paste viscosity (CPV) were recorded (Figure 1). The stability (HPV/PV) and setback ratios (CPV/HPV) were calculated.

Statistical analysis

PROC MEAN and PROC CORR procedures (SAS, 1992) were used to calculate the descriptive statistics and Pearson's correlation coefficients between variables.

Results and Discussion

Root dry matter and starch content

Root DM and total starch content of the 106 sweetpotato clones varied widely. Root DM ranged from 19.9 to 45.4% and starch content from 11.1 to 33.5% on a fresh weight basis (fwb), with an average total starch content of 21.6% (Table 2) or 61.5% dwb. These values are within the ranges reported in the literature (Woolfe, 1992). The 106 clones were initially selected for high DM content based on CIP data, which explains the high average of 34.9% (Table 2). Most of the white/cream- (58%) and yellow-fleshed clones (85%) had a DM content > 35% (Figure 2). Sixty percent of the orange-fleshed clones (including yellow

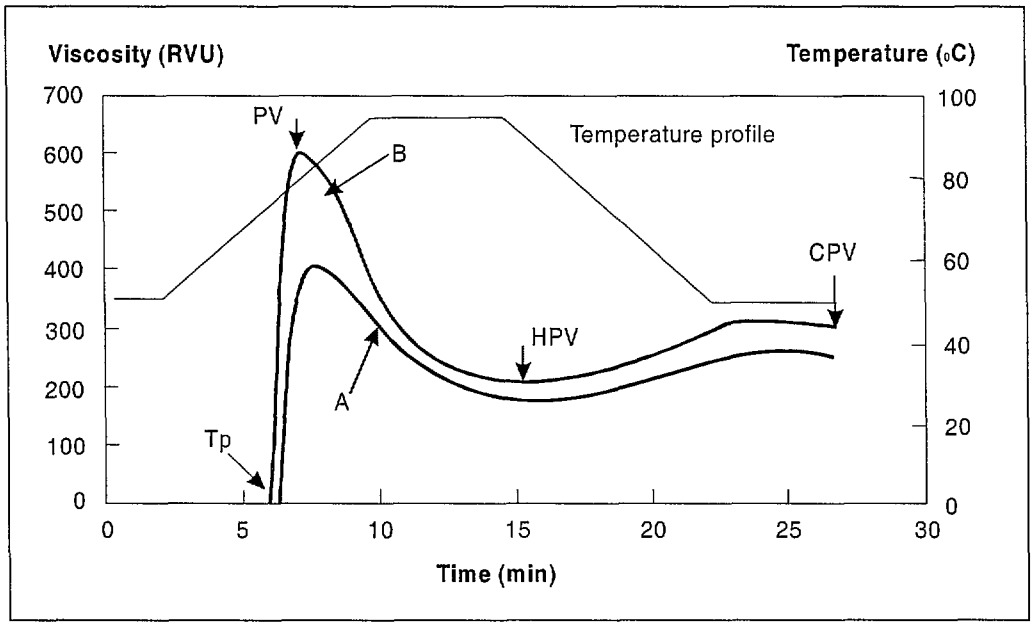

Figure 1. Typical RVA viscosity profiles of sweetpotato starch suspension of 9% (dwb/w) in distilled water observed in 106 clones selected from the gene bank held at CIP, Lima, Peru. Position of pasting temperature (Tp), peak viscosity (PV), hot-paste viscosity (HPV), and cool-paste viscosity (CPV) is indicated. Profiles A (CIP440029, Feng Shou Bai, China, white/cream-fleshed clone) and B (CIP440068, IITA-TIS 5081, Nigeria, yellow/orange-fleshed clone) correspond to the lowest and highest PV values.

Table 2. Variability of root dry matter and total starch content, extractable starch, and starch physicochemical properties[a] among 106 sweetpotato clones selected from the gene bank held at CIP, Lima, Peru.

Variables[a]	Range	Mean	Standard Deviation	Coefficient of variation (%)	Literature range[b]
Dry matter (%)	19.9 - 45.4	34.9	4.5	13	13.6 - 48.2
Total starch (%, fwb[c])	11.1 - 33.5	21.6	4.5	21	5.3 - 28.4
Extractable starch[d] (%, fwb)	6.5 - 25.7	17.3	3.6	21	/ - /
Starch pH	5.1 - 7.0	6.1	0.5	9	5.9 - 6.8
Amylose (%)	18.6 - 27.1	21.8	1.3	6	8.5 - 38
Tp[e] (°C)	70.2 - 76.6	73.8	1.4	2	66.5 - 86.3
PV[e] (RVA)	410 - 600	494.0	38.0	8	329 - 428
HPV[e] (RVA)	161 - 243	204.0	16.0	8	127 - 203
CPV[e] (RVA)	242 - 342	285.0	23.0	8	208 - 284
Stability ratio (HPV/PV)	0.31 - 0.52	0.41	0.04	10	0.35 - 0.55
Setback ratio (CPV/HPV)	1.22 - 1.62	1.4	0.08	6	1.40 - 1.67

[a] Analyses were done at least in duplicate, except for extractable starch, and starch amylose content and pasting properties

[b] Dry matter and total starch (Woolfe, 1992); Amylose and Tp (Tian et al., 1991); Starch pH and pasting properties, except Tp (Collado and Corke, 1997).

[c] Fresh weight basis.

[d] 14% moisture content.

[e] Starch pasting properties: Tp = Pasting temperature, PV = Peak viscosity, HPV = Hot-paste viscosity, CPV = Cool-paste viscosity, RVA = Rapid Visco-Analyzer unit.

orange) had a DM content > 30%, with 10 clones > 35%. The Peruvian clone (CIP420053, Capadito), which is strongly pigmented with anthocyanins, had a DM content of 39.1%. These results suggest the potential for increasing DM content in sweetpotato roots by using these clones in breeding programs. Many varieties now cultivated have a DM content too low (25-30%) to be used in the processing industry (Mok et al., 1997), which prefers a DM content > 30-35%.

Extractable starch ranged from 6.5 to 25.7% fwb, with an average of 17.3% (Table 2). That represents an average recovery rate of 80.3% (ratio of starch at standard 14% MC to total starch content in roots), with values ranging from 54.6 to 91.4%. Wheatley (1996) found a highly significant positive correlation ($r = 0.90$, $P < 0.01$) between laboratory and industrial extraction rates. That demonstrates the usefulness of the laboratory method used in this study for screening clones for the starch industry. White/cream- and yellow-fleshed clones averaged higher extractable starch (18.3% and 19.1%, respectively) than orange-fleshed clones (15.2%). Sixty-two percent of the white/cream-fleshed clones and 70% of the yellow-fleshed clones had extractable starch values between 15 and 20%, whereas about half of the orange-fleshed clones had values < 15% (Figure 2). Approximately 29% of the white/cream-fleshed clones, 30% of the yellow, and 18% of the orange were in the highest extractable starch range of 20-26%.

A small amount of latex (3 rating) was produced in fresh roots of approximately 40% of the 106 clones; 12% produced abundant latex (7 rating) (Figure 2). Compared to the orange-fleshed clones of which 28% produced little latex and 20% abundant latex, a higher proportion of white/

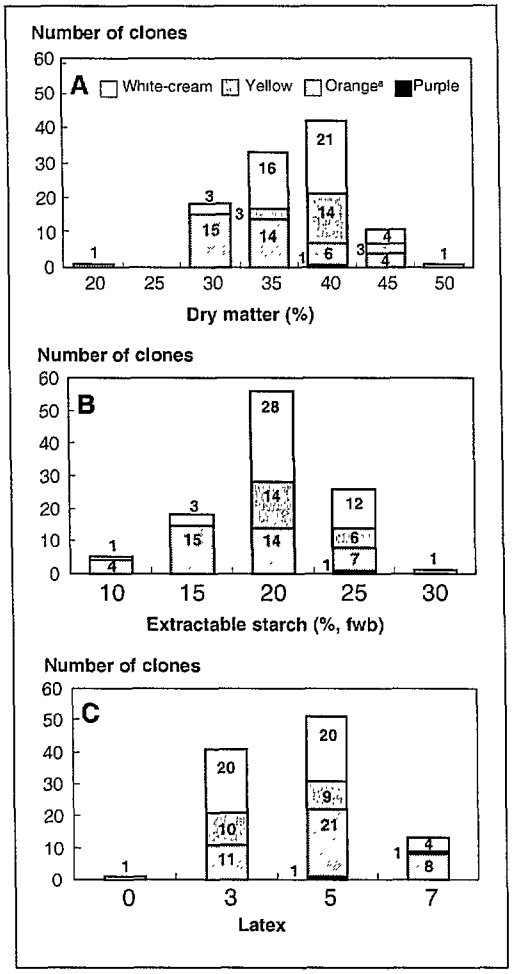

Figure 2. Frequency distribution of (A) dry matter content, (B) extractable starch at 14% MC, and (C) latex production in fresh roots for 106 sweetpotato clones selected from the gene bank held at CIP, Lima, Peru. Latex (C) was assessed visually using the scale 0 = latex not discernible, 3 = little latex, 5 = some latex, and 7 = abundant latex. Analyses were done at least in duplicate, except for extractable starch. (a. Including yellow/orange- to orange-fleshed clones.)

cream- (47%) and yellow-fleshed clones (50%) produced a small amount of latex, and a lower proportion of these clones (9% and 5%, respectively) produced an abundant amount.

Carotenoid pigment responsible for the orange flesh color of sweetpotato roots and anthocyanin pigment, which is responsible for purple flesh color, make the production of a white starch difficult. Hence white/cream- and yellow-fleshed clones are the most suitable for the starch industry. Seven light-fleshed clones with high extractable starch and low latex production in fresh roots have been identified from the 106 sweetpotato clones (Table 3).

A highly significant positive correlation was found between extractable starch and both root DM and total starch content ($r = 0.92$, $P < 0.001$ for both). A similar result was reported by Mok et al. (1997). Thus, root DM content, which is simple, fast, and cheap to determine, can be used to select sweetpotato clones with high extractable starch. That would be particularly useful in breeding programs in the first or second generation when a large number of clones are evaluated. Extractable starch in advanced clones could then be measured in the laboratory and confirmed in the field.

Starch properties

Amylose content and pasting properties are among the most important quality traits of starch. When an aqueous suspension of starch is heated above a critical temperature, granules swell irreversibly and amylose leaches out into the aqueous phase, resulting in increased viscosity (pasting). At this stage the granules are highly susceptible to thermal or mechanical breakdown, which leads to a decrease in starch paste viscosity. Upon cooling, the starch paste forms a gel (gelification) along with increased viscosity. Pasting and gelification are important properties in determining starch behavior in various food and industrial applications. They affect starch-based product quality such as texture, stability, and digestibility. The RVA provides as good a method for measuring these functional properties and describing starch potential end-uses as the Brabender viscoamylograph, which is usually used but consumes more time and sample.

Table 3. Sweetpotato clones selected for high extractable starch and low latex production[a] in fresh roots from the gene bank held at CIP, Lima, Peru.

CIP Number	Name	Origin	Predominant root flesh color	Latex[a,b]	Dry matter[a] (%)	Total starch[a] (%, fwb[c])	Extractable starch[a] (%, fwb)
187016.1	Caplina	Peru	White/cream	3	41.0	27.3	21.4
187016.3	TN89.315	Peru	White/cream	3	39.8	25.6	20.0
188004.3	LM88.113	Peru	Yellow	3	39.4	24.8	22.6
440041	Papota	Puerto Rico	White/cream	3	39.3	25.9	23.3
440046	Viola	Puerto Rico	White/cream	3	38.9	25.5	21.0
440341	101273	Thailand	Yellow	3	38.4	24.4	20.2
440376	Woksaken	Papua New Guinea	White/cream	3	39.2	26.8	21.7

[a] Analyses were done at least in duplicate, except for extractable starch.
[b] Assessed visually using the scale 0=latex not discernible, 3=little latex, 5=some latex, and 7=abundant latex.
[c] Fresh weight basis.

Amylose content. Amylose content varied from 18.6% in the yellow-fleshed clone CIP187001.2 to 27.1% in the orange-fleshed clone CIP420012, with an average of 21.8% in all clones (Table 2). These values are within the ranges reported in the literature (Tian et al., 1991). Over 50% of the 106 clones had an amylose content of between 20 and 23%.

Pasting properties. Pasting properties also varied among the 106 sweetpotato clones (Table 2). The RVA viscosity profiles were all of the A type (using the starch classification of Schoch and Maywald, 1968) normally observed for root and tuber starch. They were characterized by moderate to high PV with a major breakdown and low CPV with respect to PV (Figure 1). Starch pH typically fell between 5.1 and 7 (Table 2), within the range where it usually does not affect pasting properties, as revealed by nonsignificant Pearson's correlation coefficients (not shown). Collado and Corke (1997) obtained a similar RVA pattern for 14 Philippine sweetpotato clones using the same operating conditions, but with a lower range of variation in pasting parameters, especially in PV (Table 2).

Although the importance of amylose has been established, viscoamylography was found to be a more practical and reliable method for predicting starch noodle quality (Collado and Corke, 1997). These authors found a high and positive correlation between the firmness of sweetpotato starch noodles and the RVA pasting parameters of stability ratio ($r = 0.95$), CPV ($r = 0.83$), and HPV ($r = 0.73$), $P < 0.01$. Twenty clones with the lowest and highest starch paste stability and amylose content, as well as 40 additional clones selected at random from the 106, are being evaluated for starch noodle production in Asia at Hong Kong University, to gain better information on the relationship between sweetpotato starch properties and noodle quality, and to identify suitable clones for this purpose.

Conclusions

This study is the first evaluation of starch content and properties of a large sample from the sweetpotato gene bank. These studied traits can also be affected by environmental factors such as site, season, and year, as well as root storage time (Tian et al., 1991). Results reported in this study, therefore, cannot be considered as absolute

values for each clone. Nevertheless, they are useful for general comparison and preliminary screening of sweetpotato germplasm collections for suitable root quality traits. The second phase study, already being initiated at CIP, aims to evaluate the stability of starch content and properties across different environments in Peru.

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Potential of Sweetpotato in Reducing Vitamin A Deficiency in Africa

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Recent studies have associated the consumption of foods rich in carotenoids with decreased incidence of certain cancers in humans (Gester, 1993). That and the possible role of carotenoids in immunity, fertility, and early prophylaxis of cardiovascular diseases in livestock, have generated interest in these compounds (Pfander, 1992). Carotenoids represent the most widespread group of naturally occurring pigments in nature. They are primarily of plant origin and ß-carotene, with few exceptions, predominates. ß-carotene serves as an important nutritional component in foods, as a major precursor of vitamin A, and provides pleasant yellow-orange colors to foods (Simon, 1997). Dietary vitamin A deficiency causes debilitating health problems such as xerophthalmia, corneal lesions, keratomalace, and, in many instances, death. The World Health Organization (1995) reports these problems affecting young children in Africa.

Sweetpotato has been receiving increasing attention in part because it grows on soils with limited fertility, is relatively drought tolerant, provides good ground cover, and is often cultivated without fertilizer or pesticide (Ewell, 1990). Those qualities are attractive to agriculturalists and ecologists interested in developing sustainable food production systems in the tropics. Also, it has remarkable pro-vitamin A qualities (Woolfe, 1992). In parts of West, Central, and East Africa, sweetpotato is an important staple source of calories and is consumed by all age groups. Children, the group most at risk of vitamin A deficiency, particularly like sweetpotato (Low et al., 1997). Widely consumed cultivars, however, have white or pale yellow flesh and contain very little ß-carotene (Ameny and Wilson, 1997). Orange-fleshed sweetpotato storage roots high in carotenoids and vitamin A-active ß-carotene are eaten less. Compared to light-colored, low ß-carotene sweetpotato, consumption of orange-fleshed sweetpotato roots and sweetpotato-based processed foods could provide sustainable, cost-effective, and much needed vitamin A. Therefore, the use of orange-fleshed sweetpotatoes as a food source of pro-vitamin A merits further attention.

Fresh sweetpotato roots are bulky and highly perishable. In Africa they are commonly consumed fresh, usually boiled. These roots are generally not harvested and stored for extended periods. That is, farmers keep unharvested mature sweetpotatoes in the field until they are needed for consumption or sale, a practice called piecemeal harvesting (Rose, 1970; Onueme, 1982; Smit, 1997). In semi-arid areas with a long dry season, in-ground storage is limited by attacks from sweetpotato weevils (*Cylas* spp.). Farmers have traditionally chipped or crushed sweetpotato roots and sun-dried them for storage and year-round use. Chipping, drying, and storing orange-fleshed sweetpotato can overcome seasonal shortages of pro-vitamin A in the diets of many low-income African households during the dry season when there are no fresh, green vegetables. CIP has been working to make more nutritious sweetpotato varieties available to African

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countries (Gichuki et al., 1997). Little is known, however, about the effect on carotenoid contents of drying and processing sweetpotato into flour and flour-related products.

Some inconclusive reports say that carotenoid content changes during sweetpotato storage root growth and development (Data et al., 1987). Studying variations in carotenoid content, especially pro-vitamin A carotenoid content, during storage root development is relevant in the process of maximizing the availability of that nutrient. Recommendations could then be made to farmers to start practicing piecemeal harvesting of newly introduced, high-yielding, orange-fleshed cultivars.

This work is part of a larger study reported in part elsewhere. K'osambo et al. (1998) report on the HPLC carotenoid analysis. In the HPLC analysis, one ml of total carotenoid extract from 2 g of grated sweetpotato sample was freeze-dried and reconstituted in high performance liquid chromatography (HPLC) mobile phase of 90% methanol:10% tetrahydrofuran. The reconstituted samples were ultrafiltered through 0.5 µm microfilters before injection into the HPLC system. HPLC analyses were done as described by Ruddat and Will (1985).

HPLC results reported in K'osambo et al. (1998) indicated that a good number of carotenoids occur in sweetpotato root extracts. Six of these were present in significant amounts with all-*trans*-ß-carotene predominant, accounting for more than 80% of total carotene in most orange-fleshed sweetpotato roots analyzed. All-*trans*-ß-carotene, ß-carotene-5,6-monoepoxide, ß-carotene-5,6,5',6'-diepoxide, and 2 unidentified carotenoids (designated P1 and P2) were present in all cultivars analyzed. The amount depended on the cultivar. Chromatographic profiles of sweetpotato extracts from different cultivars were compared with co-chromatography with pure carotenoid. Comparison of HPLC profiles of carotenoid standards, sweetpotato extracts, and co-chromatography indicated that three sweetpotato carotenoid peaks at 5.36, 8.61, and 14.60 min. correlated to the co-chromatographic peaks produced by ß-carotene-5,6,5',6'-diepoxide; ß-carotene-5,6-monoepoxide, and all-*trans*-ß-carotene as indicated by similar retention times (K'osambo et al., 1998).

P1 predominated in white- or cream-fleshed cultivars such as KSP 20, Naveto (CIP440131), and Kemb 10, where it formed a significant portion of total carotenoids. The probable identity of this carotenoid was postulated on the basis of its elution pattern. Craft (1992) reported that during non-aqueous reversed-phase HPLC, xanthophylls, that are more polar, partition more preferentially in the polar mobile phase and, therefore, elute earlier than the less polar carotenes. Early elution of P1, as well as that of P2, strongly suggests P1 is a xanthophyll, possibly lutein, and P2 a zeaxanthin (K'osambo et al., 1998).

This paper reports on the part of the study undertaken to identify high-yielding sweetpotatoes that are high in ß-carotene and study the effects of drying and processing on carotenoid content.

Materials and Methods

Plant material

Selected sweetpotato cultivars from Kenya and Uganda and others from CIP's pathogen-tested list (CIP, 1998) were grown in Kabete, Kenya (altitude 1,800 m, ambient temperature 20.3 ± 3°C, and annual rainfall, 1,046 mm) using a standard random complete block design. Storage root flesh colors of these cultivars ranged from white to orange. Samples of each cultivar were taken for carotenoid analysis in a two-stage random sampling. Three plants were randomly selected and three medium-sized storage roots taken at random from each plant. These were used for carotenoid extraction and analysis.

Roots were peeled, and about 2-cm-thick medial transverse slices were taken from each root. These were finely grated lengthwise using a cheese grater. These samples were thoroughly mixed, packed under N into plastic bags, and stored at -20°C until used for carotenoid extraction.

Effect of root age

The effect of root age on carotenoid content was assessed by sampling sweetpotato roots at 12, 16, 20, and 24 weeks after planting. At each stage, three plants were randomly selected and the largest storage roots piecemeal harvested from each randomly selected plant. Different plants were sampled at each harvest.

Total carotenoids in processed foods

Sweetpotato chips were dried at 65°C in a forced-air oven to a moisture content of 6-8%. The process of producing dried sweetpotato chips is that described by Hagenimana et al. (1999). To check for changes in total carotenoid contents during storage, dried chips from each cultivar were stored in an opaque paper bag and sampled for flour processing after 3, 6, and 11 months of storage under ambient air conditions. Buns, chapatis (flat unleavened bread), and mandazis (doughnuts) were prepared as described by Hagenimana et al. (1998). Carotenoid was extracted following the procedure described by Khachik et al. (1992). Total carotenoids and ß-carotene were determined spectrophotometrically as described by Imungi and Wabule (1990).

Results and Discussion

Carotenoids and vitamin A values of sweetpotato roots

Large variation was observed in carotenoid content of the cultivars studied. This was a reflection of the wide spectrum of the root flesh color of sweetpotato. White-fleshed roots such as those from cultivars Mugande, TIS 2534 (CIP440062), LM88.014 (CIP188001.2), and KSP 20 had the lowest total carotenoid. Orange-fleshed cultivars such as Camote Amarillo (CIP400014), Japon Tresmesino Selecto (CIP420009), Kakamega 4 (SPK 004), and Zapallo (CIP420027) had the highest (Table 1). Our results agree with the conclusion that carotenoids, especially ß-carotene, are largely responsible for the orange flesh color in sweetpotato storage roots (Purcell, 1962; Purcell and Walter, 1968; Almeida-Muradian et al., 1992; Takahata et al., 1993). The depth of orange flesh color was mainly a function of the concentration of all-*trans*-ß-carotene, as was similarly reported by Simonne et al. (1993). These results indicate that carotenoids from orange-fleshed sweetpotato are highly vitamin A active and are consistent with those of Jalal et al. (1998). That work showed that consumption of ß-carotene-rich foods, mainly in the form of orange-fleshed sweetpotato, increased serum retinol levels in Indonesian children and alleviated signs of vitamin A deficiency.

Since the early 1990s, the main strategy for combating vitamin A deficiency in Africa has been to distribute massive-dose capsules using donations from UNICEF (Kennedy and Oniango, 1993). Mothers who do not identify adverse physical symptoms in their children often neglect returning for additional doses. The same benefit could be achieved if children consume sufficient quantities of ß-carotene and vitamin A-rich foodstuffs. This is one of the most reliable, readily available, and most sustainable approaches to controlling vitamin A deficiency in many rural areas of Africa where chronic deficiencies are still common (Roels et al., 1958). Foods such as dairy and meat products containing preformed vitamin A are often too expensive for most people in African countries. Therefore, it is important to make available more potent and sustainable food sources of pro-vitamin A carotenoids, such as orange-fleshed sweetpotatoes, and to improve their production, shelf life, and consumer acceptance. That could make a tremendous contribution to improving African nutrition and health.

Table 1. Relationship between the flesh color and carotenoid contents of different sweetpotato cultivars.

Cultivar name	Visual flesh color	Carotenoids (μg/100 g fresh root tissue ± SD)	
		Total	β-carotene
CIP440057 (TIB11)	Orange (deep)	8823.5±654	7983.9±339
CIP400014 (Camote amarillo)	Orange (deep)	7195 4 ± 2169	6271 0 ± 1312
Unknown	Orange (pale)	7451.5±718	6234.3±92
CIP420009 (Japon Tresimesino Selecto)	Orange (deep)	6931.7 ± 4620	6175.0 ± 4251
CIP440015 (W-220)	Orange (deep)	8389.9±446	6023.1±465
CIP420010 (Teoboza)	Orange (deep)	8942.5 ± 2021	5144.5 ± 1001
CIP420027 (Zapallo)	Orange (deep)	4692.0 ± 550	4085.0 ± 10
CIP420004 (Mamala)	Orange (light)	2671.9 ± 83	2217.2 ± 311
SPK 004 (Kakamega 4)	Orange (light)	2715.5 ± 212	2130.0 ± 109
CIP187004.1 (LM87.009)	Cream	1700.3 ± 70	1071.3 ± 101
CIP440377(NG 7570)	Cream	1009.0 ± 500	847.0 ± 351
CIP440186 (Tainan No 15)	Cream	1700.3 ± 213	832.1 ± 286
CIP187004.2 (LM87.045)	Cream	1289.2 ± 109	747.4 ± 76
Kemb 10	Yellow (deep)	1006.9 ± 402	627.0 ± 219
CIP420047 (Estrella)	Cream/purple	604.1 ± 71	485.8 ± 14
K148	Cream/yellow	834.6 ± 80	473.3 ± 111
CIP440224 (CN1517-139)	Cream/yellow	736.2 ± 83	448.4 ± 90
CIP440154 (Xiang shu 6)	Cream/white	460.9 ± 70	274.0 ± 42
CIP420053 (Capadito)	Purple/white	722.5 ± 72	249.1 ± 78
CIP420031 (Cascajo morado)	Purple/ cream	784.8 ± 50	199.3 ± 124
CIP440228 (CARI 9)	Cream/yellow	473.3 ± 49	174.4 ± 93
CIP400002 (Morado maravi)	Purple/white	290.2 ± 13	161.9 ± 17
CIP440025 (Xushu 18)	Yellow (light)	168.2 ± 23	111.8 ± 45
CIP420008 (Maria Angola)	Orange (light)	390.9±28	110.6±10
KEMB 33	Yellow (light)	336.3 ± 20	99.7 ± 37
CIP440162 (Mabrouka)	Yellow (light)	137.0 ± 11	49.8 ± 9
CIP440078 (TIS70357)	Cream	248.8±39	39.3±7
CIP440023 (W-228)	White/yellow	239.2 ± 50	37.4 ± 7
KSP11	White	159.6±9	19.6±2
Ex-Diana	White	191.7±24	19.1±2
CIP440062 (TIS2534)	White	138.3±2	16.7±2
CIP440160 (Philippine)	Cream	158.5±5	Traces
CIP440066 (Ihuanco)	White	112.1 ± 10	Traces
CIP188001.1 (LM88.002)	White	106.8±11	Traces
CIP440094 (NC 1582)	White	99.7 ± 15	Traces
KEMB 20	White/yellow	93.4 ± 21	Traces
CIP440144 (IRA502)	Yellow/purple	69.8 ± 27	Traces
CIP440131 (Naveto)	White/yellow	68.5 ± 29	Traces

Continued on next page

Table 1 (cont.)

CIP440164 (K51/3251)	White/yellow	62.3 ± 22	Traces
CIP188001.2 (LM88.014)	White	56.1 ± 22	Traces
KSP 20	White	Traces	Traces
Mugande	White	Traces	Traces

Woolfe (1992) and Low et al. (1997) suggested that cultivars having more than 100 µg retinol equivalent per 100 g fresh roots were good sources of vitamin A. Hagenimana et al. (1999) reported that cultivars such as Kakamega 4 (SPK 004), Zapallo, Japon Tresmesino Selecto, unknown, W-220 (CIP440015), and TIB 11 (CIP440057) have sufficient levels of retinol equivalents to meet this criteria. Their cultivation, consumption, and use in different dishes should be encouraged in combating nutritional vitamin A deficiency in Africa.

Effect of root age

Sixteen to twenty-week-old roots contained higher carotenoid concentrations than younger roots (Table 2), except the low ß-carotene content cultivar TIS 2534, which reached its highest carotenoid content at 24 weeks. These differences in total carotenoid content between young and older roots depended on the cultivar. Sixteen-week-old roots from Kakamega 4 (SPK 004) were twofold higher in total carotenoid content than 12-week-old roots. Orange-fleshed cultivar Japon Tresmesino Selecto had two-thirds of its total carotenoid content available after just 12 wk. Concentration of total carotenoid continued to increase up to the 24th wk in low-carotenoid-content cultivars TIS 2534 (CIP440062) and Kemb 10 (Table 2). Therefore, to receive the maximum provitamin A benefits from the sweetpotato, piecemeal harvesting and consumption of roots from Japon Tresmesino Selecto could begin after 12 wk, after 16 wk from Kakamega 4 (SPK004), and after 20-24 wk from the lower carotenoid content cultivars.

Total carotenoids in processed sweetpotato products

Addition of orange-fleshed sweetpotato roots to buns, chapatis, and mandazis increased the total carotenoids and content of these products (Figure 1). Using sweetpotato flour in the recipe was one of the best means of increasing total carotenoids and ß-carotene, followed by using boiled and mashed sweetpotato, and then raw and grated roots. Adding sweetpotato also improved the products' color, giving them an attractive yellow appearance.

Boiling the roots reduced the total carotenoid content by 20%, whereas drying roots at 65°C for 12 hours reduced total carotenoid content by 30%. Storing dried chips for 11 months reduced total carotenoid content an additional 11%, from

Table 2. Total carotenoid contents of 4 sweetpotato cultivars grown at Kabete, at different root ages.

	Total carotenoid content (mg carotene equiv./100 g fresh root ± SD)			
Cultivar	12 weeks	16 weeks	20 weeks	24 weeks
KEMB 10	0.43 ± 0.02	0.75 ± 0.04	0.91 ± 0.04	1.13 ± 0.43
Japon Tresimesino Selecto	3.39 ± 0.14	5.47 ± 0.34	6.91 ± 0.39	5.17 ± 0.08
Kakamega 4	0.85 ± 0.16	2 58 ± 0.15	3.09 ± 0.38	3.03 ± 0.08
TIS 2534	0.05 ± 0.01	0.08 ± 0.03	0.06 ± 0.01	0.16 ± 0.01

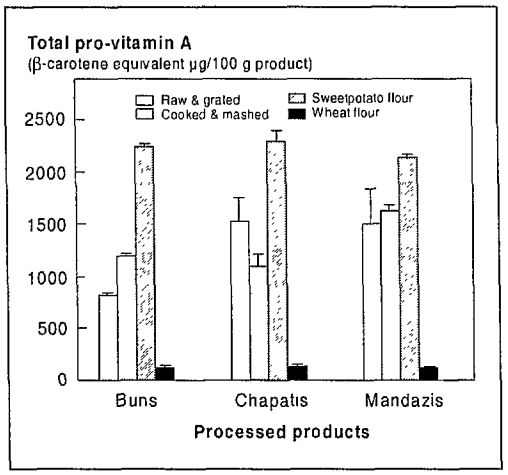

Figure 1. Improvement of pro-vitamin A in processed foods by incorporation of sweetpotato cv. CIP420027.

70% to 59% (Hagenimana et al., 1999). Although fresh sweetpotato carotenoid levels decreased during the drying process, carotenoid concentration was much higher in the dried products than in fresh roots.

Good agronomic performance and consumer acceptability of processed products combined with the high carotenoid levels of orange-fleshed sweetpotato cultivars provide an elegant and well-adapted mechanism for combating vitamin A deficiency among resource-poor urban and sweetpotato farming communities in Africa.

Conclusions

- Orange-fleshed sweetpotato roots contained higher total carotenoid and ß-carotene content than white- and cream-fleshed roots. Carotenoids from orange-fleshed sweetpotato are highly vitamin A-active and their consumption in Africa where vitamin A deficiency is prevalent should be encouraged.
- Twelve weeks after planting, the yield and amount of pro-vitamin A present in roots of orange-fleshed cultivars were high enough to potentially provide adequate dietary pro-vitamin A. Piecemeal harvesting should be started then.
- Incorporation of flour made from orange-fleshed sweetpotato roots into buns, chapatis, and mandazis significantly enriched the products in pro-vitamin A.
- Results of this study suggest that increased consumption of orange-fleshed sweetpotatoes in either fresh or processed form can contribute to alleviating dietary deficiency of vitamin A.

Acknowledgement

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Development of a Sweetpotato-Based Instant Weaning Food for Poorly Nourished Children Six Months to Three Years Old

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In Peru, as in many other developing countries, infant malnutrition is a serious problem. A recent national health and demographic survey found that over 25% of children under 5 yr of age suffer from chronic malnutrition (ENDES, 1996). Usually the percentage of malnourished children is higher in rural areas, but due to the greater urban population in Peru the majority of undernourished children live in the peri-urban areas.

The critical period for a child's growth and development is between 6 and 24 mo during the transition from a diet based on mother's milk to one akin to the family diet. During this period the child is susceptible to malnutrition and deficiencies in several micronutrients that can lead to growth retardation and susceptibility to infectious diseases (Creed-Kanashiro et al., 1990).

The situation is the result of a nutrition gap: the difference between the quantity and quality of food that the infant receives vs his/her daily requirements. This is the result of infant feeding patterns. The custom is to serve liquid or semisolid preparations, such as soups and broth, that mothers consider to be the best for their children. Foods that fill them but do not adequately nourish them. Thus, a child receives food low in energy and nutrient density. Also, the target population has limited purchasing power, lacks nutrition knowledge, and does not necessarily orient food purchases toward maximum nutritional benefit.

There is a good potential for improving the diet, and thereby a child's nutritional status, through the incorporation of sweetpotato (*Ipomoea batatas*) into the diet. Sweetpotato is produced in Peru, is easily accessible, and low-cost. Children like it. Orange-fleshed varieties are rich in highly bioavailable ß-carotene (pro-vitamin A). The use of sweetpotato offers the possibility of expanding the use of the crop while contributing to the prevention of vitamin A deficiency present in several sectors of the Peruvian population (Presidencia de la Republica del Peru, 1998).

In this context, a collaborative project was conducted by CIP with the Nutrition Research Institute (IIN), a nongovernmental organization with over 30 yr experience working with vulnerable populations in Peru. The objective of the project was to fully exploit the sweetpotato's nutritional attributes and palatability by developing a low-cost instant weaning food as a complement to breast milk for children 6 mo to 3 yr old (Figure 1).

Materials and Methods

Weaning food ingredients

Fresh sweetpotato roots of commercial cultivar Jonathan (orange) and the new cultivar Imperial-INIA (YM89-052, white), and corn, rice, soybean, pea, quinoa, and wheat flours were used to prepare the weaning food mixes. In addition, powdered whole milk, freeze-dried egg, milk whey, and soybean protein isolate (PAS), (PRO FAM 646) (Archer Daniels Midland Company) were included as protein sources.

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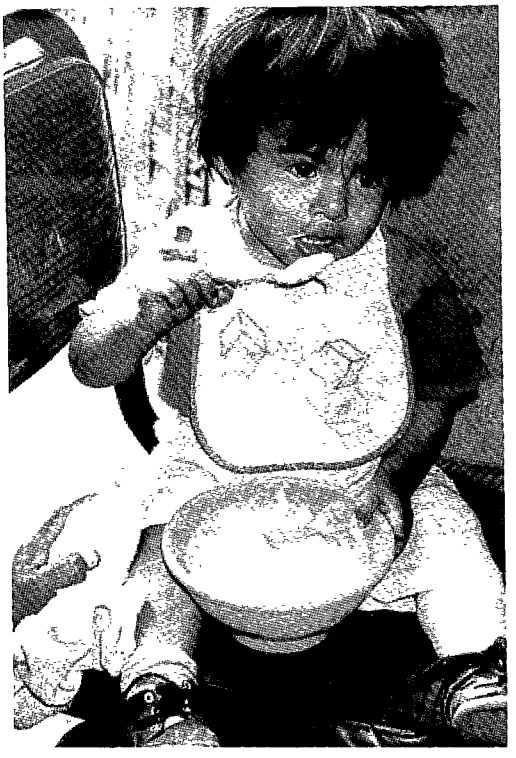

Figure 1. A young lad enjoying his weaning food during the acceptability trial.

White sugar and vegetable oil were used as energy sources, and a premixture of vitamins and minerals formulated for instant food for children (Product # 2760960, Roche S.A.) was added. Ronoxan A (Roche S.A.) was included as an antioxidant for the formula and cinnamon (Sd spray-dry, Product # 08035, Montana S.A.) to improve flavor.

Nutritional criteria for an instant weaning food

The nutritional criteria used for developing the weaning food were:

- the recommended intake of energy and protein for children under 3 yr of age and other nutrients (FAO/WHO/UNU, 1985; FAO/OMS, 1991),
- the nutritional deficit that exists between these requirements and actual food consumption by infants in Peru, and
- the minimum nutritional standard set by the Peruvian Ministry of Health (MOH, 1993). The Ministry's standards are those established for instant products used in the government's supplementary feeding program for preschool-age children.

Development and preparation of the instant weaning food

The weaning food was developed taking into consideration the:

- optimum percentage of sweetpotato that should be included in the formulation and the best form of sweetpotato flour (raw, precooked, or extruded),
- availability of the ingredients based on the calculation of different combinations for their nutritional value and cost, and
- laboratory determination of the organoleptic characteristics, size of ration, amount of water needed, and energy density.

Six formulas were selected that differed by type of sweetpotato (white or orange flesh) and flour (wheat or soybean) used.

Industrial preparation of the infant food was carried out in ASA Alimentos S.A., a private company located south of Lima in Cañete, Peru. Two preparation methods were used.

1. Precooked sweetpotato flour mixed with the other flours (rice, corn, wheat, or soybean), soybean protein (PAS), oil, and Ronoxan A. These were fed directly into the drum-dryer to obtain precooked flakes.
2. Sweetpotato puree was prepared by washing, peeling, and steam cooking fresh roots. The puree was then combined with rice, corn, wheat, or soybean flours and soybean protein (PAS) that had previously been mixed with oil and Ronoxan A. This mixture was fed directly into the drum-dryer to obtain precooked flakes.

In both cases, the flakes were ground and then mixed with the powdered milk, sugar, cinnamon, and the premix of vitamins and minerals to form the weaning food.

Nutritional and microbiological analysis

The following analyses were performed:

- Proximal analysis (total protein, fat, ash, fiber, and carbohydrates), using the standardized method of AOAC 1983.
- ß-carotene (AOAC, 1995).
- Percentage of gelatinization analysis made by DEMSA, Lima, Peru (using the method of the Mppimbianti Company, 1987).
- Digestibility in vivo analysis conducted by the Nutrition Department, Agrarian University, La Molina, Lima, Peru, using the balance of rat method.
- Amino acid content (AOAC, 1994).
- Microbiological analysis (total aerobic flora; total coliforms: *Staphylococcus aureus, Bacillus cerus,* and *Clostridium perfringens*; molds; yeast; and salmonella) using 3M Petrifilm plates (Beuchat et al., 1991) and plate dilution (AOAC, 1995).

Acceptability trial

An acceptability trial was conducted with mothers and infants living in peri-urban areas in Huáscar and Bayovar, Canto Grande, San Juan de Lurigancho District, Lima.

The trial consisted of determining the acceptability of the six different formulas by infants and their mothers through short-term feeding trials (4 d), exploring the incorporation of the weaning food into the daily diet of the infants, and evaluating mothers' perceptions of ease of preparation and use.

A double-blind design was used in coding the formulas. Tests were conducted with 120 mother-child pairs, 97 of which completed the study. Twenty-three dropped out because of illness (11) or parents did not wish to continue (12). Before the tests, the mothers were provided with 900 g of weaning food formula (sufficient for 10 d), a bowl, and two measures (one for water and the other for the formula). They were also instructed on how to prepare the weaning food to avoid the risk of contamination.

Results and Discussion

Weaning food formula

The composition of the six weaning foods is shown in Table 1 for the equivalent of a daily ration of 90 g. Weaning foods of two fat levels (30% and 33%) were prepared to optimize the industrial process. The 30% level was prepared with orange sweetpotato only (white sweetpotato was not available at the time of this preparation) (Espinola et al., 1998).

Sweetpotato root was the only fresh ingredient used in the formulation. It represented 24% of the total composition on a dry basis. All ingredients were completely cooked, resulting in a mixture which needs only hot water to prepare in the home.

In accordance with the FONCODES (1996) requirement for 20% of total protein to be provided from animal sources, powdered whole milk was included. Soybean protein (PAS), rice, maize, soybean, and sweetpotato flours provided the remaining protein. Vegetable oil contributed additional fat and refined sugar was added as a complementary source of energy (up to 11% of carbohydrates). A mixture of vitamins and minerals was added to meet the required levels. Ronoxan A (which contains a-tocoferol and palmitate of L-ascorbilo) was added to prevent oxidation. Cinnamon was added as a natural flavor. Cinnamon and Ronoxan A are permitted additives for processed products for children under 3 yr old, according to Codex Alimentarius, 1994 (FONCODES, 1996).

Nutritional and microbiological quality

The protein, carbohydrate, and energy density levels of the six weaning foods are all within the range of requirements stipulated by official standards (Table 2). The fat and fiber contents vary by type of mixture. Indeed, the 97% level of gelatinization in all formulas surpasses the official requirement, indicating that the foods were

Table 1. Ingredients of six weaning food formulations, CIP, Lima, Peru, 1997.

	Weaning foods[a] (g/90g ration[b])					
	33% fat				30% fat	
Dry ingredients	1	2	3	4	5	6
White sweetpotato[c]	—	—	21.79	21.67	—	—
Orange sweetpotato[c]	22.07	22.07	—	—	22.07	22.07
Wheat flour	6.89	—	6.92	—	7.38	—
Soybean flour	—	4.92	—	4.92	—	4.92
Rice flour	8.36	9.84	8.40	10.33	8.85	11.80
Maize flour	6.89	9.84	6.92	9.83	7.87	10.82
Whole powdered milk	27.54	27.54	27.69	27.53	27.54	24.59
Soybean protein (PAS)	3.93	1.97	3.96	1.97	3.93	2.95
Sugar	5.90	5.90	5.93	5.90	5.90	5.90
Vegetable oil	7.38	6.89	7.42	6.88	5.41	5.90
Ronoxan A	0.01	0.01	0.01	0.01	0.01	0.01
Mix of minerals/vitamins	0.09	0.09	0.09	0.09	0.09	0.09
Tricalcium phosphate	0.55	0.55	0.55	0.55	0.55	0.55
Magnesium sulfate	0.25	0.25	0.25	0.25	0.25	0.25
Natural cinnamon	0.15	0.15	0.07	0.07	0.15	0.15

[a] Weaning foods: 1) orange sweetpotato + wheat, 2) orange sweetpotato + soybean, 3) white sweetpotato + wheat, 4) white sweetpotato + soybean, 5) orange sweetpotato + wheat, 6) orange sweetpotato + soybean.

[b] To be consumed in two feedings/day.

[c] Before drum drying: orange sweetpotato fresh wt 129 g, white sweetpotato 116 g.

completely cooked, easy to digest, and met established standards for instant food (FONCODES, 1996).

The retinol content of formulations 1, 2, 5, and 6 (Table 2) exceeded official requirements for children 6 mo to 3 yr old. More importantly, the results indicate that root processing did not significantly affect ß-carotene content. Woolfe (1992) reported a similar finding in her earlier review of the literature. Hence, inclusion of orange sweetpotato roots in the weaning food permits either a contribution of vitamin A beyond that officially required, or a reduction in the level of retinol required in the formulations.

The amino acid content of each formula exceeded the FAO chemical score (FAO/WHO/UNU, 1985) for a given amino acid (Table 3). There were no limiting amino acids and the protein quality was adequate.

Throughout preparation—mixing, cooking, packaging, and transporting—care was taken to prevent contamination of the product. Microbiological analyses show the weaning food to be well within the prescribed limits of aerobic flora, total coliforms, molds, and yeast, and salmonella, permitted for an infant food, in accordance with the FONCODES (1996) requirements.

However, when the acceptability trials were started (6 wk after preparation), the bags containing formula 1 were externally contaminated by fungi. As a result, this formulation was dropped from the acceptability trials.

Table 2. Peruvian Ministry of Health's requirements for an instant weaning food, and the results of nutritional analyses of six weaning foods, CIP, Lima, Peru, 1997.

	Requirement[a]	Weaning foods[b]					
		Fat 33%			Fat 30%		
Ration		1	2	3	4	5	6
Energy (kcal)	350-400	375.0	390.0	396.0	385.0	373	377.0
Moisture (%)	<5%	2.7	3.2	2.7	3.4	2.6	3.2
Protein (12-15% total kcal)	48-60 kcal	55.0	54.4	59.2	49.6	53.2	47.8
Fat (25-30% total kcal)	100-120 kcal	83.7	114.6	129.6	113.4	73.4	88.0
Sugar (g)	Up to 11% CHO	11.0	10.9	11.6	10.8	9.7	9.9
Fiber (g)	≤2.0	1.7	1.7	2.8	2.5	1.5	1.8
Energy density (kcal/g)	1 to 1.5	1.1	1.2	1.2	1.1	1.1	1.1
Gelatinization (%)	>94	97.8	98.5	98.3	98.0	98.0	97.6
Retinol (μg)	400	510.0	563.0	75.3	101.0	518.0	500.6
Chemical score (%)	>85%	>100%	>100%	>100%	>100%	>100%	>100%
α-tocaferol (mg/kg)	300 max.	60	60	60	60	60	60

[a] FONCODES (1996).

[b] Weaning foods: 1) orange sweetpotato + wheat, 2) orange sweetpotato + soybean, 3) white sweetpotato + wheat, 4) white sweetpotato + soybean, 5) orange sweetpotato + wheat, 6) orange sweetpotato + soybean.

Table 3. Analysis of the amino acids of the weaning foods formula vs chemical score for preschoolers.

	Sweetpotato weaning foods[a]					
	2	3	4	5	6	Chemical score[b]
	(mg/g protein)					
Isoleucine	35.5	49.6	49.1	44.4	48.1	28
Leucine	81.1	87.7	92.1	84.6	89.9	66
Lysine	67.3	66.9	70.0	67.2	65.0	58
Methionine + cystine	30.6	35.4	37.8	29.8	42.8	25
Phenyalanine + tyrosine	86.0	83.7	94.3	89.7	92.8	63
Threonine	41.0	45.9	45.9	43.2	44.4	34
Valine	38.1	52.5	52.1	48.1	52.4	35

[a] Weaning foods: 2 = Orange sweetpotato + soybean (33% fat), 3 = white sweetpotato + wheat (33% fat), 4 = white sweetpotato + soybean (33% fat), 5 = orange sweetpotato + wheat (30% fat), 6 = orange sweetpotato + soybean (30% fat).

[b] For children under 5 yr old (FAO/WHO/UNU, 1985).

Acceptability by mothers and children

Acceptability of the weaning foods was evaluated using the method developed by the IIN, based on ISO-6658 (ISO, 1985) and Watts et al. (1992). Each formulation was evaluated for the number of times consumed each day, amount consumed, and the mother's perception of her child's acceptance of the formula. A score was assigned to each of these criteria to develop an acceptability rating. Seventy-five percent was considered good acceptance, in accordance with the requirements established by FONCODES (1996). On this basis, formulations 2 (orange sweetpotato + soybean flour), 4 (white sweetpotato + soybean flour), and 5 (orange sweetpotato + wheat flour) were rated acceptable.

Consumption of the weaning foods increased on the 2nd and 3rd days as children became accustomed to them. Consuming these foods between main meals changed the child's eating patterns, principally through replacing between meal snacks, e.g., banana, porridge, cookies, or milk. In general, the weaning food contributed to increasing the child's total food intake.

Almost all mothers found the formulations beneficial. Eighty-seven percent said that the instant preparation, using just warm, boiled water and mixing, helped them in their daily activities, both in saving time and in satisfying the child. These mothers perceived their children to be quiet and well fed. A few children disliked the food, accounting for the 13% of mothers who did not consider it beneficial.

With the results of the acceptability trials, formulations 2, 4, 5 were selected (Table 4). Formulation 2 had lower fiber and higher retinol that Formulation 4, the only ration with a higher acceptability rating. Formulation 5 closely followed 2 in acceptability, but had a slightly lower retinol and was made with only 30% fat.

Production cost

We prepared preliminary estimates of the costs and returns to production of the weaning food. They were based in part on actual trial runs at the Cañete plant, assuming a raw material price for sweetpotato of US$0.03/kg. We made one set of calculations assuming the plant running at 100% capacity and a second set assuming a 70% use factor. The costs of water, gas, or electricity were not quantified.

Assuming the plant running at 100% capacity, the cost per ration ranged from US$0.16 to US$0.17 for the six formulations. Assuming operation at 70% capacity, the cost per ration ranged from US$0.16 to US$0.18 (Table 4). The estimated costs using both assumptions were well below

Table 4. Final characteristics for the selection of weaning food, 90g ration, CIP, Lima, Peru, 1997.

Weaning food[a]	Acceptability (%)	Fiber (g)	Fat (%)	Retinol (μg)	Modified costs (US$)
4	82	2.46	33	101	0.17
2	80	1.74	33	563	0.17
5	75	1.50	30	518	0.18
6	70	1.80	30	500	0.16
3	66	2.84	33	75	0.18

[a] Weaning foods: 2) orange sweetpotato + soybean, 3) white sweetpotato + wheat, 4) white sweetpotato + soybean, 5) orange sweetpotato + wheat, 6) orange sweetpotato + soybean.

the MOH acceptable prices for a weaning food of US$0.26 per 90 g ration. They were also below the average price of US$0.19 per 90g ration for the IIN-FONCODES supplementary feeding program for preschool children.

Formulation 6 was the lowest cost (US$.16), followed by 2 and 4 (US$.17). Although it is not the lowest cost, Formulation 2 was judged to be the best candidate for success because it combined high acceptability, low fiber, and high retinol.

Conclusions

- Sweetpotato roots are an excellent ingredient for weaning foods, which can be used to contribute to optimum nutrition of children in this critical growth period.
- Using a system of precooking sweetpotato before converting it into flour, orange-fleshed sweetpotato retained most of its ß-carotene content resulting in a weaning food with a higher retinol content.
- Formulation 2 is nourishing (high retinol, low fiber), easy to prepare, and readily accepted by children and mothers. Its low cost makes it competitive with other foods offered in the government supplementary feeding programs for preschool children.

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AFLP Assessment of Sweetpotato Genetic Diversity in Four Tropical American Regions

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Sweetpotato (*Ipomoea batatas* (L.) Lam.) was originally domesticated in the New World (Austin, 1988). The exact site of origin and domestication of the sweetpotato has not been well defined; neither has the wild ancestor of this species been found. Based on the numerical analysis of key morphological characters of sweetpotato and the wild *Ipomoea* species, Austin (1988) postulated that the center of origin of *I. batatas* was somewhere between the Yucatán Peninsula of Mexico and the mouth of the Orinoco River in Venezuela.

Linguistic evidence suggests that sweetpotato was dispersed to the rest of the world in three lines. The *kumara* line is prehistoric and based on lexical parallels between the Quechua name and Polynesian word *kumara*. That could explain the transfer of sweetpotato by Peruvian or Polynesian voyagers from northern South America to eastern Polynesia around AD 400. The *batata* line dates from the first voyage of Columbus in 1492, which resulted in the introduction of West Indian sweetpotatoes to Western Europe. Portuguese explorers transferred sweetpotatoes grown in western Mediterranean Europe to Africa, India, and the East Indies in the 16th century. The plant was recorded in South China by 1594 and in southern Japan by 1698. The *camote* (name derived from the word *camotli* in the Mayan language Nahuatl) line represents the direct transfer of Mexican sweetpotatoes by Spanish trading galleons between Acapulco, Mexico, and Manila, Philippines, in the 16th century (O'Brien, 1972; Yen, 1982).

Today sweetpotato, with an annual production of 124 million t, is the world's seventh most important crop after wheat, rice, maize, potato, barley, and cassava (CIP, 1996). It is widely grown in tropical, subtropical, and warm temperate regions. Developing countries account for 98% of the world's sweetpotato production. Its wide adaptability on marginal land and rich nutritional content provide an enormous potential for preventing malnutrition and enhancing food security in the developing world.

CIP has carried out numerous sweetpotato-collecting expeditions in Latin America and the Caribbean since 1985. Donations from other countries and the transfer of sweetpotato collections previously maintained in other international research centers further expanded the collection. The sweetpotato gene bank maintained at CIP now contains 5,526 cultivated accessions from 57 countries, 2,589 of them from Latin America. Peru alone contributed 1,099 accessions (Huamán and Zhang, 1997).

The success of any genetic conservation and breeding program is dependent on understanding the amount and distribution of genetic diversity present in the gene pool. For example, information on diversity distribution and domestic history is crucial for constructing core collections. They are a limited subset of accessions, derived from a larger germplasm collection, chosen to represent the genetic spectrum in the whole collection. Maximum genetic diversity is

1 CIP, Lima, Peru.
2 CIP, Nairobi, Kenya.

the key to establishing a good core subset (Brown, 1989).

In the present study, we applied amplified fragment length polymorphism (AFLP) fingerprinting to a group of Latin American sweetpotato cultivars maintained at CIP to answer two basic questions related to genetic structure in this gene pool:

1. Is there any regional differentiation in the sweetpotato diversity from tropical America? For purposes of this study, we defined four regions: (1) Central America, (2) Colombia-Venezuela, (3) Peru-Ecuador, and (4) Caribbean.
2. What is the geographical pattern of genetic diversity in these regions?

This survey is part of CIP's molecular assessment of genetic diversity in the sweetpotato collection. The information obtained will enhance our understanding of the genetic structure in the American sweetpotato gene pool and help to rationalize its management.

Materials and Methods

Plant materials

Four to ten sweetpotato cultivars were randomly selected from each country of the four regions, which resulted in a total of eighty cultivars with a geographical coverage ranging from Mexico to southern Peru (Table 1). The plant materials were obtained from the sweetpotato gene bank at CIP. Healthy young leaves were collected from accessions maintained in a screenhouse and in vitro. The leaf tissue was immediately immersed in liquid N and then transferred to –80°C, freeze-dried, and stored at room temperature until use.

AFLP protocol

A modified DNA miniprep procedure of Doyle and Doyle (1990) was used to extract DNA. The AFLP technique is described by Vos et al. (1995). DNA restriction uses the enzyme combination *Eco*RI/*Mse*I. After adapter ligation, DNA fragments are amplified using polymerase chain reaction (PCR). Primer annealing is targeted at the adapter and restriction-site sequence. Three-nucleotide extensions on both *Eco*RI and *Mse*I primers cause selective amplification of fragments. Primer combinations were chosen to produce a high number of unambiguous polymorphisms in a set of 10 sweetpotato genotypes tested. The eight primer combinations that were used are presented in Table 2.

Scoring and data analysis. Different fragments produced with each primer were treated as a unit character and numbered sequentially. Genotypes were scored for the presence (1) or absence (0) of each fragment. Only those fragments with medium or high intensity were taken into account. Fragments with the same mobility on the gel, but with different intensities, were not distinguished from each other when cultivars were compared. Monomorphic fragments were not scored.

From these data, a matrix of pairwise Euclidean distances defined by Excoffier et al., (1992) and a matrix of similarity based on simple matching coefficients (Sneath and Sokal, 1973) were calculated using the package RAPDistance v1.03 (Armstrong et al., 1995).

The similarity-based relationships between the 80 cultivars were then presented in a dendrogram following the unweighted pair group method with arithmetic mean algorithm (UPGMA) using SAHN clustering analysis of NTSYSpc (Rohlf, 1992).

Based on the Euclidean distances, the analysis of molecular variance (AMOVA) procedure (Excoffier et al., 1992) was applied to estimate variance components for AFLP phenotypes. Individual variation was partitioned within and between regions. The variance components of interest were extracted and tested using nonparametric permutational procedures. Variation between regions was then partitioned into pairwise distance between

Table 1. Name, collection number, and origin of 80 sweetpotato cultivars from the collection held at CIP.

No.	Name	Collection No.	Country of origin	No.	Name	Collection No.	Country origin
1	Cuba 9	CTX 34	Mexico	43	Catemaco	DLP 868	Venezuela
2	Linea 96	CTX 9	Mexico	44	Unknown	DLP 869	Venezuela
3	Cuba 3	CTX 5	Mexico	45	Chaco Morado	DLP 2869	Venezuela
4	Linea 475	CTX 16	Mexico	46	Unknown	DLP 2902	Venezuela
5	Unknown	DLP 3874	Panama	47	Unknown	DLP 2884	Venezuela
6	Columbiaorado	DLP 3892	Panama	48	Unknown	DLP 842	Venezuela
7	Unknown	DLP 3837	Panama	49	Unknown	DLP 824	Venezuela
8	Unknown	DLP 3834	Panama	50	Patatilla	DLP 806	Venezuela
9	Unknown	DLP 4617	Nicaragua	51	Chaco Columbiaorado	DLP 2868	Venezuela
10	Unknown	DLP 4678	Nicaragua	52	Morado	DLP 2896	Venezuela
11	Unknown	DLP 4686	Nicaragua	53	Unknown	DLP 1870	Colombia
12	Unknown	DLP 4675	Nicaragua	54	Unknown	DLP 1685	Colombia
13	Camote Blanco	GUA 494	Guatemala	55	Blanca	DLP 1731	Colombia
14	Santa Rosa (A)	GUA STRA	Guatemala	56	Morada	DLP 1793	Colombia
15	Camote Morado	GUA 940	Guatemala	57	Unknown	DLP 1858	Colombia
16	Camote Morado	GUA 948	Guatemala	58	Exquisita	DLP 1736	Colombia
17	Unknown	DLP 4545	Honduras	59	Camota	DLP 1771	Colombia
18	Unknown	DLP 4494	Honduras	60	Morado	DLP 1011	Colombia
19	Unknown	DLP 4521	Honduras	61	Blanca	DLP 1792	Colombia
20	Unknown	DLP 4558	Honduras	62	Unknown	DLP 2104	Colombia
21	Gumbs	SVG 12	El Salvador	63	Horse Money	DLP 3205	Jamaica
22	Lover's Nome	SVG 24	El Salvador	64	Tis-2544	DLP 3247	Jamaica
23	Six Weeks White	SVG 27	El Salvador	65	Clipperu	DLP 3211	Jamaica
24	Rasta	SVG 8	El Salvador	66	Tis-5093	DLP 3232	Jamaica
25	Papa Blanca	INVT 72	Cuba	67	Papota	SPV 44	Puerto Rico
26	Jiquima	INVT 51	Cuba	68	Sunny	SPV 43	Puerto Rico
27	Nigua	INVT 63	Cuba	69	Mojave	SPV 65	Puerto Rico
28	Pata de Gallina	INVT 74	Cuba	70	Toquecita	SPV 55	Puerto Rico
29	Unknown	CSDA 22	Dominican Rep	71	Unknown	DLP 3433	Peru
30	3-c-n	3-C-N	Dominican Rep	72	Unknown	DLP 253	Peru
31	Tunita	DLP 1567	Dominican Rep	73	Unknown	RCB IN-199	Peru
32	Yema de Huevo	SOSA 33	Dominican Rep	74	Unknown	DLP 909	Peru
33	Unknown	DLP 1257	Ecuador	75	Unknown	DLP 1921	Peru
34	De Dulce	DLP 1149	Ecuador	76	Unknown	RCB IN- 90	Peru
35	Blanco Papa	DLP 1435	Ecuador	77	Unknown	ARB 355	Peru
36	Camote de Dulce	DLP 1231	Ecuador	78	Unknown	ARB 455	Peru
37	Bunuelo	DLP 1484	Ecuador	79	Unknown	DLP 2298	Peru
38	Irizo Blanco	DLP 1405	Ecuador	80	Unknown	ARB 97	Peru
39	Unknown	DLP 1186	Ecuador				
40	Niguilla	DLP 1397	Ecuador				
41	Unknown	DLP 1157	Ecuador				
42	Camote Dulce	DLP 1498	Ecuador				

Table 2. Primer combinations used in AFLP analysis of sweetpotato diversity.

Number	E+3/M+3 nucleotide extensions
E34/M33	5'-GACTGCGTACCAATTC AAT-3'
	5'-GATGAGTCCTGAGTAA AAG-3'
E38/M38	5'-GACTGCGTACCAATTC ACT-3'
	5'-GATGAGTCCTGAGTAA ACT-3'
E33/M38	5'-GACTGCGTACCAATTC AAG-3'
	5'-GATGAGTCCTGAGTAA ACT-3'
E38/M32	5'-GACTGCGTACCAATTC ACT-3'
	5'-GATGAGTCCTGAGTAA AAC-3'
E36/M37	5'-GACTGCGTACCAATTC ACC-3'
	5'-GATGAGTCCTGAGTAA ACG-3'
E38/M34	5'-GACTGCGTACCAATTC ACT-3'
	5'-GATGAGTCCTGAGTAA AAT-3'
E36/M33	5'-GACTGCGTACCAATTC ACC-3'
	5'-GATGAGTCCTGAGTAA AAG-3'
E36/M34	5'-GACTGCGTACCAATTC ACC-3'
	5'-GATGAGTCCTGAGTAA AAT-3'

regions to examine the regional contribution to total molecular diversity (Excoffier et al., 1994).

Results

AFLP profile, similarity and cluster analysis

The eight primer combinations generated 210 polymorphic and clearly scorable fragments across the 80 cultivars. There were no region-specific markers (present in one region but absent in the other). However, the mean genetic similarities vary considerably between regions, ranging from 0.592 for Central America to 0.660 for Peru-Ecuador (Table 3).

The overall geographic proximity is low as reflected by the UPGMA dendrogram (Figure 1). No clusters clearly distinguished cultivars from Central America, Caribbean, and Colombia-Venezuela. Within each cluster, however, cultivars from the same geographical origins tend to group together. In sharp contrast with the closer relationship between cultivars from Central America, the Caribbean, and Colombia-Venezuela, the Peruvian-Ecuadorian cultivars were clearly distinguishable from the others. All of the 40 cultivars from Peru-Ecuador were grouped into one single cluster at a higher similarity level.

The mean similarity and the UPGMA dendrogram both suggest that Central American cultivars apparently have the highest genetic diversity, whereas Peru-Ecuador cultivars have the lowest. The Caribbean and Colombia-Venezuela cultivars have an intermediate level. The cluster analysis demonstrated a substantial regional differentiation in the Latin American sweetpotato cultivars. Sweetpotatoes from Peru-Ecuador contributed most to the regional differentiation.

Analysis of molecular variance

The results of AMOVA (Table 4) revealed large within-region variations, which accounted for 91.3% of the total molecular variance. This large within-region variation could be the contributions from two sources. The first is the expected large

Table 3. Number of AFLP-generated polymorphic markers and mean similarity in sweetpotato cultivars from four Latin American regions.

Region	Accessions (no.)	Polymorphic fragments within regions	Mean similarities within regions (no.)
Central America	24	213	0.592
Colombia-Venezuela	20	210	0.611
Caribbean	16	202	0.639
Peru-Ecuador	20	195	0.660

variation between individual cultivars, because sweetpotato is an outcrossing hexaploid, therefore the variation due to sexual reproduction is large. The second source is the between-country variation within a region. In this study, each region included more than one country, and the between-country variation was confounded by the between-individual variation. The between-country component was not separated in the analysis because the sample sizes in some countries, particularly those from Central America and the Caribbean, were too small to represent one country.

The between-region variation, although accounting for only 8.7% of total molecular variance, was statistically significant using a nonparametric test (Excoffier, 1994). That means there is measurable divergence between the four regions. Individuals from different regions were more divergent, on average, than individuals from the same regions.

Partitioning between-region variability into pairwise distance gave a clearer picture of the extent to which each region contributes to the total molecular diversity (Table 5). Pairwise distances between regions differ greatly. The shortest distance was between Central America and the Caribbean (0.0234), whereas the longest distance was between Central America and Peru-Ecuador (0.1269). Peru-Ecuador has the greatest mean distance to the rest of the regions (0.1007), indicating that sweetpotato from Peru-Ecuador has the most differentiation thus contributed most to the between-region variation. This result fully agreed with the observed grouping pattern of Peru-Ecuador cultivars in the cluster analysis.

There is a significant geographic pattern of diversity distribution (Table 4). The Central America region contains the most internal diversity (0.1990), whereas the Peru-Ecuador region contains the least (0.1677). The intermediate within-region diversities were found in Colombia-Venezuela (0.1837) and the Caribbean (0.1795). This pattern is the same as that based on mean similarity and cluster analysis. It thus confirms the higher level of genetic diversity in Central America. The diversity level decreased as sweetpotato was dispersed from the center of origin toward the south and the east.

Discussion

This study is the first case of applying AFLP fingerprints for diversity assessment in sweetpotato. The high polymorphism of AFLP makes it a powerful tool for genotyping a large number of accessions. It is suitable for genetic diversity assessment in large sweetpotato gene banks.

Austin (1988) postulated that the center of origin of *I. batatas* was somewhere between the Yucatán Peninsula of Mexico

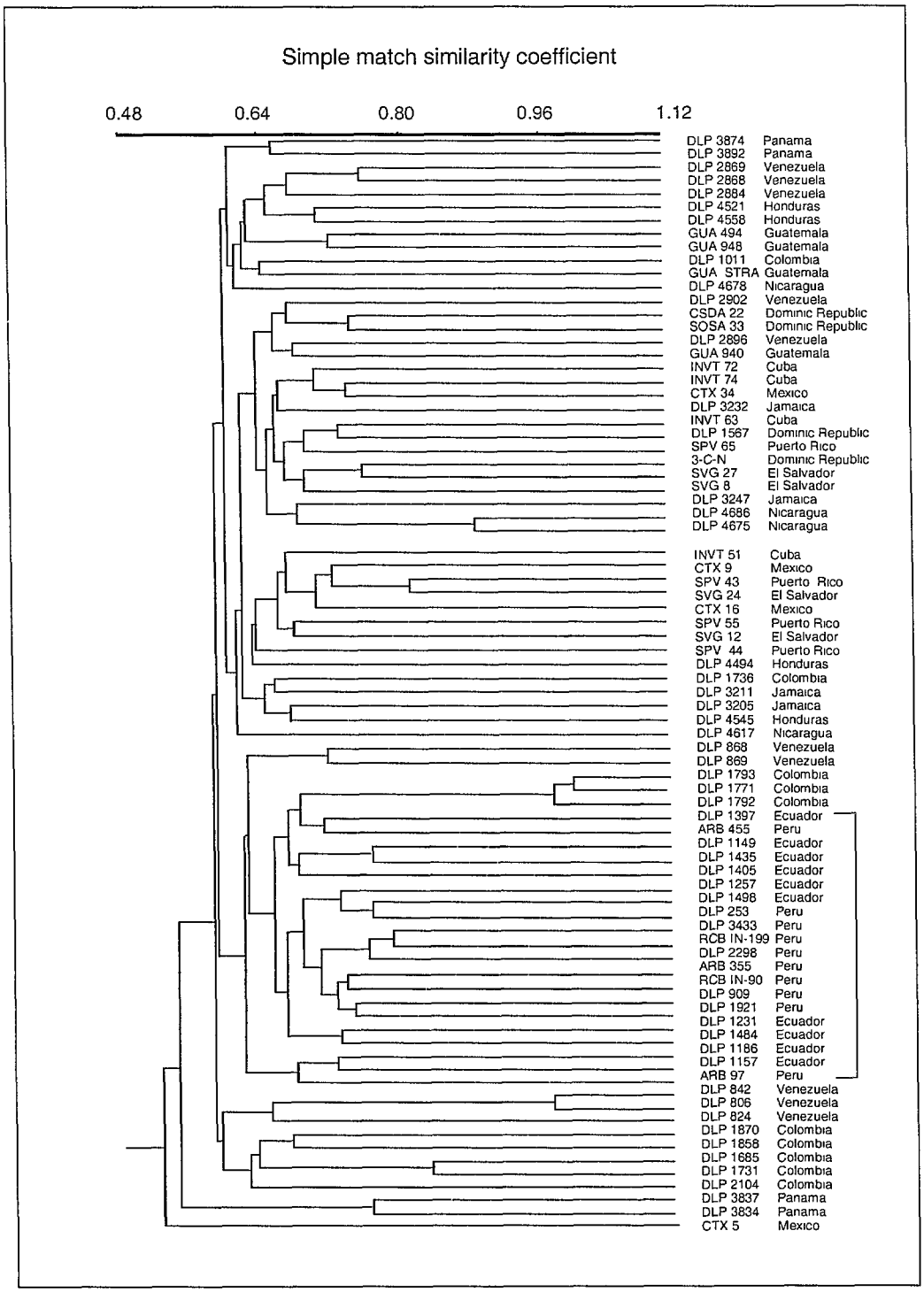

Figure 1. UPGMA dendrogram of 80 sweetpotato varieties based on simple matching coefficients from AFLP markers.] = Regional differentiation of Peru-Ecuador varieties and the lower internal diversities in the region.

Table 4. AMOVA format for the extraction of components of AFLP variation of sweetpotato clones between regions, and between individuals within regions.

Variation source	Df	SSD	MSD[a]	Variance component	Total[b] (%)	P value[c]
Between regions	3	1.593	0.531	0.0174	8.55	<0.001
Individuals within regions	76	14.129	0.1859	0.1859	91.45	
Central America	23	4.5758	0.1990			
Colombia-Venezuela	19	3.6745	0.1837			
Peru-Ecuador	19	3.1868	0.1677			
Caribbean	15	2.6920	0.1795			
Total	**79**	**15.722**				

a. Mean squared deviations.
b. Percent of total molecular variance.
c. Probability of obtaining a larger component estimate. Number of permutations = 1000

Table 5. Genetic distances between sweetpotato cultivars from four Latin American regions (Distances = PhiST between pairs of regions).

Regions	Central America	Colombia-Venezuela	Peru-Ecuador	Caribbean
Central America	0.0000	0.0391	0.1269	0.0234
Colombia-Venezuela	0.0391	0.0000	0.1130	0.0622
Peru-Ecuador	0.1269	0.1130	0.0000	0.0622
Caribbean	0.0234	0.0622	0.0622	0.0000
Mean distance to other regions	0.0631	0.0714	0.1007	0.0493

and the mouth of the Orinoco River in Venezuela. That is where *I. trifida* might have been crossed with another putative ancestor, *I. triloba*, and might have produced the wild ancestor of *I. batatas*. By at least 2,500 BC, the cultigen had most likely been spread by the local people to almost the limits for cultivation in Central and South America that existed when the Europeans arrived nearly 4,000 years later. The greater molecular diversity in Central America provides strong evidence that Central America is the primary center of diversity. It should also be the center of origin as well, considering the richness of wild *Ipomoea* species that are closely related to sweetpotato.

The much lower molecular diversity found in Peru-Ecuador suggests that cultivars in this region constitute a subset from the center of primary diversity. This result reflects the traditional pattern of crop distribution from the primary center of origin. As the crop dispersed along migration and trade routes, and through exchanges between native communities, the diversity level decreased due to the limited donor populations. A similar pattern was demonstrated in our previous work on a group of Papua New Guinea sweetpotatoes (Zhang et al., 1998).

Sweetpotato, however, is an ancient crop in Peru (Engel, 1970; Yen, 1974). The

unique ancient agriculture and other ethnographic factors may have led to a greater morphological diversity based on relatively narrow donor diversity. That could explain why Peru-Ecuador hosts a large number of sweetpotato cultivars but has a lower level of diversity. The natural and human selection forces also caused a significant regional differentiation, which was reflected as the greater genetic distance between Peru-Ecuador and the other regions. Therefore, Peru-Ecuador could be considered as a secondary center of sweetpotato diversity.

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Introduction and Use of Exotic Germplasm in the Chinese Sweetpotato Breeding Program

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Sweetpotato (*Ipomoea batatas*) was introduced to China over 400 years ago. Its high yield, wide adaptability, tolerance of abiotic stresses, and versatility have contributed to its traditional and continuing importance in Chinese agriculture. Sweetpotato ranks fourth among crops in planted area, about 5.6 million ha, with mean yields higher than those almost anywhere else in the world. In the 1950s and 1960s, the crop was used mostly for food and feed, with only 10% of total production going to starch extraction and food processing. In the 1990s, that has risen to about 45% of total production. Given the changes in use pattern, it is clear that high dry matter (DM) or high starch content is becoming more important. Most Chinese cultivars have low or moderate DM content of <30% (XSPRC, 1993). Over the last 20 years, many provincial breeding programs worked to increase DM content and yield with little success. Given the lack of progress, there appears to be a need for an infusion of new sources of genetic diversity.

Chinese Sweetpotato Breeding: Past and Present

Over the past 400 years, a number of local cultivars emerged due to selection pressure by farmers and environmental changes. Forty-eight were listed in the Catalog of Sweetpotato Cultivars in China (XSPRC, 1993), which contained 184 important cultivars. Those cultivars possess tolerance of biotic stress and resistance to abiotic stresses. They are still grown in small areas in South China. However, most of them had low yield and poor adaptability when planted away from their place of origin. That has been a serious constraint to the expansion of sweetpotato production. In 1938, Nancy Hall was introduced from the USA. Preliminary evaluations were conducted in Nanjing and Sichuan. In 1941, the Japanese cultivar Okinawa 100 was introduced and soon became the most widely grown in northern China. Nancy Hall and Okinawa 100 became important in both production and in breeding.

Modern breeding programs

Modern sweetpotato breeding began in the late 1940s and early 1950s when the population explosion and severe food shortages led the government to emphasize sweetpotato production. Major efforts were devoted to sweetpotato breeding in provinces with large sweetpotato planting areas. A number of new cultivars were developed using Okinawa 100, Nancy Hall, and some local cultivars as parents. Most of the new cultivars had medium to low DM content. Xushu 18 is the cultivar most widely grown, with a planted area of 1.5 million ha. Its DM content is about 25% (summer cropping in sandy loam soil in Xuzhou) and extractable starch content is 11-15% (XSPRC, 1993). Various institutes released many cultivars. One of most successful after Xushu 18 was Nanshu 88, which was released in 1988 by the Nanchong Agricultural Research Institute. It is, however, grown only in Sichuan Province.

To increase production and efficiency, key breeding units in China were organized into a national collaborative sweetpotato breeding project. Greatly improved collaboration among provincial- and city-level

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research units resulted. Conventional hybridization is still the principal approach for sweetpotato breeding. Since the late 1970s, Jiangsu Academy of Agricultural Sciences (AAS) and Shandong AAS paid more attention to collection, evaluation, and use of wild-relative species. Some newly developed cultivars, such as Sushu 2 and Pushu 83-91, were bred with the introgression of genes from wild relatives. New cultivars, Yi 306, Lushu 7, and Yushu 7, were selected from crosses with the Japanese cultivar Minamiyutaka, which has 12.5% of wild species genes in its pedigree. Mutation breeding with ^{60}Co radiation used to induce somaclonal variation has been used to improve sweetpotato. This work was done at Beijing Agricultural University. As a result, Nongda 601, highly resistant to black rot caused by *Ceratosystis fimbriata*, was selected from Xushu 18; and, Nongda 321-10, with resistance to stem nematode (or brown ring caused by *Ditylenchus destructor*), was selected from Ning 12-17. Yantai Institute of Agricultural Sciences selected a number of cultivars using fast neutron radiation. These selected cultivars are high yielding and have high vitamin C content. The Xuzhou Sweetpotato Research Center (XSPRC) selfed elite clones, and selected two superior clones, Xuzi 39 and Pengwei S_1-12-48. None of these efforts, however, resulted in a cultivar superior to Xushu 18.

In recent years, postharvest processing of sweetpotato has become an important way for farmers to increase their income. That requires a high-yielding sweetpotato high in DM content. Existing cultivars do not meet these demands. Disease-resistant cultivars with high starch content and high DM yield are urgently needed.

Inbreeding tendency in sweetpotato breeding

Nancy Hall and Okinawa 100 have been widely used as parental material since the beginning of the modern breeding program. According to Lu (1990), who analyzed the pedigree of cultivars listed in the Catalog of Sweetpotato Cultivars (1981), 41 cultivars have been released from crosses with Okinawa 100 as a parent, and 33 from Nancy Hall. Thirty-one cultivars were developed from cross combinations between the two, including important cultivars such as Lizixiang, Yiwohong, Fengshouhuang, and Huabei 52-45. Nancy Hall and Okinawa 100 were dominant among parents in breeding programs in Beijing and Nanjing. In Beijing, Huabei 117, Huabei 166, Beijing 553, Beijing 284, Beijing 169, and others were selected from crosses of these two parents. More than 70 cultivars were selected from the crosses of Nancy Hall and Okinawa 100 after provincial breeding units were established in the early 1950s. Some of them, such as Yiwohong, Beijing 553, and Lizixiang are still planted in some places.

In turn, Xushu 18, which has 75% of its genes from Nancy Hall and Okinawa 100, has been widely used as parental material.

Although the use of Nancy Hall and Okinawa 100 led to the development of many successful cultivars, the genetic background of sweetpotato has become narrow and limited. From 1986 to 1990, 21 of 23 cultivars released in China carried a substantial number of genes from Nancy Hall and Okinawa 100. Nanshu 88 and Ji 18-1 were the only two exceptions. Of 21 new cultivars registered from 1990 to 1995, only Sushu 4 and Sushu 6 were not genetically related to these two parents.

The General Seed Company of China (1989) listed 42 cultivars grown on more than 667 ha. Of these, 26 were considered closely related to Nancy Hall or Okinawa 100 or both, in that they have more than 12.5% of their genes in common.

Sweetpotato breeding programs all over China have extensively used Nancy Hall, Okinawa 100, Xushu 18, and other closely related cultivars as parents. This practice caused severe inbreeding during selection, and limited the release of new, promising cultivars, especially those with high DM content. Although more than 30 new

cultivars have been released since 1990, none can replace Xushu 18. These new cultivars have low to medium DM content compared with many Japanese cultivars.

In recent years, more and more exotic germplasm has been introduced through international cooperation. The breeding strategy of CIP (Mok et al., 1998) strongly influenced sweetpotato breeding in China. Breeders paid more attention to broadening the genetic base by introducing exotic germplasm. With the introduction of superior germplasm from CIP and Japan, the inbreeding tendency can be reversed to achieve higher yields and DM content. Breeding materials from various sources, including those from South America and Africa, are expected to further broaden the genetic base to incorporate resistance to viruses and other diseases. The challenge is to introgress these new genetic resources into highly-adapted, high-yielding Chinese commercial cultivars. Obviously, cultivar introduction alone will not achieve these goals. There is a need for further breeding.

Material and Methods

Various sources of seed families have been evaluated in China. Seed families from CIP-Lima had high DM content with resistance to root-knot nematode (*Meloidogyne* spp.). CIP-Nairobi sent seed families of high DM content with sweetpotato virus disease resistance. Those from CIP-Bogor had high DM content with wide adaptability. Seeds were also received from the cooperative shuttle breeding project with Japan (Table 1). Seven advanced clones were introduced from CIP-Bogor. They had been selected at three sites in Indonesia: Bogor (humid tropics, poor soil, 200 m), Lembang (highland, cooler climate, 1600 m) and Malang (highly fertile soil, 700 m). These clones were initially selected based on yield, DM content, starch content, and adaptability to poor soils. Two clones (190070-1 and 194039-1) selected at Xuzhou from CIP-Lima seeds were included. Xushu 18 was used as a check.

Seedling evaluation was done at Xuzhou by planting during the first week of June. Advanced clones were multiplied at XSPRC and evaluated at Chengdu, Jinan, and Xuzhou. Clones were planted in random complete block design with three replications. The size of a single plot was 9.4 m^2. Cultivation was done according to the standard method of each provincial AAS. Harvest was 120 d after planting. DM content of storage root was measured using 200 g of longitudinally sliced strips. Drying oven temperature was set at 70°C until the samples reached constant weight.

Results and Discussion

Botanical seed families from CIP have been introduced into China since 1990; more than 34,000 seeds have been evaluated. The number of families and their origin are listed in Table 1. Seeds introduced in the early 1990s had poor germination and low adaptability, resulting in a low selection

Table 1. Evaluation of botanical seeds introduced to XSPRC from CIP.

Year	Crosses	Seeds received	Seedlings planted	Clones selected	Origin
1992	33	1,700	600	12	CIP-Lima
1994	100	8,100	3,571	34	CIP-Lima, CIP-Bogor
1995	80	6,700	4,000	70	CIP-Lima, CIP-Bogor, CIP-Nairobi
1996	30	2,650	1,010	22	CIP-Lima, CIP-Bogor
1997	14	1,483	920	30	Shuttle-breeding families
1998	160	12,000	8,600	400	CIP-Lima, CIP-Bogor
1999	148	20,520			CIP-Lima, CIP-Bogor

ratio. Selected high-yielding clones such as 490074-2 (from CIP-Lima, 1992) and B0080-1 (from CIP-Bogor, 1994) had low DM content. These clones have already been discarded from the CIP breeding program.

In 1995, large quantities of seeds were introduced, most of them from crosses of high DM-content parents. Two clones from CIP-Lima were selected, 194038-3 and 194039-1. Both had high DM content, 35% for 194038-3 and 32% for 194039. They had higher dry matter content than that of Xushu 18 (25-26%). After initial selection at XSPRC, the 2 clones were sent to more than 10 breeding units around the country for further evaluation. Although the clones were not released as cultivars, they were used as parental material in many provinces. In 1996, 22 good clones were selected from CIP seed families. Of these, Kawa 090-1 had 30% DM content, 4% higher than Xushu 18. Further evaluation was done in 1998 with about 12,000 seeds, 9,600 of which came from CIP-Lima, 2,200 from CIP-Bogor, and 524 from the National Agriculture Research Center (NARC), Japan. The Japanese seeds were produced as a part of CIP-NARC's shuttle-breeding activity. With the adoption of improved seed germination methods, about 90% of seeds germinated. After inferior plants in the nursery were discarded, 8,600 seedlings were transplanted to the field. Finally, 400 good clones were selected from the first year seedling evaluation. Selection was based on good root shape and high DM content.

In 1998, seven clones were introduced from CIP-Bogor. Of these, enough planting material was produced to test three clones (Group I) in Xuzhou, Jinan, and Chengdu. Four clones (Group II) that did not produce enough cuttings were tested only in Xuzhou. The result of the evaluation of Group I is presented in Table 2, and that of Group II in Table 3. The results indicated that AB94001.8 (code name CIP-2) had high DM content and high yield. Fresh storage root yield of CIP-2 was almost the same as Xushu 18 (Table 2), but DM content was higher than Xushu 18 at all three sites. This clone will be tested in demonstration trials in 1999.

Clone AB94001.8 was initially selected in Indonesia from seed families obtained through shuttle breeding. In evaluations of various introductions from many countries, seed families from Japan were observed to produce progenies having very high DM content. The parental clones of these families also had high DM content in Japan (Tarumoto, 1989; Yamakawa, 1995).

Table 2. Multilocation trial of introduced high DM-content clones (Group I), China, 1998.

Clone	Xuzhou			Chengdu			Jinan			Mean		
	DM (%)	FY (t/ha)	DY (t/ha)	DM (%)	FY (t/ha)	DY (t/ha)	DM (%)	FY (t/ha)	DY (t/ha)	DM (%)	FY (t/ha)	DY (t/ha)
AB94001.8	30.2	19.5ab[a]	5.9a	32.3	28.4a	9.2a	39.4	11.2a	4.1ab	34.0	19.7	6.4
AB95002.3	30.4	8.5c	2.6 b	27.8	13.2 c	3.7 c	41.6	3.9 b	1.6 c	33.3	8.5	2.6
AB97001.1	28.2	14.4abc	4.1ab	28.3	13.2 c	3.7 c	38.5	6.2 b	2.4 bc	31.6	11.3	3.4
190070-1	31.8	12.1bc	3.8ab	33.3	13.5 c	4.5 bc	43.6	5.1 b	2.2 c	36.2	10.2	3.5
194039-1	30.2	21.2ab	6.4a	32.3	17.1 b	5.5 b	40.6	8.2ab	3.3abc	34.4	15.5	5.1
Xushu 18	24.4	24.2a	5.9a	30.3	30.7a	9.3a	35.1	12.4a	4.3a	29.9	22.4	6.5

DM = dry matter content, FY = fresh storage root yield, DY = dry matter yield.
a. Mean separation within columns by Duncan's multiple range test at P = 0.05.

Table 3. Single-location trial of introduced high DM-content clones (Group II), Xuzhou, China, 1998.

Clone	DM (%)	FY (t/ha)	DY (t/ha)
AB94002.7	29.7	4.9	1.46
AB95002.7	32.8	10.8	3.54
AB94078.1	33.7	13.8	4.65
AB95012.4	25.0	8.4	2.10
Xushu 18	24.0	20.6	4.94

DM = dry matter content, FY = fresh storage root yield, DY = dry matter yield.

Obtaining botanical seeds in quantity from Japan was difficult due to the cost of seed production. Moreover, all of the recently-released cultivars, which are frequently used for hybridization, are protected under the breeders' rights law in Japan. To overcome these limitations, shuttle breeding was suggested (Takagi, H., Japanese International Research Center for Agricultural Science and Komaki, K., National Agricultural Research Center, pers. comm.). CIP sent a trainee to NARC to learn hybridization techniques using high DM-content cultivars such as Minamiyutaka, Satsumahikari, and Hi-starch. *Ipomoea nil*, a dwarf morning glory, which had strong flowering induction ability, was used as grafting stock. Three trainees from developing countries were sent to Japan, one each in 1996, 1997, and 1998. Hybrid seeds produced were evaluated in China, Indonesia, and Vietnam. DM content in the breeding population was rapidly increased using these seed families.

Another clone, AB94078.1, was selected at CIP-Bogor from seed families of CIP-Lima. This clone had the highest DM content of all clones tested at Xuzhou (Tables 2 and 3), and also gave the highest DM content (39%) at three distinctively different environments in Indonesia (Mok et al., 1997a). This clone has already been distributed to other breeding units in China.

Two main selection criteria at CIP-Bogor were high DM content and wide adaptability (Mok et al., 1997b). These *AB series* clones, selected for wide adaptability in Indonesia, seemed to perform satisfactorily at the evaluation sites in China. Clones selected in Indonesia for high DM content almost always tested high for DM content in China. The heritability of DM content was 61.2% (Mok et al., 1997b). It is likely that this trait could have a small genotype by environment interaction.

Conclusion

In China, popular sweetpotato cultivars mostly have low to medium DM content. Two major reasons for this are the narrow genetic base and the high yield focus of breeding programs. Recent developments in starch processing from sweetpotato in China require cultivars with high DM content and high starch content. Collaborative research with CIP makes the exchange of genetic resources possible with unprecedented speed. As a result, a number of high DM clones have been selected and introduced. These materials are under evaluation in many provinces where sweetpotato is important. These preliminary results indicate it is possible to select cultivars for high DM content, high yield, and wide adaptability in China. This effort will have a major impact in many provinces where starch processing is a major source of farmers' income.

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Farmer Maintenance of Sweetpotato Diversity in Asia: Dominant Cultivars and Implications for In Situ Conservation

G. Prain and D. Campilan[1]

In situ conservation of plant genetic diversity has received growing attention in the last 30-40 years, primarily in relation to wild species. In Asia, the number of protected areas tripled between the 1960s and early 1990s (MacKinnon, 1995). In situ maintenance of crop genetic diversity, however, was not considered a viable conservation strategy by international organizations or leading specialists until recently (Williams, 1988; Frankel, 1970). The earlier assumption was that landraces were used only in traditional agricultural systems. Technological modernization then, especially the introduction of new cultivars, would inevitably lead to the loss of landraces in most cases. Since it would be both impracticable and immoral to preserve an entire system in its traditional state, it was argued, ex situ rather than in situ conservation was the only solution.

In fact, the cultivation of diversity has survived enormous historical changes in these supposed unchanging societies (Wolf, 1982). There is clear evidence that landraces continue to be cultivated under modern conditions and with modern technology (Brush, 1991, 1993). Nevertheless, some of these findings give rise to concern. Modern or selected commercial cultivars seem to have contributed in some cases to the decline of area, fragmentation into pockets or islands of production, and even the disappearance of indigenous cultivars altogether (Brush, 1993).

That is an important issue for sweetpotato (*Ipomoea batatas* (L.) Lam.) in Asia, the secondary center of diversity and the primary center of production and use of the crop. There is an urgent need to identify adequate national conservation strategies to ensure the continued availability of genetic diversity to farmers and plant breeders. In situ conservation could provide greater accessibility to diversity and, by spreading the costs of conservation, reduce the vulnerability of publicly funded ex situ genebanks. It could maintain diversity and habitat viability where continued crop evolution could take place provided a few commercial cultivars do not dominate and displace local crop genetic diversity.

To gauge the real potential of in situ conservation, it is necessary to fully understand cultivar maintenance practices of households under different socioeconomic and ecological conditions, and the dynamics of varietal dominance. Does dominance mean displacement? This paper draws conclusions for the future role of in situ maintenance in crop conservation strategies. It is based on case studies in three areas where varietal dominance is important.

Approach and Methods

To document and evaluate sweetpotato diversity in Asia and to understand how farmers maintain cultivars, CIP has supported germplasm collection and socioeconomic studies in the Philippines, Indonesia, and Vietnam since the early 1990s. Fieldwork methods have varied considerably. Some focused on collection and characterization with minimum documentation of

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indigenous knowledge. Others are extremely detailed, long-term documentation of local practices using participatory rural appraisal, ethnobotanical techniques, and monitoring of local germplasm collections.

The studies undertaken by UPWARD (Users' Perspective with Agricultural Research and Development), a CIP network, have identified four major sweetpotato production systems: (1) shifting cultivation in hillside and mountain areas, (2) home gardens, (3) upland rotations, and (4) lowland postrice systems (Prain, 1995). The last is the most commercialized production system in Southeast Asia and by volume the most important system in Vietnam, Indonesia, and the Philippines. The different systems influ-ence farmer maintenance of sweetpotato diversity.

Case Study 1. Shifting Cultivation in Mountain Environments

The case study on shifting cultivation in mountain environments is based on published and unpublished data collected in Wagawaga, Central Irian Jaya, Indonesia (Schneider and Yaku, 1996; Schneider et al., 1997; and Prain, Widiastuti, and Yaku, unpubl.). Wagawaga is in the northern part of the Baliem Valley, a large, flat agricultural area. The valley is surrounded by steeply rising mountain walls, which also support shifting agriculture. There are two main sweetpotato production systems. In one, *hipere wen*, sweetpotato is planted in individual mounds on high ridges surrounded by deep drainage ditches. The other, *yabu waganak*, is similar to *hipere wen* but without the drainage ditches. *Yabu waganak* is sometimes practiced in gardens near the compounds, particularly on hillsides.

As in most parts of highland Irian Jaya, steamed or baked sweetpotato is the staple food of Wagawaga families, accounting for as much as 90% of their diet (Heider, 1979). Production systems are designed to supply freshly harvested sweetpotato year-round. Households maintain several beds at different stages of development as well as mixtures of cultivars in each bed to ensure supplies. Mixtures are important. Local people compare the mixing of many sweetpotato cultivars in one garden bed with the need to *mix up* the clans for marriage to ensure the continuity of the tribe. Short duration cultivars are important components of the mixtures. The number of cultivars maintained per bed ranged from 7 to 20, with an average of 12. Women who maintain multiple sweetpotato beds do not plant the same set in each bed, but the most important cultivars are likely to be common in all beds.

Wagawaga was designated as an in situ site in 1994. A preliminary study on the genetic diversity (Yuliantiningsih, 1995) identified 47 cultivars in the 30 beds of the in situ study garden. A follow-up documentation of 30 beds in 1998 also documented 47 cultivars, but only 27 of these were the same as the cultivars planted in 1994 (Table 1). The distribution of the different sets of cultivars in 1994 and in 1998 are quite similar, although the beds documented in 1998 were not exactly the same as those in the 1994 study since beds are periodically remade within the same garden area. We can better understand the cultivar distribution by considering two key characteristics of farmers' cultivar management: the number of plants of a cultivar and the frequency with which the cultivar is planted in different beds (Figures 1 and 2). The planting density of cultivars was calculated differently in 1994 and 1998. In 1994, the total number of plants in the garden was counted and the percentage of the total calculated for each cultivar. In 1998, each bed was mapped and the percentage each cultivar occupied in the bed was calculated.

Helaleke asli was the most widely planted cultivar in both 1994 and in 1998, with 34.9% of bed area in 1994 and 42% in 1998 (Cluster 1, Figures 1 and 2). This cultivar is the most important human food in Wagawaga and, in particular, is the

Table 1. Cultivars planted in Wagawaga, Irian Jaya in 1994 and 1998.

Cultivars present 1994	Cultivars present 1998	Cultivars present 1994	Cultivars present 1998	Cultivars 1994	Cultivars present 1998
Helaleke asli	Helaleke asli	Ponai	-	-	Kafiar
Hupuk	Hupuk	Tuke asli	-	-	Suweal baru
Hopoye	Hopoye	Puluk	-	-	Leget pilodok
Musan	Musan	Mikmak	Mikmak	-	Kakum eka
Namukera	Namukera	Musaneken baru	-	-	Musan baru
Musaneken	Musaneken	Saporeken	Saporeken	-	Kentang
Abukul	Abukul	Salisike	Salisike	-	Wiyayuken
Alukulek	Arukulek	Suweal	Suweal	-	Tinta hitam
Kilaake	Kilaake	Sabolok	-	-	Juaiken baru
Helakeke baru	Helakeke baru	Tabogole	Tabogole	-	Wopem
Inin	-	Tinta	Tinta	-	Tinta putih
Juaiken	Juaiken	Tamue	Tamue	-	Kulameke
Duak	-	Welelom Sumunah	Welelom Sumunah	-	Tinta merah
Ebe asli	-	Welelum Baru	Welelum Baru	-	Yakik
Fibisak	Hibisak	Wenaboge Molah	-	-	Hoboak
Ogopem	-	Wenaboge	Wenaboge	-	Lisuge
Nobokum	Nobokum	Wereneh	Wereneh	-	Baruke
Hulok	Hulok	Helaleke Hulek	-	-	Aluage
Hupaleke	-	Helaleke Walagin	-		
Kilu	-	Yibilaken	-		
Hupuk Sumunah	-	Wosilolo	Wosilolo		
Pilka	Pilka	Kumbuk Aidek	-		
Pogoreken	-	Mayugwe	-		
Pulugia	-		Wortel		

appropriate food for women to present to men. The second most widely planted cultivar, in area and in number of beds where it was grown, was Musan. It occupied 16% of bed area in 1994 (Figure 1) and 24% in 1998 (Figure 2). This cultivar produces large roots and is an important source of pig feed in the area. According to women (who plant and tend the beds), the proportion of beds dedicated to particular cultivars varies, depending on the proportion of people and pigs in households and compounds.

The second clustering (Cluster 2, Figures 1 and 2) includes cultivars planted in more than 10 beds and which occupy more than 1% of bed area. These clusters comprise cultivars that are also important, but for different reasons. One is connected with the use of sweetpotato for baby food, such as cultivars Arukulek, Welelom, and Welelum Baru. The rapid diffusion of the new cultivar Wortel between 1994 and 1998 seems to be due to its orange color and less floury texture, preferred characteristics for baby food. Some, such as Hupuk are ancestral cultivars. They must be planted, often before other cultivars and by the fertility chief, for the sake of the ancestors and to ensure a bountiful harvest. Many of these cultivars are valued as adult food and are also fed to pigs, especially the smaller roots.

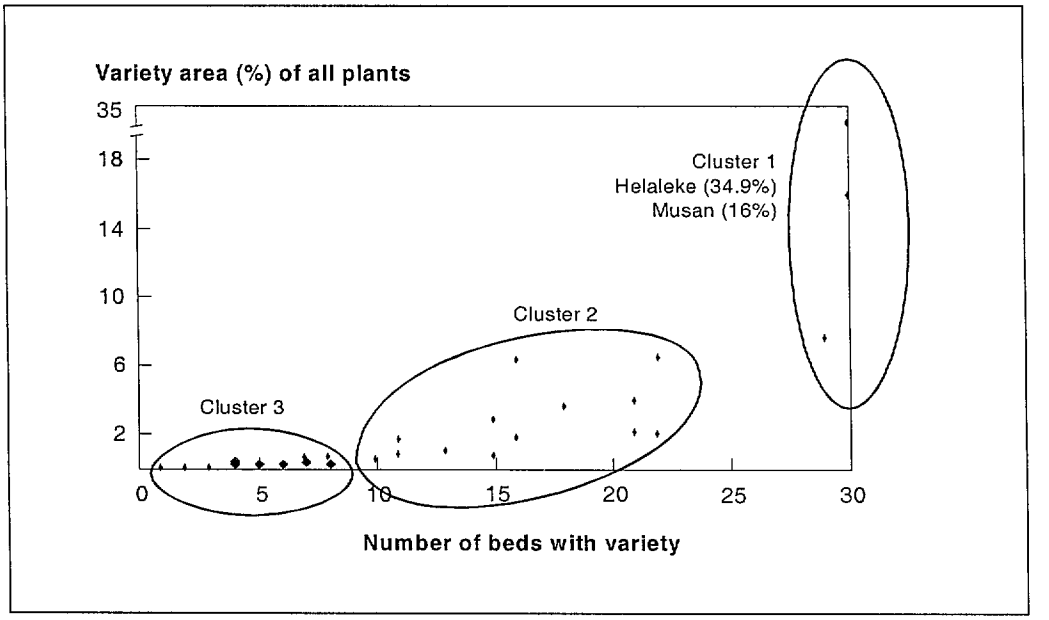

Figure 1. Distribution of 47 sweetpotato cultivars in 30 beds, Wagawaga, Irian Jaya, Indonesia, 1994.

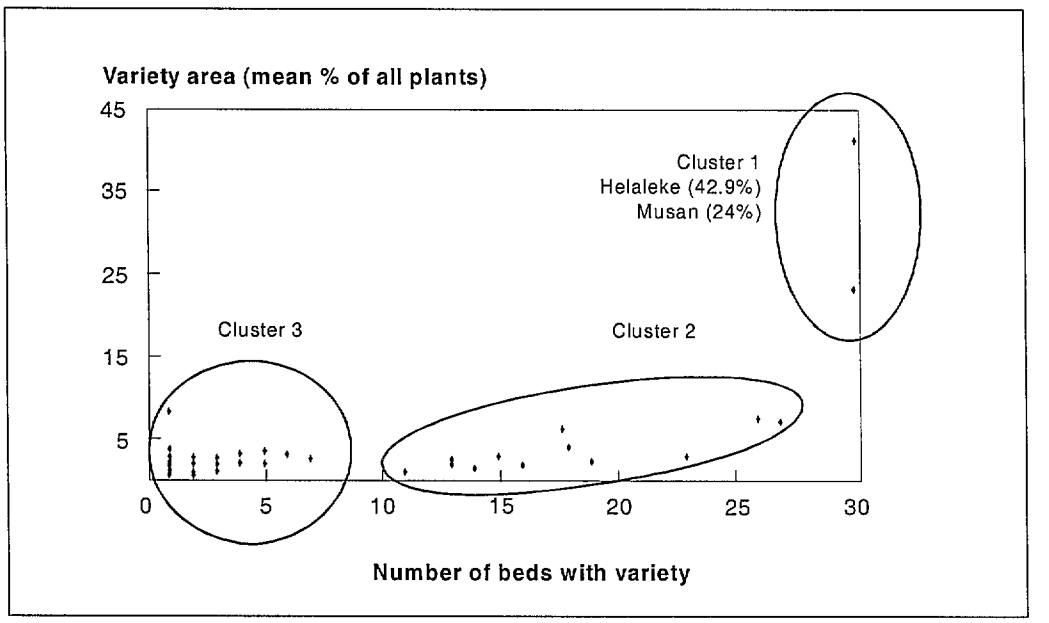

Figure 2. Distribution of 47 sweetpotato varieties in 30 beds, Wagawaga, Irian Jaya, Indonesia, 1998.

Cluster 3 involves cultivars that appear *residual*. In 1994, 30 of the 47 cultivars were grown in fewer than 10 beds and accounted for only 4% of area. In 1998, 33 cultivars were grown in fewer than 10 beds and accounted for 6% of area. Women say they do not *forget* to plant any of the cultivars, even these with such tiny representation. However, they may not replant some cultivars if they do not find cuttings,

which is especially possible with this last cluster. These cultivars account for most of the variation between 1994 and 1998 as they slip in and out of the system. Of the 20 cultivars that disappeared, almost all covered less than 0.5% of beds and were planted in fewer than 5 beds.

A similar situation applies to the newly introduced cultivars in 1998. Almost all were found in fewer than 5 of the 30 beds, with very small area planted. Exceptions are Tinta (in 18 beds in 1998) and Wortel (14 beds). Tinta is grown as pig feed. Wortel is grown as baby food and for sale to non-Irianese consumers who like its yellow flesh. Both cultivars are new (*baru*), meaning they have recently been introduced or identified as novel types, probably having emerged as seedlings.

Case Study 2. Upland Semicommercial Rotations

The upland rotations case study involves a semicommercial system practiced in Maambong Province on Mindanao, the southernmost of the larger Philippine islands (Prain and Piniero, 1999). It is one of the wettest areas of the country with well-distributed rainfall allowing crops to be planted throughout the year. That favors sweetpotato conservation, because vegetative planting material is readily available for replanting. Maambong is situated in the relatively flat, northern part of a generally undulating grassland plateau, crosscut with deep river valleys.

Farmers practice adapted plow agriculture and rotations on the plateau and in the hills, especially for maize, root crops, and, more recently, vegetables. Another common production system is the home garden, which normally supports a large amount of biodiversity. Sweetpotato is a supplementary staple in both systems. There has been a steady increase in sweetpotato genetic diversity with the influx of cultivars brought by migrants from the northern coast and from nearby smaller islands. However, the growth in diversity may have peaked around the early 1980s. That was around the time a multinational pineapple plantation became an increasingly important employer in the area; this increased opportunities for vegetable production.

Through an agreement with an informal group of women in Maambong, a *conservation garden* was established. The garden, initially consisting of 24 beds, was modeled after household gardens. Following initial experimentation, however, the women adopted a rotation system with peanut for replanting their root crop collections. Each woman cultivated her own plot and initially planted cultivars from her own fields and garden, leading to considerable duplication of cultivars across the plots.

There was a sharp rise in sweetpotato diversity in the second planting, from 11 to 19 cultivars, with one lost (Table 2). That can be explained by several factors, the most important of which is the influence of the project itself. The considerable interest and enthusiasm among the women in diversity maintenance resulted in their scouring the locality for additional cultivars. However, five of the added cultivars had already disappeared from the garden by the third planting; all had disappeared by the fifth planting. It was felt that the project had heightened the normal practice of evaluating any new cultivar for which planting material is available.

That impression was supported by the similar pattern that characterized subsequent plantings, with a few rare local or exotic cultivars added only to be abandoned later. A cluster of preferred cultivars present from the beginning of the garden (Klarin, Five Fingers, Igorot Pula, Igorot Puti, Amerikano, Kamada, and Tapol) were consistently planted by most women and gradually became the main cultivars (Table 2). Furthermore, in later plantings there was a tendency to reduce the numbers of plants of other cultivars in favor of the preferred cultivars. That was particularly true of Klarin and Five Fingers, which are popular

Table 2. Sweetpotato cultivars planted in the Maambong genebank over five seasons.

First planting	Second planting	Third planting	Fourth planting	Fifth planting
Klarin	Klarin	Klarin	Klarin	Klarin
5-fingers	5-fingers	5-fingers	5-fingers	5-fingers
Igorot Pula	Igorot Pula	Igorot Pula	Igorot Pula	Igorot Pula
Tapol	Tapol	Tapol	Tapol	Tapol
Amerikano	Amerikano	Amerikano	Amerikano	Amerikano
Bilaka	Bilaka	Bilaka	Bilaka	
Igorot Puti	Igorot Puti	Igorot Puti	Igorot Puti	Igorot Puti
Kamada	Kamada	Kamada	Kamada	Kamada
Valencia	Valencia	Valencia	*Valencia*	
Kinampay	*Kinampay*	**Kinampay**	Kinampay	*Kinampay*
Kaligatos	Kaligatos	Kaligatos	*Kaligatos*	Kaligatos
	Tinangkong	Tinangkong	Tinangkong	*Tinangkong*
	Kapitlok	Kapitlok	*Kaligatos*	
	Kabohol	Kabohol	*Kabohol*	
	Sil-ipon	Sil-ipon	*Sil-ipon*	
	Magtuko	*Magtuko*		
	Maranding	*Maranding*		
	Senorita	*Senorita*		
	Imelda	*Imelda*		
	Kitam-is	*Kitam-is*		
		Lila	*Lila*	
		Initlog	*Intilog*	
			PNGL	PNGL
			Kawakwak	Kawakwak
			P16	P16
			NPSP	PNSP
			Salayaw	*Salayaw*
			UPLSP	UPLSP
			Kabato	*Kabato*
			Turay	*Turay*
Total 11	19	17	17	13
Additions	+ 9	+ 3	+ 8	+ 1
Losses	- 1	- 5	- 8	- 5

Note: Cultivars in bold are additions.
Cultivars in italics are losses.

in the fresh market. Characteristics of the preferred cultivars are given in Table 3. The wide genetic diversity suggests close relation between diversity of use and genetic diversity.

Case Study 3. Lowland Postrice Systems

The lowland postrice sweetpotato production system case study (Anganon et al., 1998; Data et al., 1997) is based on the key commercial sweetpotato producing

Table 3. Morphological characterization[a] of continuously planted, dominant cultivars in the Maambong, Philippines, genebank, 1998.

Cultivar	Plant type	Vine color	Leaf vein	Leaf shape	Immature leaf col.	Petiole pigment	Root shape	Skin color	Flesh color	Extracts of farmers' characterizations
Klarin	7	1	2	5332	32	1	8	830	100	Grows easily; roots dry, sweet; tops for vegetable, forage; salable
Five Fingers	7	3	5	6755	72	3	3	634	442	Early maturing; leaves for vegetable; roots sweet, watery; salable
Amerikano	7	7	8	3131	95	9	8	126	543	Profuse vines; few big roots; roots sweet, powdery
Igorot Puti	9	3	3	5332	62	3	8	230	200	Profuse foliage, good for weed control, forage; roots sweet, dry
Igorot Pula	7	3	5	5334	92	8	3	230	100	Roots dry, sweet; leaves for vegetable; salable
Tapol	5	7	8	3151	95	9	2	930	196	Easy to maintain; Roots unsweet, watery; leaves for vegetable; good market for this color; small area
Kamada	5	1	2	5332	23	3	3	520	100	Early maturing; easily harvested; root sweet, watery; tops suitable for forage

Key· Plant type = 1 erect, 9 extremely spreading. Vine color = 1 green, 9 totally dark purple. Leaf vein color = 1 yellow, 2 green, 3 purple spots main rib, 4 purple spots several veins, 5 main rib partially purple, 6 main rib mostly purple, 7 all veins partially purple, 8 all veins mostly purple, 9 lower surface and veins totally purple. Leaf shape (combination of 4 numbers): 1st Outline = 1 rounded, 7 almost divided; 2nd Type of lobe = 1 none, 9 very deep; 3rd Lobe number; 4th Shape of central lobe = 0 absent, 9 linear. Immature and mature leaf color (combination of 2 numbers) = 1 yellow-green, 9 totally purple. Petiole pigment = 1 green, 2 green with purple near stem, 3 green with purple near leaf, 4 green with purple both ends, 5 green with purple spots throughout, 6 green with purple stripes, 7 purple with green near leaf, 8 some petioles purple, some green, 9 totally/mostly purple. Root shape = 1 round, 9 long, irregular or curved. Skin color (combination of 3 numbers): main = 1 white, 9 dark purple; intensity = 1 pale, 3 dark; secondary = 0 absent, 9 dark purple. Flesh color (combination of 3 numbers): main = 1 white, 9 strongly pigmented; second color = 0 absent, 9 dark purple, distribution of color = 0 absent, 9 covering all.

region in Central Luzon, the Philippines. Located about 50 km north of Manila, it is the main supplier for the urban fresh root market. Sweetpotato is commercially grown in ricefields during the dry months from December to April, with peak harvest in March. Central Luzon's six provinces had a sweetpotato production area of approximately 9,000 ha in the early 1990s. Recently, the area has expanded to 10,000 ha through increased demand for sweetpotato as a raw material for large-scale starch processing. Moreover, destructive flows of volcanic debris resulting from the eruption of Mount Pinatubo in 1991 forced the shift from rice and sugarcane to sweetpotato.

A total of 25 sweetpotato cultivars have been grown in the region since the early 20th century, according to farmers. Only four are now widely grown and a single cultivar Superbureau covers at least 80% of the total production area. High root yield, marketability, and early maturity are the most important traits considered by farmers. Historically, farmers grew a mix of cultivars for both general and specialized uses. For instance, two popular cultivars, Bureau and Taiwan, were preferred for the high quality of their boiled roots. Girayan and Lampangog were grown because they commanded high prices for their use in traditional dishes. Finally, the establishment of starch factories created a demand for Superbureau as a processing cultivar.

Availability of planting materials has also been a major determinant of cultivar. Most farmers maintain their own mini-seedplots of preferred cultivars. With the high demand for planting materials at the start of a cropping season, some enterprising farmers have offered specialized seed production and marketing services. The cultivars propagated by these commercial suppliers determine the varietal combinations for the next season. For instance, Tarlac farmers, faced with the acute shortage of their preferred Bureau, resorted to planting Superbureau, the only material available from seed suppliers from the neighboring province. The seed suppliers have in turn been responding to agroecological and socioeconomic changes in the region. Bureau was being severely affected by feathery mottle virus (SPFMV) and possibly other viruses in the early 1990s and seed growers began looking for an alternative cultivar. Superbureau had many of the characteristics of Bureau, but was more resistant to SPFMV and more appropriate for the developing processing industry. In 1998, Superbureau itself began exhibiting a similar susceptibility to the virus complex, prompting farmers to seek newer, more tolerant cultivars. Meanwhile, with increasing attention to the processing market, cultivars high in dry matter became important.

Despite the relative uniformity of the postrice system in Central Luzon, agroecological variation affecting cultivar choice still exists. Variation may be stable and long-term such as in soils, topography, drainage, etc. For example, in some areas Superbureau performs very poorly. Or variation may be produced through natural disasters such as the accumulating volcanic debris in agricultural land after the Mount Pinatubo eruption. For instance, there has been greater preference for Ube over Binicol in some affected areas.

Patterns of Diversity: Maintenance, Dominant Cultivars, and In Situ Conservation

In all three case studies, one or two cultivars are preferred. They are planted by most farmers and over much larger areas than other cultivars. That reflects the fact that the dominant local concerns will be reflected in the one or two cultivars that best address those concerns. Even when dominant concerns are the same, such as cultivars for home consumption or for sale in the market, they can result in different dominant cultivars. That is because the agroecological conditions themselves vary and different cultivars adapt in different ways such as between provinces in Central Luzon or between Irian Jaya's hill-dwelling

and valley-bottom farmers. Similarly, in Mindanao comparative studies of neighboring communities revealed that different, but isomorphic, genotypes essentially fulfil the same function (Prain and Piniero, 1999). Given the variability of the environment that exists in the uplands, especially in the mountains, we can expect to find considerable genetic diversity, even when cultural preferences are similar.

When we observe cultivar maintenance along the dimensions of frequency of planting in different beds and the more common measure of plant density per bed, the regular and often substantial occurrence of other cultivars indicates other important societal concerns. In Maambong, in addition to the two dominant cultivars grown primarily for the fresh market, other cultivars are maintained for early maturity, vegetable use, pig feed, etc. In Wagawaga, while Helaleke asli and Musan are the main sources of food and feed, respectively, several cultivars are also maintained for infant food or for sale. The most striking example of what we can call *cultural saliency*, however, is the role of particular cultivars in rituals of first planting and consecration of land.

In both Wagawaga and Maambong, the dynamism of local maintenance appears to occur primarily among cultivars that are planted in a few beds with few plants per bed. Ritual cultivars also have few plants per bed, but the many women who plant them do not let them disappear. The old cultivars are planted first, not only to comply with custom but because they are said to need more fertilization than exotic cultivars. The extreme case is Inin, which is planted in a pile of ash from burnt branches of cleared garden to ensure production. This careful management contrasts with the treatment of cultivars in few beds and small areas. These residual or experimental cultivars, which might certainly include the products of fortuitous seed germination, usually enter and exit individual collections quite rapidly. Occasionally, a cultivar like Wotel or Tinta will be taken up by increasing numbers of farmers.

The Central Luzon case indicates that in the past diversity of use stimulated diversity of cultivar. More recently there has been a shift from spatial to temporal diversity, a process shared with other highly commercial areas (Prain and Fano, 1991). The one or two commercial cultivars covering a wide area are quite rapidly replaced as their productivity declines due to disease, they are outperformed by new cultivars, or market demand changes.

Conclusions

These findings have implications for in situ conservation strategies. A more comprehensive analysis of dominance suggests that evolution toward modern sweetpotato agriculture dominated by a single cultivar is not inevitable. Even if sweetpotato were to become a more commercial crop in Wagawaga, the maintenance practices are resilient enough to incorporate one or two commercially dominant cultivars without overall decline in variability. Maambong also gives reason for optimism. There the same kind of cultural salience characterizes several cultivars besides those dominant in plant density. Moreover, in the upland, particularly the hillside environments of these regions, there is isomorphic variability. That is, genetically diverse cultivars with similar cultural salience are found at different sites in a region. One could therefore envision a network approach to in situ conservation. Sets of culturally salient and genetically highly diverse cultivars could be maintained in selected sites within a region. The contribution of the national genetic resources conservation system toward this type of farmer-led conservation should focus on five things.

1. Public recognition of the value of local germplasm and local knowledge of it.
2. Public recognition of the participation of site representatives in a national conservation effort.

3. Simple reward system involving agricultural seeds and low-input technologies.
4. Facilitating access to exotic germplasm from other sites and from breeding programs.
5. Supporting continuing diversification of use and the cultural salience of different cultivars.

Although the kinds of lowlands represented by Central Luzon are unlikely to become repositories of genetic diversity, in situ conservation strategies at least should attempt to increase local diversity through diversifying uses (Amihan-Vega and Bacusmo, 1999). That could help to avoid the serious consequences that virus disease is now having on the mono-cultivar crop in Central Luzon.

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Sweetpotato for the New Millennium: Trends in Production and Utilization in Developing Countries

G.J. Scott and L. Maldonado[1]

Sweetpotato (*Ipomoea batatas L.* Lam.) is among the world's most important, versatile, and underexploited food crops. With more than 133 million tons (FAOSTAT, 1998) in annual production, sweetpotato currently ranks as the fifth most important food crop on a fresh-weight basis in developing countries after rice, wheat, maize, and cassava. Sweetpotato is cultivated in over 100 developing countries and ranks among the five most important food crops in more than half of them (FAOSTAT, June 1998). Only in the last decade has the crop been the focus of an intense, coordinated, global effort to realize its full potential as a source of food, feed, processed products, and income for millions of small farmers and low-income consumers in Africa, Asia, and Latin America.

Sweetpotato is also one of the most misunderstood of the major food crops. Not all sweetpotatoes are particularly sweet—many have a neutral to dry flavor. None are like potato, where the tubers are harvested. Instead sweetpotato roots are dug and eaten like carrots or cassava. Potato foliage is not used for human consumption. But sweetpotato leaves and tips are an important source of vitamin A in several developing countries in Asia and Africa. They are a trendy, luxury vegetable in Japan. Still, relatively few sweetpotatoes are produced and consumed in industrialized countries. Over 98% of global sweetpotato output is currently harvested and utilized in developing countries.

This paper analyzes recent trends in sweetpotato production and use from a global, regional, and sub-regional perspective. Developments in Asia, China in particular and Sub-Saharan Africa merit particular attention as upward trends in output are linked to the changing role of sweetpotato in local food systems. The results presented serve as the basis for recommendations for policymakers and research scientists and are aimed at building on the local momentum to fully exploit sweetpotato's untapped potential in the new millennium.

Materials and Methods

Analysis done for this paper relies heavily, although not exclusively, on FAO production and utilization data (FAOSTAT, June 1998). These statistics are supplemented with information from other sources including official publications of national governments, survey results, and related analyses found in scientific papers and the gray literature.

Estimated growth rates for production for particular time periods and descriptive statistics on utilization for selected years were calculated on an average annual basis. These figures are presented for different regions and countries to provide the matrix for comparative analysis.

Results and Discussion

Four facts have generated growing interest in trends in sweetpotato production and utilization. First, sweetpotato is typically a small-farmer crop and often grown on marginal soils with limited outputs. Furthermore, although the crop is widely cultivated in Asia (31 countries), Africa (39), and

1 CIP, Lima, Peru.

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Latin America (31), production tends to be concentrated in those countries with lower per capita incomes (Figure 1) and within those countries in regions such as Sichuan Province in China or western Kenya where income levels are relatively low. Hence, increasing sweetpotato production is often considered as a means to improve food security among the poorer segments of the rural and urban population. Similarly, expanding utilization through improvements in processing and feed use is seen as a way to raise incomes and thereby reduce poverty.

Second, average yields in several countries are well below the average of 15 t/ha for developing countries as a whole (Table 1). This average in turn is well below current average yields obtained in countries such as China. Potential yield increases based on experiment station trials are much higher still. Some recent developments—such as the tendency in some Asian countries to push the crop onto more marginal land—do raise additional challenges to develop and diffuse yield-increasing technologies for sweetpotato and help explain the prevailing yield gap. Nevertheless, rapid improvements in productivity are considered more readily feasible with relatively less investment in research and extension for sweetpotato than other crops, such as rice. This is because farmers' yields are far below what has been shown already to be technically feasible, and because by using standard scientific techniques can raise experimental yields even higher.

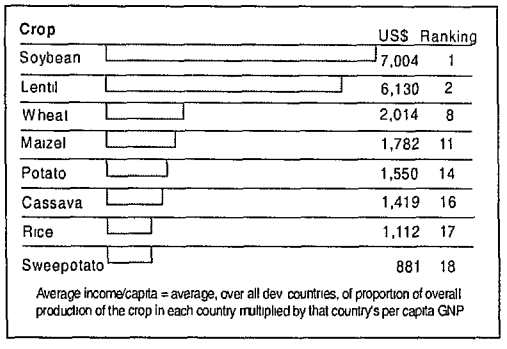

Figure 1. Average income per capita and commodity ranking of major food crop production in developing countries. (Source: Scott and Maldonado, 1999.)

Third, the last decade has witnessed a return to a positive growth rate for sweetpotato production in China—a remarkable reversal of previous trends in a country where some 85% of the world's output is harvested (Figure 2). Similar upward trends have emerged in a number of other developing countries. Some of these trends are evident from FAO statistics; others are not.

Fourth, several eastern and southern African countries have witnessed major increases in sweetpotato production in recent years. With this expansion in output have come shifts in both the orientation of production and the utilization of the harvested crop. Given the heightened concern about food security and poverty alleviation in many of these locations as well as for the region as a whole, these developments have raised the prospects for a more prominent and diversified role for sweetpotato in these countries in the decades ahead.

Sweetpotato Utilization: Food, Cash, Feed and Processed Products

Though commonly categorized as strictly a "subsistence," "food security" or "famine relief" crop, sweetpotato uses have diversified considerably in developing countries over the last four decades. Hence, while these longstanding uses are still important in some countries or some regions within these countries, other uses have clearly emerged, particularly in Asia (Table 2), where the share used as feed has increased from 14.5% in 1961–63 to 44.6% in 1993–95. Many of these changes are either not quantified or blurred in the published aggregate utilization figures. Among the most notable examples are (1) the use of vines in addition to roots for animal feed—this is simply not quantified into the estimates of feed use as these are typically based solely on estimated root production,

Table 1. Average sweetpotato production, yield, and area in developing countries.

Region/country	1995-97 Production (000 t)	1995-97 Area (000 ha)	1995-97 Yield (t/ha)	Average annual growth rate[a] Production (%) 1	Production (%) 2	Area (%) 1	Area (%) 2	Yield (%) 1	Yield (%) 2
Asia[b] (n=31)	125,058	7,178	17	1.1	0.8	1.4	-0.3	2.5	1.1
China	117,848	6,160	19	1.2	1.0	-1.5	-0.1	2.7	1.1
Indonesia	2,013	212	10	-1.2	-0.4	-2.3	-1.5	1.1	1.1
Vietnam	1,675	292	6	1.1	-1.7	0.6	-1.1	0.5	-0.5
Africa[c] (n= 39)	6,957[d]	1,519[d]	5[d]	2.1	1.5/2.7[e]	2.6	1.9/2.3[e]	-0.4	-0.4/0.3[e]
Uganda	1,888	513	4	3.7	0.9	3.5	2.8	0.1	-1.9
Rwanda	967	150	6	1.9	0.5	2.1	1.5	-0.2	-1.0
Malawi	962[f]	99[f]	10[f]	n.a.	25.3	n.a.	14.0	n.a.	9.7
Kenya	725	74	10	4.7	3.7	3.2	3.8	1.5	-0.1
Burundi	663	108	6	1.7	1.0	1.7	1.4	-0.1	-0.4
Latin America (n=31)	1,850	247	7	-1.2	-1.7	-1.0	-2.2	-0.2	0.5
Brazil	655	58	11	-2.3	-1.5	-2.7	-2.9	0.4	1.5
Argentina	339	20	17	-0.3	-1.1	-1.8	-3.9	1.5	2.9
Cuba	220	60	4	0.4	-2.6	0.9	0.2	-0.5	-2.8
Peru	191	11	18	0.7	3.6	-1.2	-0.7	1.9	4.3
Developing countries	133,865[d]	8,944[d]	15[d]	1.1	0.8[d]	-1.0	0.0[d]	2.1	0.8[d]

Source: Scott and Maldonado, (1999); (Source for Malawi data only, Ministry of Agriculture and Irrigation, Malawi).

[a] 1. 1961-63 to 1995-97, 2. 1985-87 to 1995-97.

[b] Asia (excluding Japan, Israel) + Oceania (excluding Australia, New Zealand).

[c] Excludes South Africa.

[d] Totals do not include data for Malawi.

[e] Includes data for Malawi.

[f] For 1995/96 to 1997/98.

and (2) the lack of division in the share of output devoted to food consumption between fresh roots and processed products, e.g., noodles made from starch. Consequently, any analysis of the trends in utilization for sweetpotato must be done with considerable caution.

Average annual per capita consumption of fresh roots for 1994-96 is estimated at: Africa, 9 kg; Asia, 18 kg; Oceania, 73 kg; Latin America, 2 kg; Japan, 9 kg; and USA, 2 kg (FAOSTAT, June1998). In contrast to potato, per capita sweetpotato consumption in Canada, Europe, and Australia is extremely limited and often confined to an immigrant population.

The quantities of sweetpotato consumed can vary tremendously within developing country regions. In Africa, for example, annual per capita sweetpotato consumption in Rwanda is estimated at 160 kg; Burundi, 102 kg; and Uganda 85 kg. Sweetpotato consumption also varies within countries by regions, by time of year, and by income group. In northeast Uganda, one of the poorest parts of that country, sweetpotato becomes a seasonal staple during the dry season when supplies of most other food

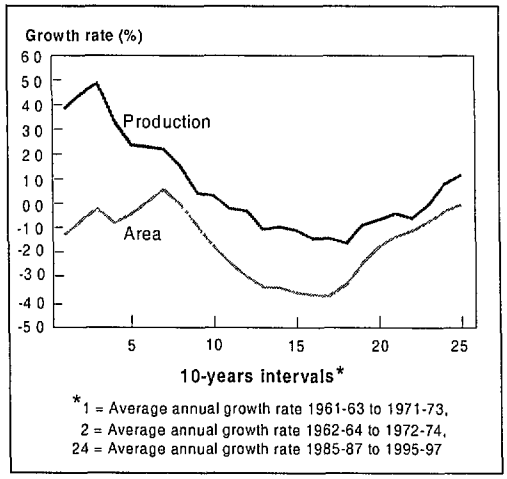

Figure 2. Average annual growth rates (%) for sweetpotato in China calculated in 10-year intervals from 1961-97. (Source: Scott et al., 1999.)

stuffs are exhausted (Hall et al., 1998). Even under such circumstances the importance of the crop may be underestimated given the increasingly apparent flaws in the calculation of such estimates.

For developing countries as a whole, per capita consumption of sweetpotato, particularly in fresh form, has declined over time. According to available statistics, average per capita consumption fell from 37.5 kg/yr in 1961-63 to 18.8 kg/yr in 1994-96 (FAOSTAT, June 1998). As incomes increased, urbanization accelerated, and the availability of cheaper, more preferred substitutes (meat, wheat breads, etc.) became more abundant in many parts of Latin America and Asia, in particular, consumers on and off the farm reduced their intake of fresh sweetpotato. However, the trend has been more volatile in Sub-Saharan Africa with consumption rising and falling and then rising again. In some countries of the region, e.g., Malawi, the trend has been a rapid rise in consumption. For the mostly poor consumers in eastern and southern Africa, per capita sweetpotato consumption has either stayed roughly constant or risen as real incomes have deteriorated, imports of traditional substitutes have been cut back, and production of (other) local staples stagnated or shrank as a consequence of weaknesses in the overall economy and continued strong population growth. In some cases this was exacerbated by problems in specific commodity subsectors, e.g., maize in Malawi, cassava in Uganda. In Asia, rapid expansion of consumption of processed sweetpotato in the form of such products as noodles has helped offset the decline in fresh consumption.

Table 2. Distribution of the uses of sweetpotato in Africa, Asia, Latin America, and the industrialized countries, 1961-63 and 1993-95.

	1961-63 (%)				1993-95 (%)			
	AF	AS	LA	IC	AF	AS	LA	IC
Total (000 t)	2,755	87,143	2,578	7,483	5,748	120,771	1,628	2,284
Food	84.8	79.7	65.8	60.1	85.3	49.9	71.1	65.5
Feed	3.7	14.5	24.5	23.6	2.9	44.6	18.5	19.3
Processing	0.0	0.0	0.0	10.7	0.0	0.2	0.0	9.1
Seed	1.1	0.2	0.2	3.8	0.7	0.0	0.3	3.5
Waste	10.4	5.5	9.5	1.8	11.0	5.2	9.6	2.6
Net export[a]	0.0	-	0.0	-	0.1	0.1	0.6	-

Source: FAOSTAT (June 1997, accessed July 1997).
Note: AF = Africa; AS = Asia; LA = Latin America; IC = Industrialized countries. Regions as defined by FAOSTAT.
[a] - = None recorded.

Tastes and preferences for fresh sweetpotato are also highly variable and show some signs of evolving as well. Some consumers prefer sweet varieties with a floury taste; others prefer bland roots. Yellow-to-orange fleshed cultivars with high ß-carotene content have been introduced and diffused recently in East Africa as part of an integrated effort to reduce vitamin A deficiency (Low et al., 1997). Wide genetic variability found in sweetpotato means that these and a number of other desirable traits can be found in existing germplasm.

Recent research has documented the widespread use of sweetpotato by small farmers in their efforts to sustain local livestock production systems (Scott, 1992; Woolfe, 1992). In fact, virtually wherever sweetpotato is cultivated, from Brazil to Madagascar to China, some part of the plant in some form is used in some type of animal production. The steady increase in the use of sweetpotato roots and vines in pig and other livestock systems in China over the last 30 years now means that from 30 to 50 million tons or more are used annually as feed. Vines also play an underexploited, but important role in animal production in other Asian countries such as Indonesia, the Philippines, and Vietnam.

Processed products made from sweetpotato including starch, noodles, candy, desserts, and flour have long been made by farm households to extend the availability, diversify the use, and increase the value-added for the crop. In China, in particular, production of sweetpotato starch in recent years has evolved into a cottage industry that utilizes millions of tons of roots per year as raw material inputs. The magnitude of these new uses is not easy to quantify in a systematic way; partly for that reason, available statistics on processing do not always reflect their true level of importance. Recent estimates from China suggest that 3 to 5 million tons of sweetpotatoes are transformed into starch to make noodles for both the domestic and export market (see Fuglie et al., 1999).

Sweetpotato Production

Driven by strong demand for feed and starch, growth rates for sweetpotato output and area planted have turned upward in China after years of decline (Figure 2). Trends for other countries and regions have been mixed (Table 1). Given weaknesses in the data, these figures should be interpreted with caution.

Asia. Sweetpotato production in Asia has been characterized by four trends. (1) The continued overwhelming dominance of China with recent positive growth rates reversing an earlier decline. (2) Shrinking area planted in sweetpotatoes—a trend that accelerated in much of the region during the last ten years. (3) Leveling off of yields as the rate of growth has slowed in many countries, including China. As sweetpotato cultivation has been pushed onto more marginal land and average yields have improved to 17 t/ha, it has become more difficult to maintain the rate of growth of improvement in yields. (4) The possible shift in the future prospects for regional sweetpotato production due to recent changes in relative prices for sweetpotato versus traditional substitutes such as imported wheat flour, as a consequence of the economic crises in Southeast Asia.

Latin America and the Caribbean. For much of this region, production and area planted to sweetpotato is most important in smaller, poorer countries such as Cuba, Haiti, and Paraguay. In Cuba, a recent sharp decline reflects the pressure on sweetpotato yields resulting from a shortage of chemical pesticides in the current transition to biological control of important pests. In bigger and/or wealthier countries, the decline during the last decade represents more of a long-term trend toward higher-value crops, the use of farmland for alternative purposes, or the migration of small farmers to other occupations outside agriculture. In Peru, production and yields rose spectacularly over the last decade as agro-climatic conditions improved, the general economy went through structural adjustment, and many small growers turned

to sweetpotato because of the shortage of farm credit and the low costs of production per hectare.

Africa. The continent produces nearly 7 million tons of sweetpotato yearly and nearly all of it south of the Sahara; Egypt in North Africa is the prominent exception. Growth rates in sweetpotato production and, in particular, area planted are the highest of any region though most of the major producers saw growth rates decline over the last decade. As area planted continued to expand, the annual average rate of improvement in yields turned negative in some cases (e.g., Uganda: –1.9%), and offset what would have otherwise been faster rates of growth in production. In other words, as planting took place under more marginal conditions, and perhaps by farmers less acquainted with the most appropriate cultural practices, yields suffered in the process.

An average yield of 5 t/ha for sweetpotato in Africa (Table 1) is the lowest of any developing region, and less than a third of the average yield in Asia. This suggests ample room for improvement in productivity in the years ahead even taking into consideration the common criticism that FAO data underestimate average yields for sweetpotato in this region. Prospects are brightest for the adoption of yield-increasing production technology for sweetpotato in Eastern and Southern Africa where cash sales of fresh roots have risen in importance in a number of countries. Although only a minor share of current consumption, the emerging demand for processed products made from sweetpotato shows signs of increasing. This should further bolster prospects for additional production. African farmers will continue to increase their production of sweetpotato for food security and income generation in response to continued high population growth and the economic hardships associated with political instability, natural disasters and limited production infrastructure.

A Word of Caution

Any review of the recent trends in sweetpotato production, consumption, and use in developing countries would be incomplete were it not to draw attention to discrepancies in data for this commodity. It is difficult to estimate production for a crop produced by small farmers on non-contiguous plots, harvested several times a year, and not sold through regulated domestic marketing channels or traded abroad in appreciable quantities. Therefore, FAO statisticians frequently resort to using the available national statistics to estimate production, area, and yield. Unfortunately, there are often discrepancies between FAO figures and national data. For example, FAO reports Malawi produces no sweetpotato, while Ministry of Agriculture figures show the country harvested over 800,000 t during 1995-97 (Phiri, 1998). This is not an isolated case, especially when one goes beyond the national statistics and compares those figures with data gathered in farm surveys as reported in the gray literature or consults with commodity specialists based in the countries themselves. Similar problems apply in the case of the figures for utilization. In conclusion, readers are advised to use these "trends" with caution.

Conclusions

Sweetpotato is an important source of food, cash, feed, and raw material for processing in developing countries. Although production is highly concentrated in China, recent years have witnessed a surge in sweetpotato output in a number of Sub-Saharan African countries. With the germplasm for sweetpotato largely underexploited, ample prospects exist to develop varieties with particular traits in addition to yield to satisfy the emerging demand for diversified end uses. Development of the crop's full potential in the new millennium will require a fully integrated approach in which efforts aimed at germplasm improvement are closely tied to the following.

- Identification of market segments for which there is the greatest demand—currently this involves feed and starch in East Asia, and flour and fresh uses in Latin America and Africa.
- Improvements in the technical efficiency of processing (e.g., via new or improved small equipment) as well as feed use and preparation (e.g., vine fermentation).
- Reductions in per unit production and marketing costs through better cultural practices and trading procedures.
- Strengthening linkages of producers as sources of raw material to processors, managerial improvements in sweetpotato processing at the enterprise level as well as more informed utilization of fresh and processed sweetpotato by final consumers.

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Sweetpotato in Ugandan Food Systems: Enhancing Food Security and Alleviating Poverty

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Uganda is one of the world's poorest and least developed countries with a GNP per capita of US$320 (World Bank, 1998/99). Uganda's economy and 90% of its population depend on agriculture for food, employment, and income (UNDP, 1999). Current population stands at slightly over 20 million and is growing at over 2.8%/yr. (UNDP, 1999). Some 85% of the people reside in rural areas.

Given the fragile balance between population, food production, and economic growth, government policy seeks to ensure the country's continued ability to sustain food self-sufficiency. Increases in agricultural productivity and agroenterprise development are key elements in the government's strategy to increase the incomes of rural households and to facilitate further expansion of the overall economy. These concerns are particularly acute in the Eastern Region in Soroti and Kumi districts, and in the Northern Region in Lira and Apac districts. These districts are among the poorest in the country (UNDP, 1999).

Uganda is the biggest sweetpotato (*Ipomoea batatas*) producer in Africa with an annual average output of nearly 2 million t (Scott and Maldonado, 1999). Output has steadily expanded in recent years. Consequently researchers, development project personnel, and Ministry of Agriculture officials have become increasingly interested in the role of sweetpotato in Ugandan food systems and its potential to enhance food security and increase rural incomes (Bashaasha et al., 1995; Fowler and Stabrawa, 1992; Hall et al., 1998). The attention to sweetpotato also reflects a more general interest in roots and tubers, and matooke (cooking banana) over the last decade (Bashaasha and Mwanga, 1992; Otim-Nape and Opio-Odongo, 1992). These crops account for a major share of annual food production and consumption. The focus on sweetpotato in Uganda has also intensified since 1990 with the spread of the more virulent Ugandan form of the cassava mosaic virus disease (CMD).

This paper analyzes trends in sweetpotato production, area planted, prices, consumption, and use in Uganda over the last 10-15 yr. After a brief review of food production and use nationwide, the analysis turns to particular regions and districts. The analysis addresses the following key questions regarding the evolving role of sweetpotato in Ugandan food systems:

- What has been the evolution of production and area planted nationally by region and by district?
- Has this evolution shifted the distribution of sweetpotato production across the country and its relative importance in local food systems, especially in areas where it substitutes for or complements cassava?
- What has been the effect of increased production on prices, relative prices, consumption, and use?
- How have these trends affected the role of sweetpotato in Ugandan food systems, particularly in the poorer regions and districts of the country?

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Material and Methods

Information resources

This paper draws upon a range of primary and secondary sources. Secondary information includes (1) official Ugandan statistics on production, prices, and consumption, (2) FAO estimates of the calories and protein provided by these commodities in relation to other major foods, and (3) a selective review of the recent literature on sweetpotato and other root and tuber crops in Uganda. Primary sources include information gathered in informal interviews with key informants in 1994, 1996, and 1998, as well as with knowledgeable specialists in organizations elsewhere, e.g., Natural Resources Institute, UK, and FAO-Rome, and participant observation of rural and urban root crop processing and marketing.

Conceptual framework

This study uses a food systems conceptual framework consisting of four central traits. One is the focus on the interrelation and interaction between different subsystems, e.g., farming (production), marketing (exchange), and use (consumption) systems.

A second feature is that each subsystem is considered as a horizontal concept. In this framework, farming systems as a concept encompasses all aspects of rural activity (cropping, livestock, and forestry systems) associated with agricultural production. In contrast, the food system is essentially a vertical concept. The focus of analysis then is not the interrelation of activities at a particular horizontal level but rather the interrelation between subsystems of the food system — from production through the marketing chain to the consumer (both rural and urban), including any processing and value-added activities (Hall et al., 1998).

A third key feature is that of a historical perspective. Instead of analyzing in detail interactions at a given point in time, the food systems approach focuses more on medium- to long-term trends in key variables. In this way we capture the evolving nature of the interrelation between subsystems.

Finally, within a country, the food systems approach frequently examines national and interregional developments as opposed to more location-specific trends. This aspect of the food systems approach is intended as a macrocomplement to analysis of particular agricultural activities at the microlevel (Morris, 1995).

Results and Discussion

Role of sweetpotato in Ugandan food systems

The average Ugandan diet contains staples such as matooke, cassava, sweetpotato or cereals such as maize. The typical meal consists of one or more of these commodities accompanied by a sauce made of beans, vegetables, fish, or meat (Bashaasha et al., 1995). Hall et al. (1998) identified at least five distinct roles for sweetpotato in Ugandan food systems, four of them peculiar to rural areas and one associated primarily with urban areas. They are:

1. A predominant staple providing the majority of calories for most of the year (sweetpotato production is seasonal and processed roots rarely last 4 mo). Examples are found in Soroti, Kumi, and parts of northern districts (Figure 1).
2. One of a number of major complementary staples consumed throughout the year but with seasonal peaks, for example, in Kabarole, Masindi, Kabale, and Iganga districts.
3. A famine reserve staple typically consumed only in significant quantities during shortages of the dominant staple.
4. A source of cash income either produced strictly for sale as in Mpigi District near Kampala (Bashaasha et al., 1995), or more commonly as a source of revenue from petty trading. That is especially true in the Northern and Eastern regions

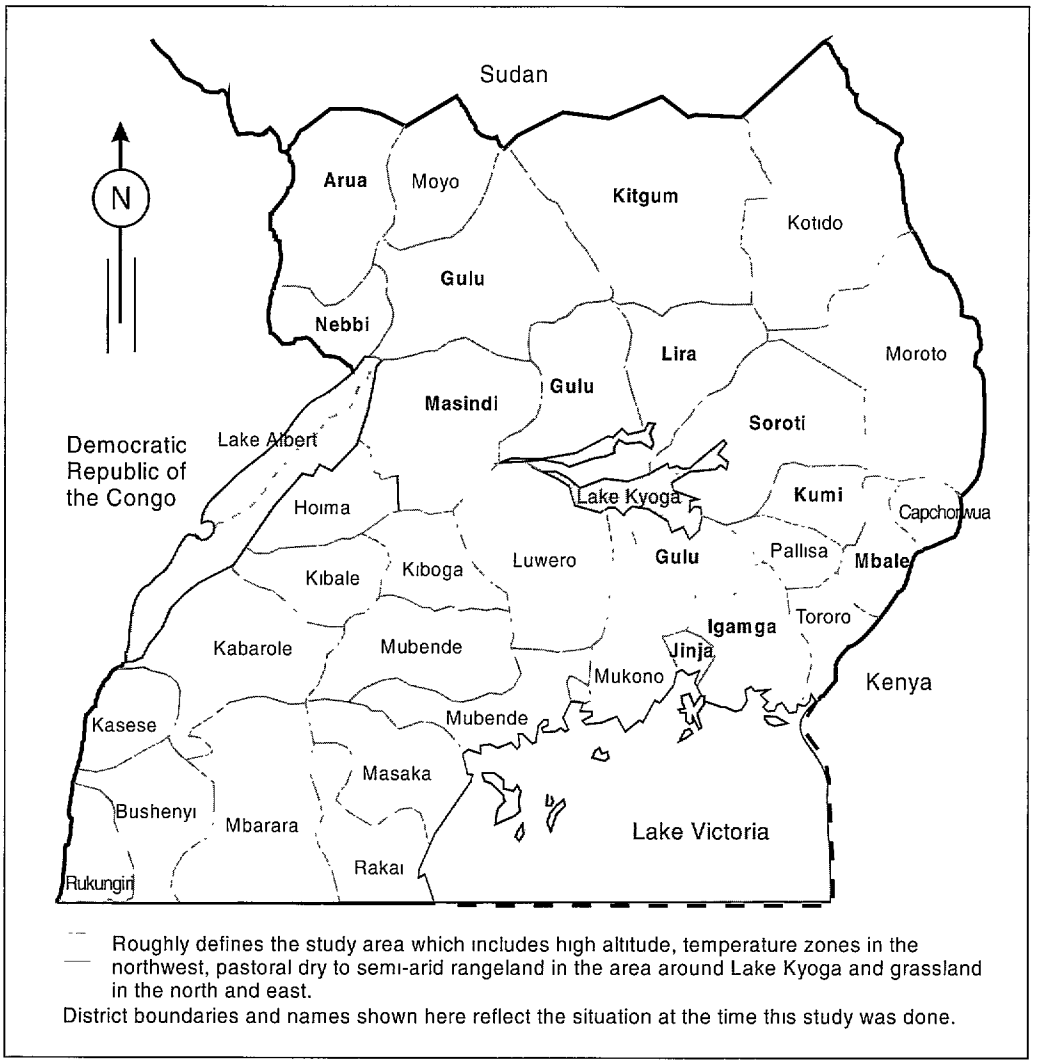

Figure 1. Ugandan administrative districts and agroecological zones.

where small farmers have relatively few opportunities to earn cash.

5. A low-priced, complementary staple for the poor and lower-income urban groups (Mwesigwa, 1995).

Production trends

Sweetpotato production in Uganda rose from 1.7 to 1.9 million t, or slightly over 12%, between 1987-89 and 1995-97. During the same period, maize output jumped 70% and matooke production increased by an estimated 1.9 million t. In contrast, cassava production fell from 3.3 to 2.2 million t, or roughly 32% (Table 1). Hence, sweetpotato assumed slightly greater importance in domestic food supplies. The increase in sweetpotato production, however, was less noteworthy than the sharp decline in cassava output or the production increases for maize and matooke.

Five of the top 10 cassava-producing districts in 1987-89 were among the top 10 sweetpotato-producing districts as well. By 1995-97, the number had risen to 7 of 10. Cassava production declined in 9 of the top

Table 1. Uganda food crop production, 1987-89 vs. 1995-97.[a]

Crop	1987-89 Production (000 t)	1987-89 %	1995-97 Production (000 t)	1995-97 %
Matooke (cooking banana)	7,267	50.3	9,153	57.0
Cassava	3,313	22.9	2,253	14.0
Sweetpotato	1,683	11.6	1,888	11.8
Maize	474	3.3	804	5.0
Millet	569	3.9	525	3.3
Sorghum	335	2.3	330	2.1
Beans	341	2.4	282	1.8
Potato	207	1.4	360	2.2
Groundnuts	134	0.9	120	0.7
Rice		0.0	80	0.5
Soybean	13	0.1	83	0.5
Sesame	35	0.2	72	0.5
Pigeonpeas	38	0.3	58	0.4
Cowpeas	38	0.3	46	0.3
	14,446		16,055	

Source: Ministry of Agriculture.

[a] Estimates are of economic production (after making allowance for postharvest losses) not of harvested product

10 districts between 1987-89 and 1995-97. Furthermore, the top 10 producing districts in 1995-97 accounted for nearly 50% of the 1.1 million t decline in national production since 1987-89.

The opposite occurred in the top 10 sweetpotato districts (Table 2). The average increase in sweetpotato production for these districts for the period was just 9,155 t. In addition to the advance of CMD, the period 1987-1990 was marked by civil unrest in certain eastern districts that temporarily reduced production of all food crops. Between 1987-89 and 1995-97, only Kitgum showed a sharp increase in sweetpotato output (26,567 t) in relation to the decline in cassava production (-17,536 t). In Gulu, cassava output increased over the period by 5,176 t, but sweetpotato production jumped by 48%, or 29,681 t. For the other top 10 districts, the increase in sweetpotato output per se was modest and also in relation to the much larger decline in cassava. Only three of the cassava-producing districts recorded a combination of a sharp decline in cassava output and a jump in sweetpotato production. In some districts production of both crops declined, although typically the drop was much greater for cassava than for sweetpotato.

Following a policy of decentralization, Uganda has created a number of new districts by subdividing some larger districts, e.g., Katakwi out of Soroti. The change in the number of districts and their respective size may affect our analysis of district production figures for 1987-89 and 1995-97. The accuracy of district-level data on acreage and yields may also suffer. However, there is little reason to believe that the data for sweetpotato are more accurate or less accurate than those for other root crops. The relation between major production increases in sweetpotato

Table 2. Uganda sweetpotato and cassava production, variation (%) and ranking, 1987-89 versus 1995-97.[a]

	Sweetpotato				Cassava		
District	Production 1995-97 (000 t)	Change (%) vs 1987-89	Ranking 1987-89	District	Production 1995-97 (000 t)	Change (%) vs 1987-89	Ranking 1987-89
Mbale	127	5.6	1	Mbale	169	-37.4	1
Iganga	105	2.8	2	Iganga	169	-12.8	5
Hoima	98	1.1	3	Apac	141	-27.4	4
Apac	98	7.9	7	Arua	139	-41.7	2
Kitgum	94	39.5	11	Kitgum	125	-12.3	11
Masindi	93	22.2	9	Gulu	119	4.6	16
Kumi	92	-2.8	5	Lira	118	-33.8	7
Gulu	91	48.3	13	Kumi	117	-38.7	6
Kamuli	80	1.2	8	Kamuli	107	-39.1	8
Soroti	72	3.4	10	Nebbi	100	-26.2	13
Total	**1,888**	**12.2**		**Total**	**2,253**	**-32.0**	

Source: Ministry of Agriculture.

[a]These district-level data are for the top ten sweetpotato- and cassava-producing districts in 1995-97 only. The totals are for all districts.

and declines in cassava at the district level has been limited to a small number of districts.

Sweetpotato rose in importance in both the Eastern and Northern regions (Table 3). Matooke accounted for the largest absolute increase in food production in the Eastern Region followed by maize and sweetpotato (Table 3). These three crops then substituted for the decline in cassava output. In contrast, cassava fell sharply in absolute output and in relation to the other principal food crops. In the Eastern Region farmers increasingly see sweetpotato as a source of cash income, particularly in the absence of cassava. That is consistent with Uganda's objective of raising rural incomes in the region given the greater incidence of poverty and lower levels of human development (Table 4).

In the Northern Region, the increase in sweetpotato production (151,000 t) was higher than any other crop in absolute tonnage (Table 3). Maize production rose by 142,000 t. The increase in matooke output has also been noteworthy (84,000 t). But not on the scale of growth in the Eastern Region where growing conditions for matooke are more favorable. These production changes are particularly important because the Northern Region and its districts are the poorest in all the country (Table 4).

Statistics for cassava and sweetpotato production in the Eastern and Northern regions in 1997 indicate that the slight upturn in cassava output has been accompanied by a similar rebound for sweetpotato (Figure 2). That suggests farmers are producing more of **both** crops rather than opting for one over the other.

Price trends

Fresh cassava and sweetpotato, along with matooke, serve as substitutes in

Table 3. Food crop production in the Eastern and Northern regions of Uganda, 1987-89 vs. 1994-96.[1]

Crop	1987-89				1994-96			
	Production (000 t)		%		Production (000 t)		%	
	East	North	East	North	East	North	East	North
Matooke (cooking banana)	1,024	138	28.7	7.3	1,401	222	36.1	9.9
Sweetpotato	631	349	17.7	18.5	794	500	20.5	22.4
Cassava	1,198	854	33.6	45.5	782	656	20.1	29.4
Maize	186	105	5.2	5.6	345	247	8.9	11.1
Millet	259	167	7.3	8.9	261	212	6.7	9.5
Potato	9	2	0.2	0.1	84	17	2.2	0.7
Beans	122	77	3.4	4.1	84	107	2.2	4.8
Sorghum	85	142	2.4	7.6	8	211	2.2	9.5
Groundnuts	49	46	1.4	2.4	46	59	1.2	2.6
Total	**3,563**	**1,880**			**3,882**	**2,230**		

Source: Ministry of Agriculture.

[1]Eastern Region includes the districts of Kapchorwa, Mbale, Katakwi, Kumi, Pallisa, Tororo, Busia, Bugiri, Soroti, Kamuli, Iganga, and Jinja; Northern Region includes the districts of Arua, Moyo, Adjumani, Kitgum, Kotido, Nebbi, Gulu, Apac, Lira, and Moroto.

Ugandan diets (Bashaasha et al., 1995). Prices for these two crops have tended to move together in recent years (Figure 2). With changes in production, however, relative prices for sweetpotato vs cassava have shifted. In a number of urban markets, sweetpotato has become cheaper than cassava, reflecting the drop in cassava production and the increase in sweetpotato output (Figure 2). That suggests urban consumers may be inclined to eat more sweetpotato, particularly those with limited food budgets.

Consumption

Roots and tubers, including matooke, account for some 44% of the average daily caloric intake of 2194 kcal in Uganda (FAO STAT, 1998). The decline in cassava production and the concomitant rise in matooke and sweetpotato output have shifted the percentage that each commodity contributes to the diet. Sweetpotato's share declined from 12% in 1984-86 to 10% in 1994-96. Cassava's share shrank from 19% to 10%.

Diets in Uganda differ by region and by time of year. Matooke, for example, is much more important in the area around Kampala for agronomic and cultural reasons (Mwesigwa, 1995). Sweetpotato assumes greater relative importance in parts of the Eastern and Northern regions and generally in July, August, and September, during and immediately after peak harvest, and during seasonal shortages of other crops (Bashaasha et al., 1995; Smit, 1997). Recent shifts in production certainly suggest sweetpotato's increasing importance in regional diets, particularly in the Northern Region.

The last decade has witnessed the emergence of sharp differences between rural and urban food expenditures (Table 5). Rural food expenditures were two-thirds of urban expenditures in 1989/90. They had dropped to nearly half of urban expenditures by 1993/94. Inasmuch as 85% of the population resides in the countryside, the national average nevertheless remained closely tied to expenditure levels in rural areas.

Table 4. Regional and selected district human development and poverty indices, 1996.

Region	Human development index[a]	Human poverty index[b]
Central	**0.4970**	**31.2**
Eastern	**0.3620**	**40.0**
Kamuli	0.3353	52.9
Soroti	0.3230	52.0
Kumi	0.2985	51.0
Iganga	0.3661	48.4
Northern	**0.3170**	**45.7**
Kitgum	0.2644	59.5
Gulu	0.3179	53.2
Lira	0.3496	51.5
Apac	0.3670	46.9
Western	**0.3730**	**39.3**
Uganda	**0.4046**	**39.3**

Source: UNDP, 1999.

[a] The human development index (HDI) measures human progress on the basis of achievement in three broad indicators: longevity, educational attainment, and standard of living. Longevity is measured by life expectancy at birth, educational attainment by a combination of adult literacy and school enrolment ratio, and standard of living by real GDP per capita (PPP$). The HDI is an aggregation of these key indicators. The index ranges from 0 to 1 where 0 indicates total absence of development and 1 indicates the highest level of development.

[b] Poverty is interpreted to mean total deprivation in a range of human capabilities. The three types of deprivation used in computing the human poverty index are only representative, but they capture a wide range of dimensions of life that matter most. The first aspect of deprivation relates to survival — the vulnerability to death at a relatively early age. The second relates to knowledge — being excluded from the world of reading and communication. The third relates to a decent standard of living.

Recent household expenditure surveys also provide information on the size and evolution of monetary outlays for sweetpotato and cassava (Table 5). They recorded not only cash purchases for food but imputed expenditure equivalents for own-produced food, especially in rural areas. Moreover, all figures are in nominal US dollars, i.e., with no adjustment for inflation. For sweetpotato, rural outlays increased both percentage-wise and nominally. Urban expenditures declined percentage-wise but rose slightly nominally. Total expenditures on food rose much more rapidly in the cities than in the countryside between 1989/90 and 1993/94. Cassava expenditures followed a similar pattern, but the nominal increases in rural areas were more modest. Consequently, expenditures on sweetpotato in rural areas both percentage-wise and nominally were higher than for cassava in 1993/94, thereby effectively reversing the situation that existed in 1989/90. For cassava, the percentage decline in expenditures in urban areas was less pronounced than for sweetpotato, but not enough to compensate for the more modest rise in rural areas. As a result, the average percentage of total food expenditures devoted to cassava nationwide declined, whereas that for sweetpotato remained constant.

Conclusions and Recommendations

Sweetpotato production has steadily increased in Uganda over the last 10-15 yr. The increase in sweetpotato output,

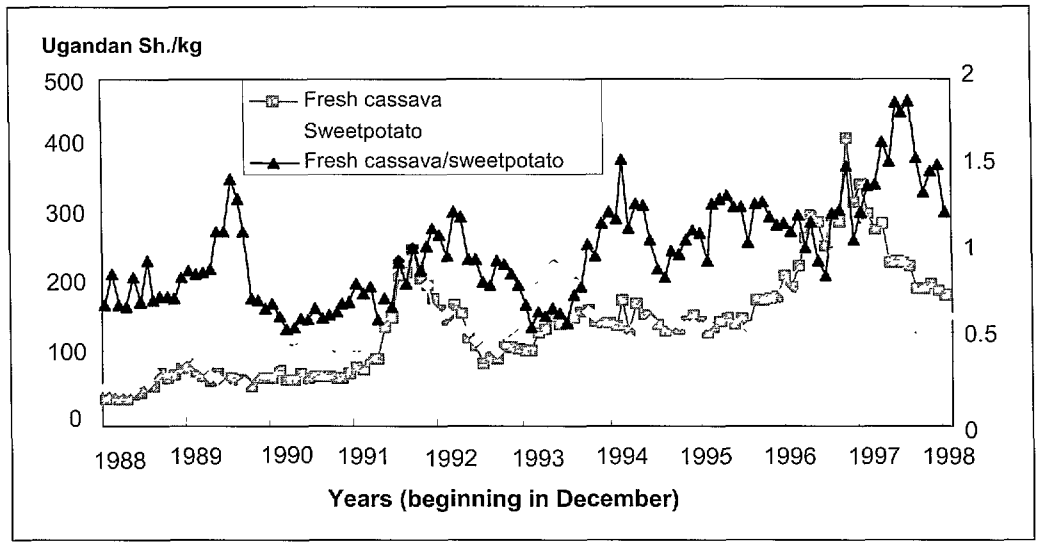

Figure 2. Trend of nominal and relative monthly prices for fresh cassava and sweetpotato prices in Kampala, Uganda, December 1988 to December 1998. Source: Statistics Department, Ministry of Finance, Planning and Economic Development, as presented in Ferris et al., 1999.

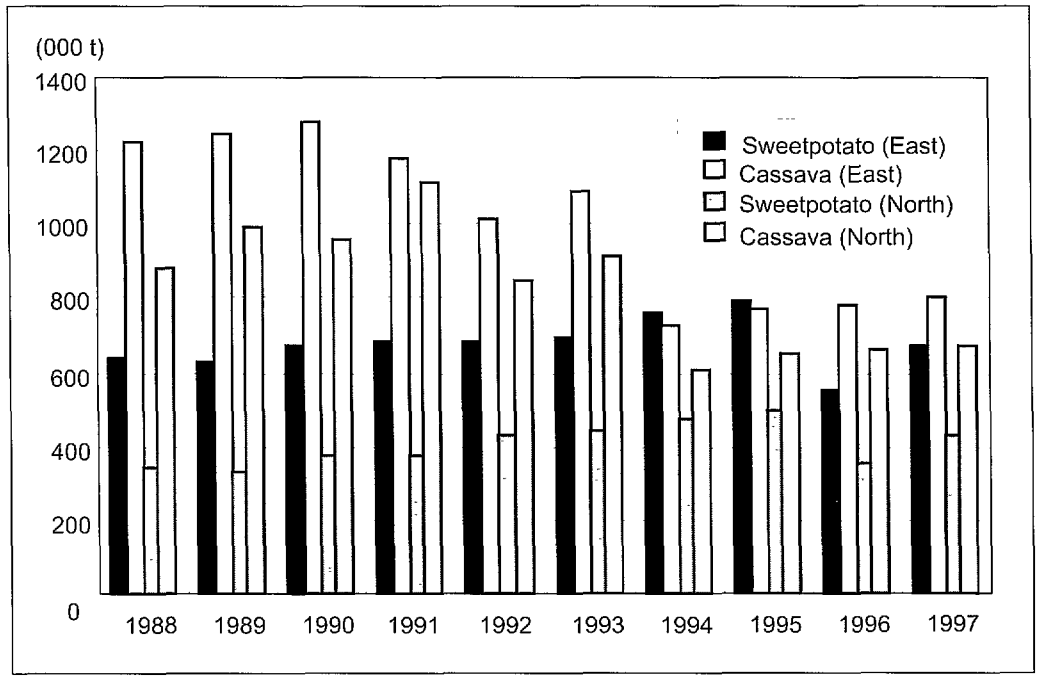

Figure 3. Cassava and sweetpotato production in Eastern and Northern Regions of Uganda, 1988-97. Source: Ministry of Agriculture.

Table 5. Expenditures on roots and tubers as a percentage of total food expenditures, Uganda.[a]

	1989/90			1993/94		
	Urban	Rural	National	Urban	Rural	National
Food expenditure						
(000 Uganda Sh.)	31.57	22.23	23.45	75.66	33.26	39.59
Total roots and tubers	8.0	14.4	13.3	10.9	24.1	19.7
Potatoes	0.8	0.9	0.9	0.8	0.7	0.7
Sweetpotato	3.7	6.4	5.9	2.1	7.7	5.9
Cassava	3.4	6.9	6.3	1.9	7.3	5.5
Yams	0.1	0.3	0.3			
Yams/other tubers				0.0	0.0	0.0
Matooke (cooking banana)			6.0	8.4	7.6	

Source: ROU, 1994; 1997.

[a] All monetary figures are in nominal Uganda Sh.; includes cash and imputed expenditures on own-produced food. (1993/94 US$1 = Uganda Sh. 1,100)

however, represents only a minor percentage of the total decline in cassava production. The data further show that the precipitous drop in cassava output in certain districts was only weakly related to changes in sweetpotato production. But at the regional level, particularly the poorer Northern Region, the shift to sweetpotato in response to the decline in cassava output was more pronounced. The recent rebound in cassava production has been accompanied by increases in sweetpotato output. Average monthly retail prices over the last 10 yr for Kampala, the capital, and four regional urban markets indicate that sweetpotato and cassava prices tend to move together. More important, sweetpotato is now less expensive than cassava. Food expenditures for sweetpotato in rural areas have also increased.

The impacts of the various trends in the role of sweetpotato in Ugandan food systems then are as follow:

- Sweetpotato has achieved a higher relative and absolute importance in cropping systems, given the simultaneous sharp decline in cassava production.
- Sweetpotato has increased in importance as a source of cash income, with lower relative prices currently making sweetpotato more competitive with cassava.
- The decline in cassava production has seen sweetpotato play a greater role in ensuring food security in the country, especially in those areas where the crop is a staple.

The bulk of the increase in sweetpotato output has been achieved as a result of increases in area planted (FAOSTAT, April 1999). Hence, the introduction and diffusion of improved germplasm has the potential to increase sweetpotato output and yields, lower costs per kilo harvested, and help to make sweetpotato even more competitive in the years to come. Increased availability and lower relative prices for sweetpotato enhance the prospects for economically viable processing activities.

Further work on product development offers the prospect of providing growers/processors with alternative markets and therefore an added incentive to adopt yield-increasing technology. Production and sale of processed sweetpotato products can

contribute even more than in the recent past to generating value-added income for retention in rural areas. That is especially true for the Eastern and Northern regions where farm households have few alternative sources of income and the incidence of rural poverty is most acute.

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In Vitro Conservation of Potato and Sweetpotato Germplasm

A. Golmirzaie and J. Toledo[1]

In vitro conservation of genetic resources has advanced considerably during this decade. Since 1975, CIP has contributed to developing tissue culture techniques for conserving germplasm of potato (*Solanum tuberosum*) (Roca, 1975), sweetpotato (*Ipomoea batatas*) (Sigueñas, 1987), and Andean root and tuber crops (Toledo et al., 1994). In vitro conservation is the most useful and efficient way to distribute clonal materials. It facilitates the availability of planting materials at any time, avoids the transfer of major pests and pathogens, and makes possible virus eradication through meristem culture (Roca et al., 1979; George, 1993). In addition, in vitro conservation is less expensive than cryopreservation of field-grown clonal materials (Florkowski and Jarret, 1990).

Short- and Medium-Term Conservation

In vitro plantlets grow in a Murashige-Skoog (MS) culture medium containing minerals, a carbon (C) source, vitamins, and a low concentration of growth regulators (Table 1). Plants exhaust the nutrients in this medium in 2-3 mo; therefore, in vitro plants have to be transferred frequently to fresh medium. The culture rooms generally have a temperature range similar to those needed to grow a given crop in the field. That is called short-term conservation. The interval between subcultures, however, can be extended through growth rate reduction by modifications to the environment or changes in some media components.

The addition of osmoticums or growth retardants to the medium has proved efficient for reducing growth rates of different plant species. Osmoticums such as mannitol or sorbitol reduce mineral uptake by cells through differences in osmotic pressures thereby retarding plant growth (Dodds and Roberts, 1985; Thompson et al., 1986). Growth retardants can produce some physiological changes or generate mutations, which can threaten the genetic stability of the materials conserved in vitro (Hughes, 1981; Lizarraga et al., 1989; Wescott, 1981). Reducing growth temperature close to 0°C for temperate plant species or several degrees below normal for tropical crops can also minimize the growth rate in many crops (Dodds and Roberts, 1985; George and Sherrington, 1984). In vitro plants growing in closed culture vessels have low concentrations of CO_2; C absorption is maintained by supplementing the medium with sugar. Reducing light intensity also affects growth rate by reducing photosynthetic requirements and therefore metabolism (Hughes, 1981).

A combination of osmoticums, low temperature, and low light intensity has been the most effective in lengthening periods between subcultures. At CIP, these procedures are applied to potato and sweetpotato with good results.

In vitro potato conservation

There are well-established protocols for micropropagation of potato (Espinoza et al., 1992), meristem culture (Lizarraga et al., 1991), in vitro tuber induction (Estrada et al., 1986), medium-term storage (Golmirzaie and Toledo, 1998), and cryopreservation (Golmirzaie and Panta, 1997).

1 CIP, Lima, Peru.

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Table 1. Components of culture media of potato and sweetpotato.

Ingredients	Potato culture media			Sweetpotato culture media[a]		
	Propagation	Conservation	Tuber induction	Propagation I	Propagation II	Conservation
MS[b] (l L)	1	1	1	1	1	1
Stock solution	Stock 1	Stock 1		Stock 2	Stock 2	Stock 1
Sucrose (g/L)	25	25	80	30	30	30
Gibberelic acid (mg/L)	0.1			1		
Espermidine (mg/L)	-	-	-	-	-	20
Naphthalene acetic acid (mg/L)	-	-		-	0.5	-
Sorbitol g/L	-	40		-	-	20
Benzylaminopurine (mg/L)	-	-	5	-	-	-
Chlorocholine chloride (g/L)	-	-	0.5	-	-	-
Phytagel (g/L)	3.5	3.5		3.5	3.5	3.5
pH	5.6	5.6	5.6	5.8	5.8	5.8
Temperature range °C	18 – 20	6 - 8	18 - 20	23 - 25	23 - 25	18 - 21

a. Liquid media is also used in sweetpotato culture.
b. Murashige-Skoog salts.
Stock solution 1: 2 mg/L glycine, 0.5 mg/L nicotinic acid, 0.5 mg/L pyridoxine, 0 4 mg/L thyamine HCl
Stock solution 2. 0 1 g/L arginine, 0.02 g/L putrescine, 0.2 g/L ascorbic acid, 0.002 g/L calcium d-panthotenic.

The protocol for medium-term in vitro conservation of the potato collection at CIP is as follows. Accessions are conserved in a conservation medium containing 4% sorbitol at a temperature of 6-8°C, and light intensity of 1,000 lux. That extends the in vitro conservation of the potato collection for 2-4 yr without subculture (Table 2). The use of sorbitol as an osmoticum is applied to many crops without any physiological changes such as callus formation or vitrification. But these undesirable reactions are produced when the media contains mannitol, which can affect potato genetic stability (Harding, 1994). After several years in in vitro culture, plantlets can recover normal growth after one to two subcultures in propagation media. This conservation method is one of the most efficient for managing a large number of potato accessions and the time interval between subcultures is longer than for other crops.

The production of microtubers in in vitro culture as an alternative method for long-term conservation of potato cultivars has also been evaluated at CIP. Microtubers are produced in 2 to 3 mo and can be stored at 10°C for up to 10 mo after harvest (Estrada, et al., 1986). The dormancy of these microtubers can be controlled by environmental changes (Estrada et al., 1986; Tovar et al., 1985). Alternatively, once the microtubers sprout, growth can be retarded, as with in vitro plants, for 2-4 yr by storing them embedded in a conservation medium.

In vitro sweetpotato conservation

In vitro techniques for micropropagation of sweetpotato cultivars are well established. Plantlets grow from 1 to 2 mo in

Table 2. Number of accessions per *Solanum* species conserved in vitro and interval between subcultures.

Solanum species	Interval between subcultures				
	2 yr	3 yr	4 yr	5 yr	Total
andigena	569	666	1,555	70	2,860
stenotomum	57	54	129	5	262
phureja	37	37	66	9	149
tuberosum	38	24	68	8	138
chaucha	23	23	61	1	108
goniocalyx	15	6	31	1	53
Juzepczukii	4	8	14	1	27
ajanhuiri	6	3	8	0	17
Other	184	125	280	18	607
Total	**933**	**946**	**2,212**	**113**	**4,204**

culture media containing minerals, a C source, polyamines, and growth regulators such as giberellic acid (propagation medium I, Table 1) in a culture room at 23-25°C and 3,000 lux (Lizarraga et al., 1990). Some plants show multiple shoot formation, phenolization, or shoot dormancy as a response to high stress. We have overcome this problem at CIP by using a culture medium containing naphthalene acetic acid (propagation medium II, Table 1).

A number of problems prevent the long-term conservation of sweetpotato. Many attempts to establish an efficient slow growth medium have failed due to a strong genotypic response to the modified culture media, low survival percentage under restrictive growth conditions, or the formation of callus and vitrification during storage.

Although plantlets cultured in growth retardants may have survival rates ranging from 70 to 90%, genotypic effects or toxic effects are seen. For example, plants grown in a medium containing abscicic acid at 5-20 mg/L had a survival rate of 70-85% after 8 mo, but showed strong genotypic effects (Desamero, 1990; Jarret et al., 1991). Plants grown with the retardant maleic hydrazide at 5 mg/L had a survival rate of 70-90% after 6 mo (Desamero, 1990). Plants grown with cycocel at 500 mg/L had the same survival rate after 1 yr (Guo et al., 1995). But toxic effects were observed with both maleic hydrazide and cycocel. Using kinetine as a growth regulator, Guo et al. (1995) achieved a 70% survival rate in 20 accessions after 1 yr in storage, but with some callus presented. Plants growing in MS medium diluted to 30% and 50% showed low survival (36-48%) after 4 mo in storage (Abreu et al., 1992; Aguilar and Lopez, 1993).

Sweetpotato plantlets can remain in 10-40 g/L sorbitol for 6-12 mo without subculture (Desamero, 1990; Acedo, 1993; Cubillas, 1997). They resume normal growth when placed in a culture medium without osmoticum. Sorbitol, however, can be metabolized by the plantlets after some months of storage and exhibit an incremental growth rate, effectively reducing storage time. Mannitol at 20-40 g/L has also been used in sweetpotato to extend the interval between subcultures to 1 yr (Aguilar and Lopez, 1993; Acedo, 1993; Mandal and Chandel, 1990; Guo et al., 1995; Desamero, 1990) but some callus formation and vitrification was reported.

Tropical crop species usually lose their viability at temperatures lower than those required for growth in the field.

Sweetpotato, however, can continue to grow at temperatures several degrees below normal field temperature. Sweetpotato plants grown at temperatures below 15°C for long periods have shown detrimental effects such as phenolization and necrosis (Desamero, 1990). CIP research has shown that temperatures of 16-18°C lengthen the storage period up to 1 yr in cultures containing 2% sorbitol. However, some detrimental effects were produced in 25% of accessions in the in vitro sweetpotato collection. Temperatures of 18-21°C are being tested. A culture medium containing 2% sorbitol, storage at 23-25°C, and 3,000 lux (Lizarraga et al., 1990) successfully maintained the sweetpotato collection at CIP 4-6 mo without subculturing. More recently, a new culture medium containing 2% sorbitol and 2% mannitol was tested using 30 accessions. Their survival rate was 82% after 16 mo of conservation (Table 3) (Cubillas, 1997). An evaluation of this method using several hundred accessions in the collection is under way.

Procedures for Optimum In Vitro Germplasm Conservation

In vitro conservation entails the risk of losing material due to cooling equipment failure, contamination of cultures, or mislabeling accessions. Therefore, the following recommendations will help to maintain an in vitro collection more efficiently.

- Frequently evaluate in vitro growth during the first month to detect plants with growth problems.
- Maintain aseptic conditions in the culture growth room to avoid sources of contamination (dust, dirt, mites, or contaminated material). Treat the room as a restricted area to prevent contamination.
- Equip the in vitro laboratory with an electronic alarm connected to a control panel that monitors environmental conditions.
- Develop a database with unique codes for each accession in the collection. Each accession should have at least two identification numbers for proper identification. Labels for the cultures should be generated directly from the database to prevent human errors while transcribing.
- Closely monitor the cultures with some frequency during in vitro storage. Isolate contaminated cultures as soon as they are detected to prevent spreading the problem to clean plantlets. Include specific antibiotics in culture media to

Table 3. Percentage of plant survival evaluated after 22 months of storage with three teatments of a modified culture medium for medium-term storage of sweetpotato.

Mo	2% mannitol 2% sorbitol	1.5% mannitol 2% sorbitol	2% sorbitol
6	100	100	100
8	98	96	94
10	92	88	84
12	87	82	79
14	85	77	70
16	82	70	61
18	76	63	53
20	71	57	43
22	66	51	37

eliminate endogenous bacteria in the cultures.

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Global Projections for Potato and Sweetpotato to the Year 2020

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Many of the developing world's poorest producers and undernourished households are highly dependent on roots and tubers—including potato and sweetpotato—as a major, if not principal, source of food, nutrition, and cash income (Alexandratos, 1995). Potato and sweetpotato are currently planted on about 27 million hectares worldwide, producing 432 million metric tons (t), 56% of this is harvested in developing countries (FAOSTAT, June 1998). By the mid-1990s, an estimated 158 million t of potato and sweetpotato were consumed annually in developing countries, representing part of the diet of several billion consumers in these regions (FAOSTAT, January 1999). An improved understanding of the importance of production, utilization, and future role of potato and sweetpotato in the global food system for the 21st century has potentially far-reaching implications for investments in agricultural research at both the international and, perhaps even more importantly, national level.

This paper represents some of the key findings of a recent collaborative study carried out by CIP and IFPRI with input from scientists at CIAT and IITA (Scott et al., 1999). It presents future projections for potato and sweetpotato to the year 2020 for the purpose of contributing to a clearer vision of the role these crops can play in the global food system in the decades ahead. Previous projections for these commodities, particularly potato, have proved to be highly misleading when compared to FAO statistics on actual output trends. Those for sweetpotato and potato are also considered suspect because the FAO production data frequently underreport production and/or yields for particular developing countries. Hence, there is a sense among commodity specialists and some global food analysts that a new set of projections using a different methodology is required in order to provide projections for potato and sweetpotato that merit consideration in the highest international agricultural policymaking circles.

In the first part of this paper, the novel elements of this approach, which emphasizes presenting disaggregate results and incorporating potato and sweetpotato in a multi-commodity model, are explained. Subsequent sections then spell out findings with regard to utilization, production, trade, and the estimated value of output according to alternative scenarios. A concluding section presents two sets of policy recommendations. One focuses on regional priorities based on the projections themselves. The other concerns the process of collecting and analyzing potato and sweetpotato data for the purpose of generating such estimates.

Material and Methods

Global food projections in this paper were calculated using IFPRI's international model for policy analysis of agricultural commodities and trade (IMPACT). The model, covering 37 countries and regions and 18 commodities, (including all cereals, soybeans, roots and tubers, meats, and dairy products, accounting for the vast majority of the world's food production and consumption), is specified as a set of country-level demand and supply equations

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linked to the rest of the world through trade. Demand is a function of prices, income, and population growth with total demand equal to the sum of food, feed, and other (non-food, non-feed) demand. Growth in crop production in each country is determined by crop prices and the future rate of productivity growth, which in turn is estimated by its component sources including advances in management and plant breeding research. Other sources of growth considered in the model include private sector investments in agricultural research and development, agricultural extension and education, markets, infrastructure, and irrigation (see Rosegrant et al., 1995, for details of the methodology). The results presented here are generated from an updated version of IMPACT that takes as its base period 1992-94. The projections are for the year 2020. Projected growth rates then are annual average rates estimated for the period 1993-2020. All other modeling methodology is consistent with the IMPACT model reported in Rosegrant et al. (1995).

In order to put the following set of results into perspective, it should be pointed out that these calculations attempt to go beyond past projections made for these crops in a number of important respects including:

- Previous attempts often focused only on a single root and tuber crop, e.g., potato (FAO, 1995), thereby making less explicit the possible linkages in production, consumption, and trade with other food commodities.
- Other attempts to model future trends for potato and sweetpotato were calculated on an aggregate basis, for roots and tubers in total, overlooking the complexities that can be more effectively captured in a disaggregate approach.
- Past efforts at estimating the future relative value of major food commodities including potato and sweetpotato have assumed fixed relative prices throughout the planning period. IMPACT specifically allows prices to vary.
- Finally, previous attempts at multi-commodity projections were often carried out without the participation of commodity specialists for roots and tubers (Rosegrant et al., 1995). Given the relative shortage of published information on potato and sweetpotato (there is no extensive body of literature on projections for these crops, particularly for developing countries), this represents an important aspect of any modeling exercise for these commodities. The results presented here represent the output of collaboration over the last three and a half years between CIP and IFPRI economists.

Results and Discussion

IMPACT posits two scenarios for future growth in demand, production, trade, and prices for potato and sweetpotato in the context of generating projections to the year 2020 for the world's major food commodities: (1) the baseline scenario; and (2) the high demand and production growth (HDP) scenario. In the baseline scenario, projections for potato and sweetpotato are driven by more conservative estimates of the effect of income growth on demand for these commodities and their derivatives. As a corollary, the rate of technological change is more modest than in the HDP scenario contributing to less rapid increases in production and yields.

Baseline scenario

IMPACT's baseline scenario for projected growth rates in food and animal feed demand from 1993 to 2020 are high and uneven across the globe. They are highest for potato with an average annual increase in total demand of 2.02%, and 2.33% for average annual food demand (Table 1). For sweetpotato, total food demand is projected to grow at 0.44% over the period reflecting reduced demand for fresh sweetpotato for direct human consumption in China.

Regional growth rates for food demand for potato are highest for Sub-Saharan Africa (3.10%) and India (3.09%), and

Table 1. Trends and projections for potato and sweetpotato in developing countries, 1987-97 vs. 1993-2020 according to different scenarios.

	Potato			Sweetpotato		
Category	1987-97[a]	1993-2020A[b]	1993-2020B[c]	1987-97[a]	1993-2020A[b]	1993-2020B[c]
Growth rates in production (average annual %)						
- Area	2.4	0.51	0.84	1.3	0.27[d]	0.35[d]
- Yield	2.0	1.50	1.85	0.9	0.97[d]	1.10[d]
- Production	4.5	2.02	2.71	2.2	1.25[d]	1.45[d]
Growth rates in utilization (average annual %)						
- Total food demand	—	2.33	2.75	—	0.44[d]	0.50[d]
- Total feed demand	—	0.37	2.66	—	1.81[d]	2.23[d]
- Total use	—	2.02[e]	2.76[e]	—	1.25[de]	1.46[de]
Net trade (mil. mt)	—	-1.2	-4.6	—	0.6[d]	0.4[d]
Value (%)	—	3.9[f]	4.9[f]	—	1.5[f]	1.9[f]

Source: Scott et al. (1999) and FAOSTAT (June 1998, accessed July 1998).

Note: Developing countries as defined by FAOSTAT.

[a] Calculated for the period 1985-87 to 1995-97, without central Asia in the case of potatoes.

[b] 1993/baseline scenario.

[c] 1993/high demand and production growth scenario.

[d] The growth rate projections are for sweetpotato and yam combined with a ratio 80/20 for sweetpotato to yam. China produces no yam.

[e] Total food, feed, and industrial (non-food, non-feed) demand.

[f] See Table 2.

lowest for other East Asian countries (e.g., North Korea), and Latin America (1.69%). These strong results reflect:

- the high status of potato as a preferred food in these regions;
- population growth, particularly strong in Africa; and,
- the extent to which the crop fits into local food systems in terms of, e.g., labor requirements, soil, and climate conditions.

For sweetpotato, regional growth rates for food demand are highest in Sub-Saharan Africa (2.74%) and lowest in China (-1.02%) with most other regions showing little or no growth. Feed demand presents just the opposite picture with strong growth in China (1.81%). This dichotomy partly reflects the relative availability of basic foodstuffs in the two regions; China is relatively well endowed and Sub-Saharan Africa much less so. Differential population and income growth rates, slower demographic expansion and more rapid economic growth increasing demand for meat in China, with an opposing scenario in Sub-Saharan Africa, also drive the dichotomy.

Projected production growth rates are variable and driven by yield increases. Average annual growth rates in production from 1993-2020 for potato (2.02%) and sweetpotato (1.25%) are dominated by growth rates in yield (1.50% and 0.97% respectively) (Table 1). However, in relation to recent actual trends in production in the period 1987-97, these estimated production growth rates are less than half that for potato, and 25% higher for sweetpotato (Table 1). Whereas in absolute terms the projected increases from 1993 to 2020 in area planted in potato (1.0 million ha, or 15%) and in sweetpotato (0.9 million ha, or 8%) are by no means insignificant, the projected average annual declines in

the growth of area planted from the periods 1987-97 to 1993-2020 is more noteworthy than the slowing of production growth over the period.

Trade is not projected to increase to any extraordinary extent, although the published FAO database for trade used for generating these projections is particularly suspect because it often lacks statistics on trade in processed products for particular countries. Current estimates suggest that processed potato exports, for example, would at least double the overall trade volume (FAO, 1995). For sweetpotato, recent research in China suggests that exports of starch-based products may be far more important and are growing more rapidly than previously realized. Notwithstanding, some marked increases in trade are projected to take place. Southeast Asia and Sub-Saharan Africa will each import 300,000 t more of seed and table potatoes in 2020 than the estimated 100,000 t imported in 1993. China's exports of sweetpotato are projected to rise by 900,000 t to 1.4 million t.

The baseline scenario projects the value of potato and sweetpotato as a share of the total value of the major food commodities in the study to fall from 6.9% in 1993 to 5.4% in 2020 (Table 2). Much of this decline is attributable to the fall in price for sweetpotato. Higher than previously estimated prices for cereals in 2020 also are driving this result (Rosegrant at al., 1995).

Table 2. Total value of selected commodities for developing countries, 1993 vs. 2020 according to different scenarios.

	1993[a]				2020A[b]				2020B[c]			
	Price (US$/t)	Production (000 t)	Value (US$) (millions)	Total (%)	Price (US$/t)	Production (000 t)	Value (US$) (millions)	Total (%)	Price (US$/t)	Production (000 t)	Value (US$) (millions)	Total (%)
Potato	160	94,336	15,094	4.1	137	161,994	22,193	3.9	145	194,006	28,131	4.9
Sweetpotato	80	124,703	9,976	2.8	56	154,722	8,606	1.5	68	163,369	11,186	1.9
All roots and tubers[d]		422,573	38,586	10.5		654,504	50,076	8.8		714,584	60,946	10.5
All cereals[e]		928,115	176,622	48.0		1,407,478	241,253	42.6		1,409,470	242,195	41.9
Soybean		57,705	15,176	4.1		106,149	24,839	4.4		106,203	24,958	4.3
All meat[f]		88,326	137,752	37.4		182,749	249,862	44.1		182,831	250,467	43.3
Total			**368,136**				**566,030**				**578,567**	
1993 share of R & T in all commodities				10.5				8.8				10.5
Share of R & T in cereals + R & T + soybean				16.7				15.8				18.6

Source: Scott et al. (1999). Note: Roots and tubers = R & T.

[a] Average for the three years; 1993 equivalent to 1992-94.

[b] Baseline scenario.

[c] High demand and production growth scenario.

[d] Includes potato, sweetpotato, cassava, yam, and other roots and tubers.

[e] Includes wheat, maize, barley, sorghum, millet, and rice. [f] Includes beef, pork, poultry, sheep, and goat meat.

High demand and production growth scenario

Recent trends indicate that the structure of demand and supply for potato and sweetpotato may be undergoing fundamental shifts in parts of the developing world (Table 1). The HDP scenario is used to examine the impact of faster supply and demand growth in selected regions.

The HDP scenario projects that growth of both food and feed uses will account for the faster growth in overall demand for potato and sweetpotato. In the HDP projection, the jump in demand for potato is almost entirely due to faster growth in food use in China and India. In China, average annual growth in food use for potato from 1993 to 2020 is 2.74% versus 2.20% for feed use. In India, average growth in food use during the period is 3.80% per year versus 3.09% for feed use. Overall average annual per capita demand for potatoes in developing countries will rise only modestly beyond the level projected in the baseline scenario—from 16.18 to 18.05kg. These consumption levels remain a minor percentage of the level currently observed in industrialized countries, 74 kg/capita/yr.

For sweetpotato, the major growth is in total feed demand (2.33% average annually from 1993 to 2020). This result largely reflects the strength of feed demand in China, where sweetpotato will become a more efficient animal feed source to help satisfy the country's growing demand for meat. This reflects higher prices for maize and improvements assumed by the HDP scenario.

Projected growth rates for production of potato (2.71%) and sweetpotato (1.45%) are higher—and for potato considerably so—than those of the baseline scenario of 2.02 and 1.25%, respectively. For potato, higher growth rates result from faster growth in China, 2.72% versus 1.49% in the baseline scenario, and in India 3.67% versus 3.10%. In both countries, production growth is a result of stronger expansion in area planted. It should be noted here that even these higher projected growth rates actually represent a major drop from recent historical levels, e.g., from 6.2% per year in China during 1987-97 (FAOSTAT, June 1998). For sweetpotato, stronger growth in area planted in Sub-Saharan Africa and moderately higher yields in China (though area planted is projected to fall by 600,000 ha) account for the accelerated growth rate for production of sweetpotato (roughly 2.7%).

In the case of trade, the big change is with potato—although the lack of data on processed products still applies. From 1993 to 2020, total imports for developing countries jump from 1.2 to 4.6 million t as China, India, and the West Asian and North African regions go from net exporters to net importers. Strong demand under the HDP scenario is likely to generate greater imports of processed potato products for human consumption (e.g., frozen french fries, chips) from industrialized countries.

The shares of potato and sweetpotato in the projected value of the commodities is projected to remain stable, if not rise (Table 2). This result is the combined effect of the faster growth rates in production and a moderately slower rate of decline in prices for these commodities with the bulk of the increase due to faster production. Furthermore, all of the more rapid projected increases are well within the range of recent trends in production and utilization for roots and tubers in developing countries as derived from FAOSTAT statistics. The additional expansion in area planted in roots and tubers is a small fraction of the total land area devoted to crop production in 2020.

Conclusions

The implications of these projections for the location of potato and sweetpotato production in the year 2020 and the value of production for these crops can be summarized briefly.

Potato and sweetpotato are, as far as developing countries are concerned, overwhelmingly Asian commodities (Figure 1). Based on these projections, particularly the HDP scenario, they will become increasingly so in the years ahead, albeit for different reasons. Rising incomes will stimulate added consumption of potatoes as consumers look to diversify their largely cereal-based diets. This increased consumption of potatoes will include high percentage increases, but modest in absolute quantities on a per capita basis, in the consumption of fast foods and snacks as Asia's largely rural-based population becomes more urbanized and incomes improve.

For sweetpotato, rising incomes and urbanization will catalyze increased use of the roots and vines for animal feed and processed food products such as noodles made from starch.

From a global perspective, the relatively minor importance of potato and sweetpotato in Africa is noteworthy. However, potato and sweetpotato will maintain, if not rise, in relative importance in particular sub-regions within Africa, particularly in East Africa.

Finally, the estimates of the value of production permit us to calculate the geographic distribution of the future value of production for potato and sweetpotato. This comparison highlights the importance of China and India for potato and China and Sub-Saharan Africa for sweetpotato (Figure 2). Policymakers and research scientists should keep these consumption and production trends in mind when formulating plans for future research and related development efforts.

Recommendations

Experience in working with the available data to generate these projections suggests a series of measures are needed to improve the process.

First, an international effort is needed to examine the databases for potato and sweetpotato in a select number of developing countries with the specific intent of reducing the margin of difference between FAO statistics and national data, as well as

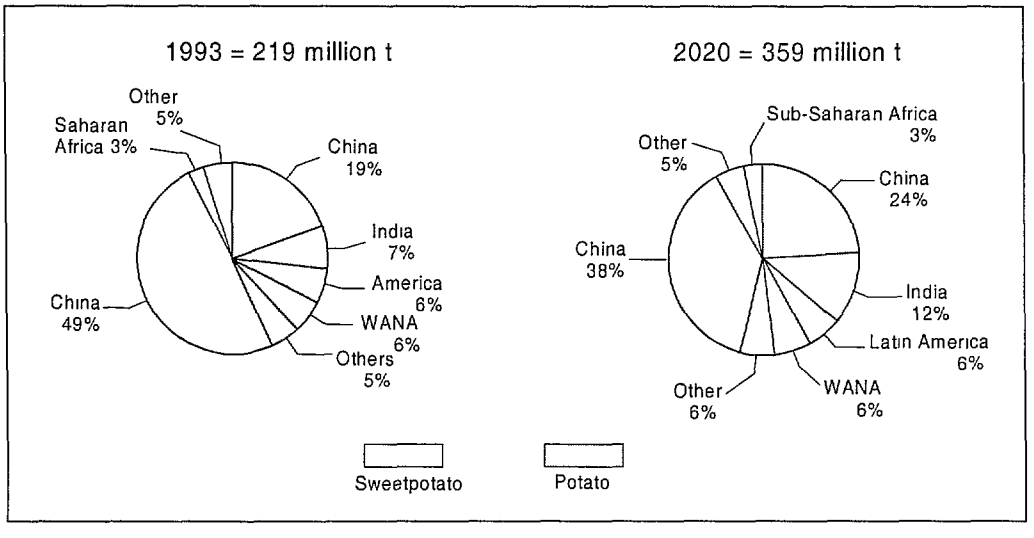

Figure 1. Potato and sweetpotato production (million t) in developing countries 1993 vs. 2020, according to the HDP scenario. (Source: Scott et al., 1999.)

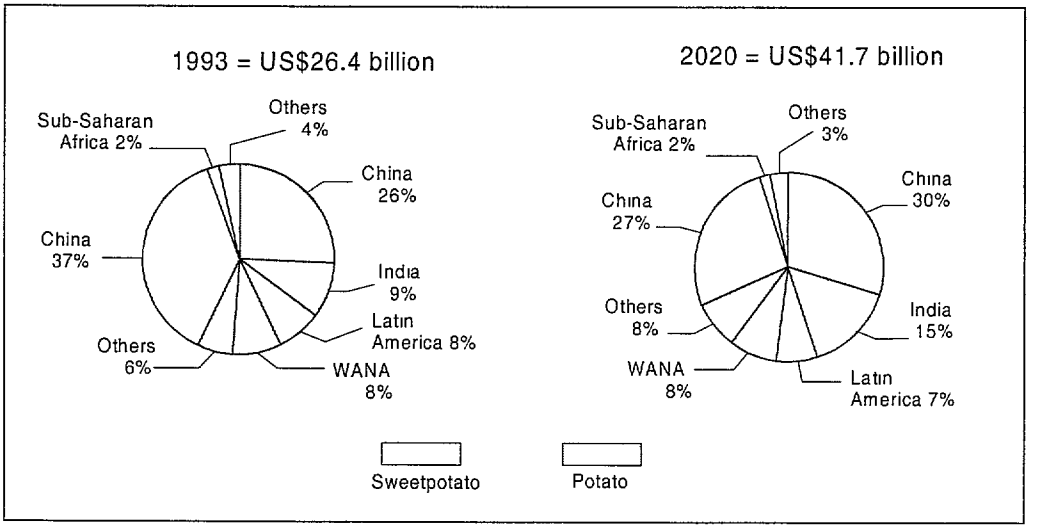

Figure 2. Value of potato and sweetpotato production (US$ billion) in developing countries 1993 vs. 2020, according to the HDP scenario. (Source: Scott et al., 1999.)

between aggregate country figures and the findings of specific case studies and farm surveys.

Second, a systematic attempt to improve the FAO Food Balance Sheet data should be undertaken. This should include reconsideration of how food and non-food categories are reported. Specifically, inclusion of sweetpotato leaves in nutrition estimates would seem to make good sense. Feed use figures should include some estimate for sweetpotato vine use; if not in the Food Balance Sheet figures themselves, then in some other internationally accepted standard of feed availability.

Third, closer statistical monitoring and publishing of trade data on potato and sweetpotato should be a goal, so as to regularly include information on at least the major processed products, e.g., frozen french fries, chips, and dehydrated products for potato as well as starch and noodles for sweetpotato. Again, perhaps an experimental pilot effort in a few key countries could help identify the types of low-cost improvements in reporting procedures, estimates of difference in results these procedures would make, as well as concrete suggestions on how the improvements might be implemented.

Impact

This joint effort of CIP and IFPRI to analyze historical trends and generate commodity projections has resulted in two major impacts. First, CIP, in conjunction with CIAT as well as IITA, and FAO are currently preparing the next set of projections for potato, sweetpotato, cassava, and yam for TAC. This more pro-active approach will reduce the need for post-publication debates about the accuracy of particular figures.

Second, the interaction between CIP and IFPRI has strengthened IFPRI's IMPACT model for the global food economy and helped CIP better appreciate the relationship between potato and sweetpotato and other major food commodities. As a result, the CGIAR's interaction with international and national policymakers will provide a more consistently accurate and optimistic outlook for these commodities in the years ahead.

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The Role of Potato and Sweetpotato in Disaster Relief: The Case of Rwandan Refugees in South Kivu, Democratic Republic of the Congo (ex-Zaire), 1994-96

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After the civil war and associated genocide in Rwanda in June and July, 1994, over one million refugees streamed over the border into neighboring areas of Zaire, a country whose new government has since changed its name to the Democratic Republic of the Congo. This area around the Great Lakes is one of the poorest and most densely populated in all of Sub-Saharan Africa. Prior to the outbreak of violence, Rwanda and then Zaire had estimated per capita incomes of US$265 and US$327, respectively (World Bank, 1992). In response to the human tragedy in 1994, refugee camps were set up under the auspices of several branches of the United Nations and a number of non-governmental organizations (NGOs). The displaced population lived in these camps for a little over two years, until they were dispersed in October 1996. Some went back to Rwanda, their home country. Others fled to locations deeper into the D.R. of the Congo. Five camps were set up near the town of Bukavu, at the southern tip of Lake Kivu (Figure 1). The agroecological conditions, farming systems, and dietary habits of the local population are very similar to those across the border in Rwanda. The refugees' presence generated a huge increase in the local demand for food. They also constituted a massive pool of hired labor for local farmers. Their presence led to a surge in the production of both potato and sweetpotato, important crops historically on both sides of the border (Scott, 1988; Tardiff-Douglin, 1991).

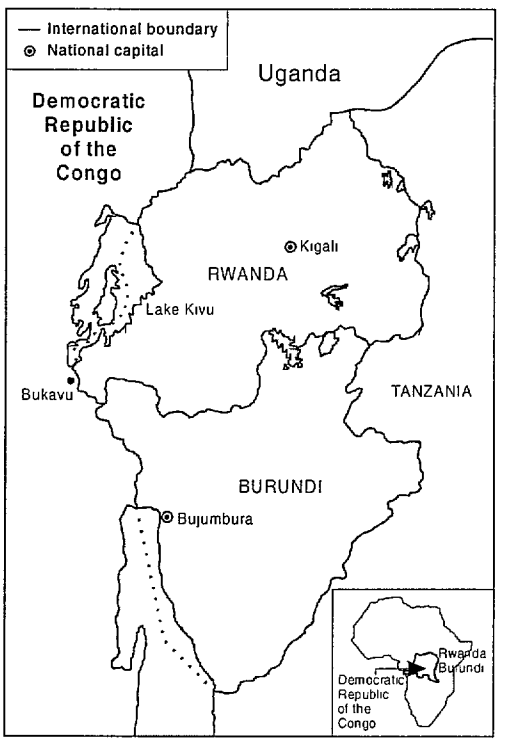

Figure 1. D.R. Congo, Rwanda, and Burundi showing Bukavu, near the five refugee camps.

Materials and Methods

The national potato and sweetpotato programs of INERA, the national agricultural research institute of D.R. of the Congo, are based at the Mulungu Research Station just outside Bukavu. The programs are part of the PRAPACE network, and have rou-

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4 CIP, Lima, Peru.

tinely received advanced germplasm and training from CIP for the past 20 years (Ewell, 1992; Rueda et al., 1996). Improved cultivars and other tested technologies were locally available. One of the refugee camps was located right on the edge of the station; others were in the immediate vicinity. The station became involved in the multiplication of planting material for local farmers, who sold their harvest directly to the refugees as well as to the relief agencies. Given these dramatic developments, researchers at Mulungu were interested in analyzing the response of local growers to these events. Among the key considerations was a better appreciation for local farmers' ability to respond quickly to upheavals in supply and demand for food, to begin to quantify the extent of this response, and to examine the role of new technology in these adjustments. To that end, a total of 128 farmers in the immediate surroundings of five refugee camps were interviewed about the impact of the crisis on local agriculture and food supplies during April and May, 1998 (Tanganik and Phezo, 1998).

Results and Discussion

The local farmers are predominantly members of the Mushi tribe. The highlands of South Kivu are mountainous, and agricultural land is located between 1,400 and 2,500 m. The predominant crop is banana, consumed primarily as local beer. The major staple crops are sweetpotato, beans, maize, cassava, and potato (Table 1). Sweetpotatoes are known as *cilera abana*, or "protector of the children", and are universally grown on a small scale for food security. Potatoes are widely grown as a cash crop, mostly by richer members of the community, in drained swamps along with other vegetables. Farmers were able to rapidly intensify production of both crops to sell to the refugees.

Potato

Most farmers increased their cropping intensity from one to two or even three crops a year (Table 2). Over half of the farmers interviewed decreased the area planted to other crops to increase potato production, at the expense of beans, maize, cassava, and sorghum. Two-thirds of them adopted new culivars. Cruza 148 (720118) was introduced into the region from Mexico in the late 1970's. It is relatively high yielding, resistant to late blight, and tolerant to bacterial wilt. Adoption has been limited by its relatively poor culinary quality that makes it difficult to market (Rueda et al., 1996). This was obviously not a major issue for the refugee market, and it quickly became the most widely grown. Other established cultivars Montsama (720049) and the Rwandan selection Mabondo were also adopted. Seed was obtained from the Mulungu research station, from agricultural extension agents as well as from NGOs. In some camps, seed was obtained from the refugees themselves, who had carried it from their homes in Rwanda.

The availability of refugees as laborers encouraged local farmers to adopt relatively labor-intensive practices. These included heavy mulching at planting, deep tillage, the preparation and application of organic compost, draining of swampy plots, and higher hilling. Over half of the farmers increased the use of fungicides to control late blight, and 42 percent rogued out diseased or other suspicious plants to improve the quality of their seed (Table 2).

Sweetpotato

The presence of a ready market encouraged a noteworthy increase in the number of plantings of sweetpotato by nearly all of the farmers interviewed, even more so than potato (Table 2). Eighty six percent of them went from one to two plantings per year, and reduced the areas dedicated to maize, beans, peanuts and vegetables. Over half of them planted new cultivars available on the Mulungu station—again even slightly more so than in the case of potato. The new cultivars had been selected primarily for earliness and high yield. Karebe II and Mugande are regional farmers' cultivars

Table 1. Sampled households reporting major annual crops in areas surrounding refugee camps in the Democratic Republic of the Congo before arrival of Rwandan refugees in July 1994.

	Site					
	Mulungu[a]	Bugobe	Kalehe	Ludaha	Nyangezi	Total
Altitude (m)	1,850	2,000	< 1,800	1,965	1,500	
Sample size	32	22	24	28	22	128
Households reporting production (%)						
Crop						
Sweetpotato	100	100	100	100	100	100
Beans	100	82	92	79	91	89
Maize	100	82	50	100	82	83
Cassava	100	64	100	21	100	77
Potato	100	100	25	100	0	65
Vegetables	19	82	50	71	19	48
Soybean	50	37	67	21	37	42
Sorghum	31	72	37	21	45	38
Peanut	19	0	83	0	36	27

[a] Mulungu is the research station of the Institut National d'Etudes et de Recherches Agricoles.

initially identified as superior by the Rwandan research program. Yanshu 1 is a very high yielding and early Chinese cultivar, which is normally scored as marginal by taste panels in Africa. Mulungu I is a local Congolese farmers' cultivar recently identified as superior by researchers. Benikomachi is a Japanese cultivar with relatively low yield but excellent taste. The low emphasis by farmers on the better tasting Benikomachi and the acceptance of the Yanshu 1 are indicative of the willingness of the market to accept cultivars with relatively low culinary quality (Yanshu 1) during the refugee crisis.

Planting material was obtained from the research station, extension agencies, and NGOs and again in some cases from the refugees themselves. Again, agricultural farmers used refugee labor to intensify production through heavy mulching at planting, the preparation and use of organic compost, better ridging, deep tillage, and draining swampy areas. Overall the movement toward improved agronomic practices was more pronounced than potato (Table 2). Insecticides were the only purchased input mentioned, but only by eight percent of the farmers.

Conclusions

The increased income from the sale of potato and sweetpotato was used to increase the wealth and status of the farmers. Dowries, livestock, home improvements, and consumer items such as bicycles and radios were the most commonly mentioned. School fees and improved diet and health for their families were rated as somewhat less important, which may imply that the most basic needs of these farm households were already met.

The departure of the refugees meant that the extraordinary surge market demand returned to pre-crisis levels, and labor was no longer so easily available. About half of the farmers said that they lost money in the season when the Rwandans left, but this may also have been partially due to the

Table 2. Impact of the presence of Rwandan refugees on potato and sweetpotato production in areas surrounding refugee camps in the Democratic Republic of the Congo, 1994-1996.[a]

	Mulungu[b]		Bugobe		Kalehe		Ludaha		Nyangezi[c]	Total	
Altitude (m)	1,850		2,000		< 1,800		1,965		1,500		
Sample size	32		22		24		28		22	106	128
	P[d]	S[d]	P	S	P	S	P	S	S	P	S
Farmers responding (%)											
1. Increased number of plantings per year?											
No	0	6	9	0	17	8	0	0	18	6	6
From 1 to 2	94	98	91	100	65	83	86	86	82	84	86
From 1 to 3	6	13	0	0	18	8	14	14	0	10	7
2. Reduced other crops to grow more potato?											
No	25	19	0	18	0	8	0	21	18	6	17
Yes[e]	69	-	82	-	17	-	36	-	-	51	-
Less beans	38	50	28	28	0	17	14	21	28	20	29
Less maize	25	25	0	19	17	67	14	21	19	14	43
Less cassava[f]	6	-	27	-	0	-	0	-	-	8	-
Less sorghum[f]	6	-	19	-	0	-	7	-	-	8	-
Less peanut[g]	-	0	-	19	-	17	-	14	27	-	15
Less vegetables[g]	-	6	-	27	-	8	-	7	9	-	12
3. Adopted new cultivars?											
No	69	50	64	45	75	100	64	14	73	68	56
Yes	13	50	36	36	25	0	36	57	27	28	34
Cruza (P) / Karebe II (S)	13	31	82	27	100	0	100	36	18	74	22
Montsama (P) / Mugande (S)	13	38	91	9	0	0	85	29	27	47	20
Mabondo (P) / Yanshu I (S)	0	35	82	9	0	0	21	30	26	10	20
Murhula (P) / Mulungu I (S)	13	19	9	0	0	0	14	0	18	9	7
Enfula (P) / Benikomachi (S)	0	6	9	0	0	0	14	0	0	6	1
4. Where seed obtained?											
Research station	100	94	72	55	0	0	100	7	72	68	45
Extension/NGO	35	0	45	36	42	0	64	43	27	47	21
Refugees	0	0	0	9	100	17	0	40	0	5	13
5. More intensive practices adopted?											
Mulching at planting	94	75	100	100	25	92	100	100	100	80	97
Deep tillage	88	19	100	100	13	100	100	100	100	75	83
Organic compost	75	75	100	100	13	100	100	100	100	72	95
Drain swamps	19	63	45	55	25	50	86	79	55	65	60
More hilling/plant on ridges	56	63	90	100	25	92	86	100	100	64	91
Fungicides/insecticides	44	6	81	0	13	0	79	0	9	54	8
Negative selection[f]	56	-	82	-	17	-	14	-	-	42	

a. Data collected April and May 1998.
b. Research station of the Institut National d'Etudes et de Recherches Agricoles, South Kivu, Democratic Republic of the Congo.
c. Additional area studied for sweetpotato production only.
d. P = potato, S = sweetpotato.
e. 'Yes' response not documented for sweetpotato production.
f. Applicable for potato production only.
g. Applicable for sweetpotato production only.

effects of the civil war in D.R. of the Congo that broke out against then President Mobutu at the same time. Nearly 100 percent of the respondents said that they immediately reduced the area planted to both crops. Nevertheless, a majority reported that they have continued to benefit from the improvements made in their farms during the upheaval, and that they continue to use improved practices to maintain higher yields than before. The major problems are shrunken market and lower prices. Local labor is available, but requires payment in cash, whereas Rwandan refugees would accept payment in the form of food.

This case study illustrates that new cultivars and labor-based technologies to improve the productivity of the farming systems are available in the region, and that they can be adopted rapidly by large numbers of farmers. The wider and more rapid adoption of yield-enhancing technologies is constrained by the size of the local market and limited effective demand and to some extent by the supply of affordable labor. Furthermore, in many areas of Sub-Saharan Africa, wars and natural disasters unfortunately seem likely to continue in the foreseeable future. Both potato and sweetpotato will have important roles to play as short-season, nutritious, locally available foods. CIP and PRAPACE will continue to work with partners and donors to make them available as quickly and efficiently as possible emergency situations, while simultaneously pursuing a longer-term strategy to expand and diversify more permanent commercial opportunities for these commodities.

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Estimating Frost Risk in Potato Production on the Altiplano Using Interpolated Climate Data

R. J. Hijmans[1]

The Altiplano is a high plateau in the Andes of Peru and Bolivia. This paper deals only with the part of the Altiplano called the TDPS System for Lake Titicaca, Desaguadero River, Lake Poopó, and Salt Lake of Coipasa (OEA, 1996), an area of 149,000 km^2 (Figure 1). That excludes the southernmost part of the Altiplano, which is rather arid, sparsely populated, and less important for agriculture. Seventy-five percent of the TDPS system, hereinafter called the Altiplano, is between 3,600 and 4,300 m; the other 25% is higher. Lake Titicaca, covering 8,400 km^2 is a conspicuous part of the topography that greatly influences local precipitation and temperature.

In 1993, the Altiplano had about 2.2 million inhabitants. About 51% of the population lives in rural settlements, down from about 59% in 1980 (OEA, 1996). Rural population density is highest along the shores of Lake Titicaca and Desaguadero River, the areas most suited for agriculture. Due to emigration to urban areas, population growth rates on the Altiplano are below national levels (1.4% vs 2.1%) (OEA, 1996). The Altiplano is one of the poorest areas of the Americas, and poorer than most other parts of Bolivia and Peru. About 76% of the population lives in poverty, with 33% of those considered to live in extreme poverty (OEA, 1996).

The severe poverty is partly due to the harsh climate that limits options for agricultural production. About 65% of the economically active population is engaged in agriculture (OEA, 1996). Large parts of the Altiplano cannot be used for crop production and have a land cover of natural grass and shrub that is used for grazing. Where crops can be grown, cold and dry conditions allow for only a small number of crops. Potato is by far the most important crop, accounting for 63% of the gross value of crop production (OEA, 1996). The potato area is about 63,000 ha (G-DRU, 1996; INEI, 1996). Potato yields are low at 5.2 t/ha in the Peruvian part and the northern Bolivian part of the Altiplano, and 3.6 t/ha in the southern part (OEA, 1996; G-DRU, 1996).

The growing season in the Altiplano is between October and March, when the warmest time of the year coincides with the rainy season. In the agricultural zones, maximum temperature is around 18°C and minimum temperature around 4°C during the growing season (INTECSA, 1993; Frère et al., 1975). There is an average frost-free period of about 140 d for the northern Altiplano and 110 d for the southern Altiplano (Le Tacon, 1989). Precipitation is highest, around 800 mm/year, in the northeast and near Lake Titicaca and lowest, about 200 mm, in the southwest. Production risk for potato is high, especially because of drought, hail, and frost. Drought is a recurrent problem that can be especially damaging in El Niño years, such as happened in 1942-43 and 1982-83 (OEA, 1996).

Frost is the condition that exists when the air temperature near the earth's surface drops below 0°C (Kalma et al., 1992). However, the temperature at which frost damage to crops occurs can be lower, depending on the crop species and cultivar.

1 CIP, Lima, Peru.

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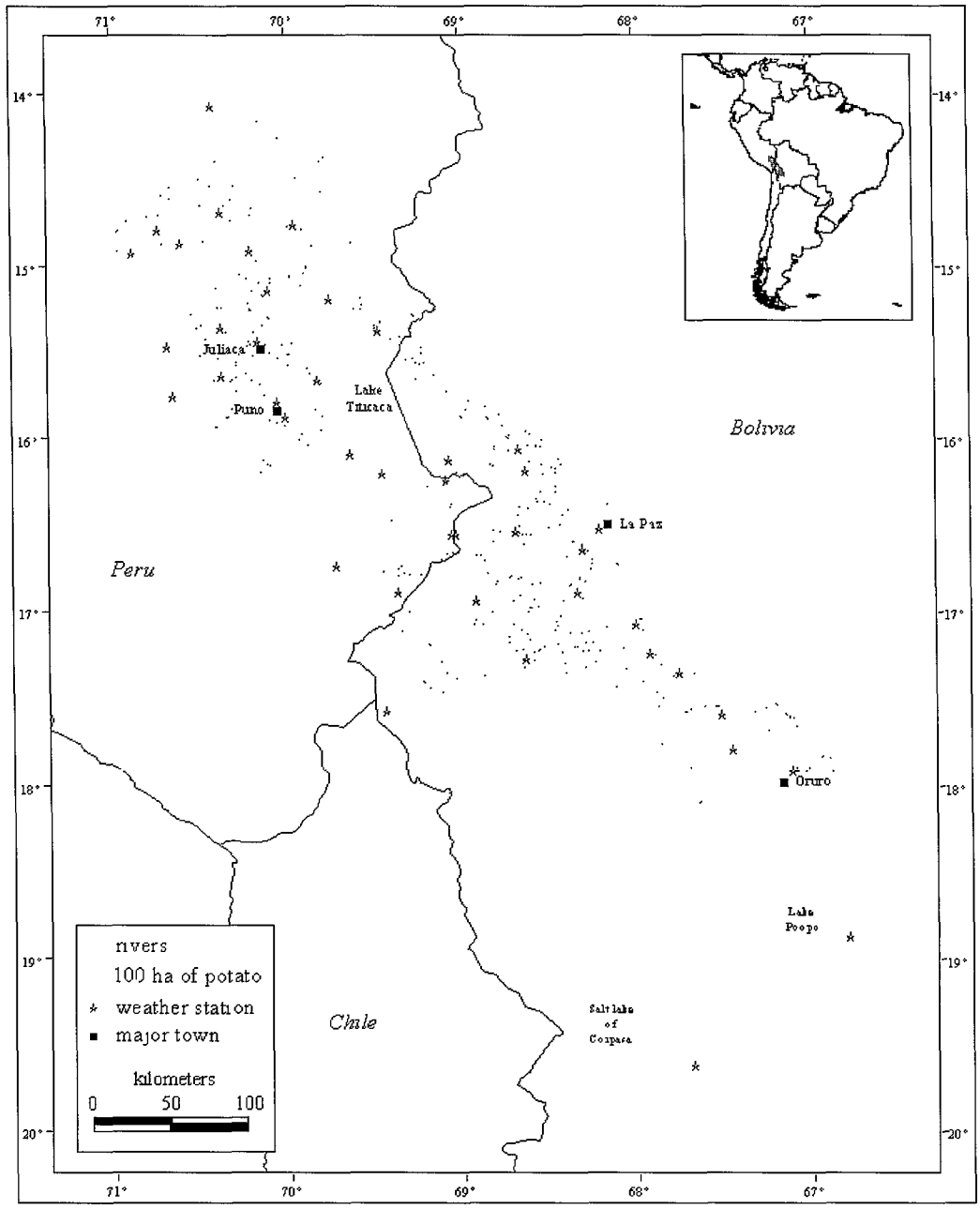

Figure 1. The Altiplano (TDPS system), distribution of potato production and sites of the weather stations used for the construction of the extreme temperature maps.

For *S. tuberosum* subsp. *andigena*, frost damage is likely to occur when the temperature drops to -2°C or lower (Carrasco et al., 1997). Therefore, we will focus on the occurrence of -2°C events. *S. tuberosum* subsp. *tuberosum*, the potato cultivated outside the Andes is slightly more susceptible and frost damage may occur at -1°C. Other cultivated potato species such as *S. ajanhuiri* and *S. curtilobum* suffer damage between -3 and -5°C (Huanco, 1992; Tapia and Saravia, 1997), whereas *S. juzepczukii*

generally tolerates -5°C and even lower temperatures (Huanco, 1992; Canahua and Aguilar, 1992; Tapia and Saravia, 1997). With the exception of *S. ajanhuiri,* the tubers of these frost-tolerant species are generally bitter due to a high level of glycoalkaloids and the need to be processed before consumption.

Frost can have a direct and indirect negative impact on potato production. The direct effect is the partial or complete loss of leaf area that leads to a reduction in photosynthesis and hence yields. In addition, crop failure may lead to a decrease in the next season's area planted due to tuber-seed shortage (Morlon, 1989). High production risk also leads to low investments in agriculture resulting in lower production in years with relatively good weather.

Farmers can avoid or reduce frost damage by selecting appropriate plant material, by careful site selection, by using appropriate cultural and management practices, and by modifying the physical environment of the crop (Kalma et al., 1992). Altiplano farmers try to diminish frost risk by planting potatoes on "warm" soils (with high thermal conductivity), and on slopes where frost incidence is lower than on the valley floor (De Bouet du Portal, 1993). Frost-related management practices include the use of smoke, rustic greenhouses (Aguirre et al., 1999), and raised beds (Smith et al., 1968; Erickson, n.d.; Sánchez de Lozada et al., 1998). In the most frost-affected areas, farmers grow frost-tolerant potato species such as *S. juzepczukii* instead of *S. tuberosum subsp. andigena.*

Frost risk can be assessed with data from climate stations, as was done for the Altiplano in Peru by Morlon (1989) and in Bolivia by Le Tacon (1989). However, given the high spatial variability of temperature and frost risk, climate stations are too far apart to draw general conclusions for the potato growing areas in the Altiplano. For the present study, maps of the probability of extreme minimum temperature events were generated. These maps were subsequently analyzed to assess the extent of frost risk in potato production on the Altiplano.

The present study was carried out in collaboration with the Fundación PROINPA (Promoción e Investigación de Productos Andinos), Bolivia, to support their project on the integrated management of abiotic stress in potato production. PROINPA's activities include breeding for frost-tolerant potato cultivars (Carrasco et al., 1997). Maps of frost risk would help target areas where new frost-tolerant cultivars might be adopted and would permit an assessment of the potential impact of these new cultivars or of other technologies.

Materials and Methods

When frost damage is reported in the literature, it is not always clear whether reference is made to temperature at screen height (1.5 to 2 m) or at canopy height. In this study, temperature refers to screen height. At the canopy level, temperature may be about 1°C lower (De Bouet du Portal, 1993).

There is a strong relation between temperature and altitude. Hence altitude is often used as a proxy for temperature and also for frost risk. However, the relation between temperature and altitude changes over space and time and cannot be extrapolated simply. Hutchinson (1995, 1997) developed a method that can be used to interpolate climate data. It fits Laplacian smoothing spline functions of two or more independent variables (longitude, latitude, and usually altitude) to the climate variable to be mapped. The method takes advantage of the strong dependence of climate (especially temperature) on altitude, but allows the size of this dependence to vary over time and space (Corbett, 1998).

Monthly extreme minimum (i.e., lowest, absolute) temperature data from 44 weather stations (Figure 1) from the database described by INTECSA (1993) were used. Depending on the weather station, data for

15-33 yr (avg. 25.2 yr) were obtained. For each station, the probability of a 0, -1, -2, -3, -4, and -5°C absolute minimum temperature event was calculated for all months of the year. It should be noted that the probability of, for example, a 0°C event does not exclude even lower absolute minimum temperatures. These probabilities were interpolated on a 30-sec (approximately 1 km^2) grid using the method of Hutchinson (1997), with altitude as the third independent variable. Altitude data were taken from the GTOPO30 database, a global digital elevation model provided by the US Geological Survey.

In the Altiplano, most potatoes are planted in October or November and harvested in April or May. Frost risk is not important before emergence. When there is frost damage just after emergence, yield loss may be limited because of re-emergence. A killing frost in April is not as harmful because there will be some crop to harvest. Therefore, in this study, the average frost risk between December and March is considered.

The probabilities of an extreme minimum temperature of 0, -1, -2, -3, -4 and -5°C were grouped in four classes: a frost event in less than 3.3% of years, between 3.4 and 10%, between 10 and 33.3%, and in more than 33.3% of years. The limits of these classes represent a frost event once in every 3, 10, and 30 yr.

A map of potato distribution in the Altiplano was made. For Peru, it was based on district level census data (INEI, 1993). For Bolivia, departmental level census data (G-DRU, 1996) and maps of crop distribution (ZONISIG, 1998) were used. Overlays (simultaneous queries) of the potato map and the frost risk maps were made to estimate frost risk in potato producing areas.

Results

Frost risk is lowest in the warmest parts of the Altiplano around Lake Titicaca and in the relatively lower parts in the southeast. It is highest in the eastern Altiplano and in the high parts of the catchment (Figure 2). Table 1 presents the probability of extreme temperature events for the potato area in the Altiplano.

Of the 63,000 ha area planted to potato, only 4% has a negligible risk of a -2°C event, and 18% has a -2°C event less than once every 10 yr. Twenty-five percent of the potato area has an extremely high frost risk, with a probability of a -2°C event once every 3 yr (>33.3%) or more. All the area in this latter class is most likely planted with potato species other than *S. tuberosum*. This assumption is supported by Canahua and Aguilar (1992) and Huanco (1992) who estimate that about one-third of the total potato area on the Peruvian Altiplano, is planted with bitter potatoes, of which 60% are *S. juzepczukii*, and 33% are *S. curtilobum* (Canahua and Aguillar, 1992). It is also supported by Rea's (1992) estimate that 15% of the potato area in Bolivia is planted to bitter potatoes. On the Altiplano there are relatively more bitter potatoes than in most other zones in Bolivia.

Table 1 indicates that the introduction of potato cultivars with increased frost tolerance could strongly reduce frost damage. If frost tolerance in potato increases from -1 to -2°C, and damage only occurs at -3°C and lower, the percentage of the current potato area with a frost event less than once every 10 yr nearly doubles, increasing from 18 to 32%. With a further increase of tolerance to -3°C, there would be another 15% increase of the current potato area with a frost event less than once every 10 yr.

Discussion and Conclusion

Current frost risk in potato production is rather high, only 18% of the potato area has

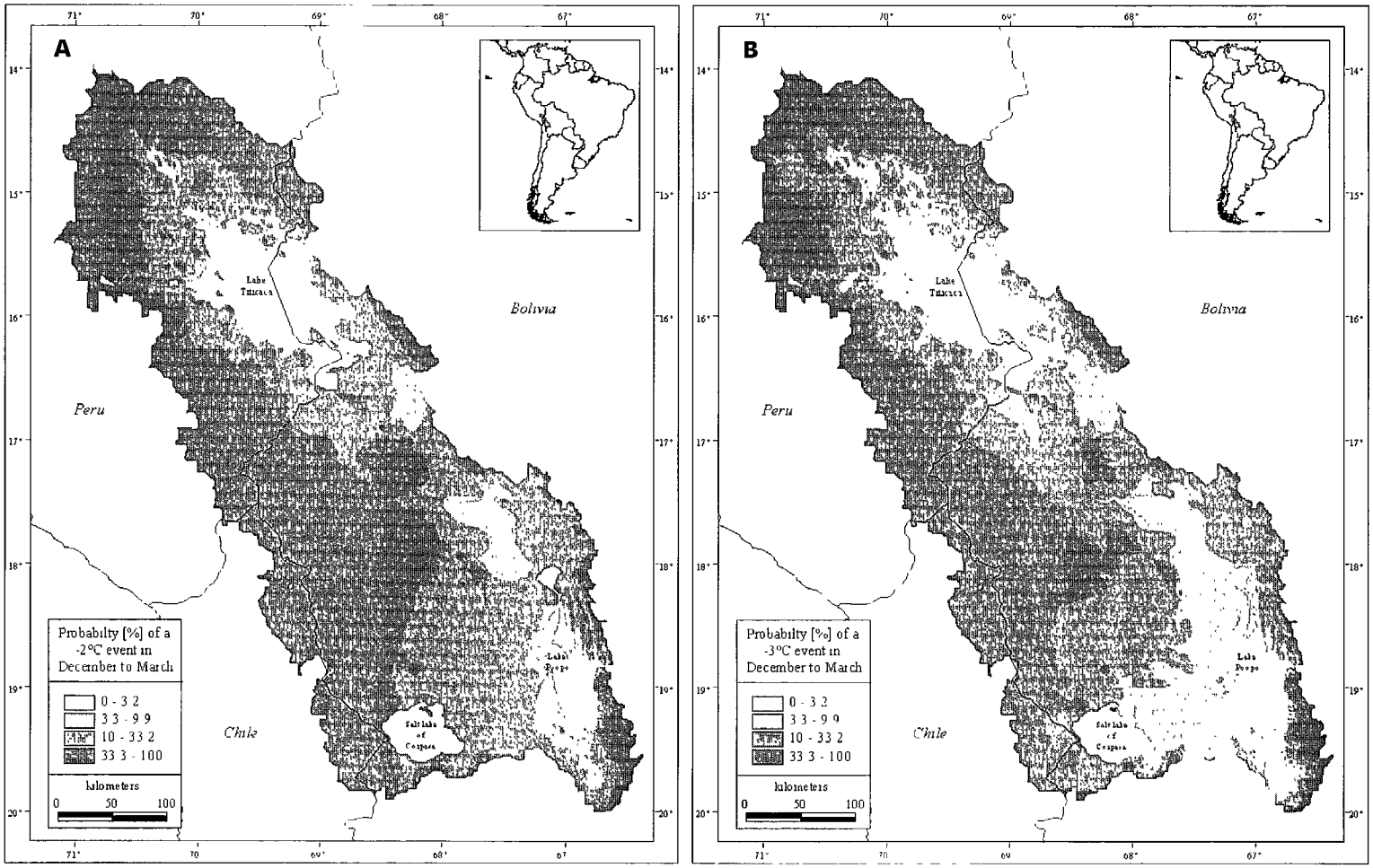

Figure 2. Probability of a -2°C (A) and a -3°C (B) event on the Altiplano between December and March.

Table 1. Distribution (%) of the potato area (63,000 ha) in the Altiplano over the extreme temperature probability classes (for the period December to March).

	Temperature (°C)					
Probability (% of yr)	0	-1	-2	-3	-4	-5
< 3.3	1	2	4	8	15	34
3.3-10	2	4	14	24	42	38
10-33.3	31	57	57	52	34	25
>33.3	66	36	25	16	9	3

a -2°C event once every 10 yr or less. That confirms the importance of the frost problem in potato production on the Altiplano. The introduction of potato cultivars with frost tolerance of -2°C could lead to a sharp decrease in frost risk and damage, and hence increased production. A further increase of tolerance to -3 or -4°C would have a similar effect. This assumes, however, having potatoes that not only resist these low extreme temperatures, but also grow well in the cold weather associated with these low absolute minimum temperatures.

Because farmers select favorable microclimates to plant potatoes, frost risk may have been overestimated. Nevertheless, the estimates may approach reality. Because of the presence of potato species more tolerant than *S. tuberosum*, and because other reports indicate similarly high frost risks, Gade (1975) distinguishes between the *effective* and the *absolute* limits of cultivation in the Andes. Beyond the effective limit, yields are unsatisfactory and crops are not important. Beyond the absolute limit, the crop will not grow or yield at all. In the Vilcanota Valley of Peru, Gade (1975) defined the effective limit, where hardy crops yielded satisfactorily in at least 60% of the years, as 3,910 m. Up to the absolute limit of 4,320 m, there were scattered fields with "pathetically low-yielding" crops, which were owned by pastoralists that do not primarily depend on crop harvests. Gade's 60% good years is close to the 33% bad years used in this paper. The results have even greater correspondence taking into account that this study considered only frost risk, ignoring other production risks such as drought or hail.

The introduction of new frost-tolerant potatoes could lead to an expansion of the potato-growing area. That could involve planting more potatoes in the current production zones or shifting toward new zones that could not be used before. With the exception of the shores of Lake Titicaca, however, the Altiplano is not densely populated and agriculture is not very intensive.

Land availability does not seem to be limiting in potato production. Instead of increasing area or shifting into new and cold areas, farmers would probably choose to increase production in the current production zones. That could make potato production more efficient and profitable. On the other hand, potential new production areas at high altitudes might be associated with better (not eroded) soils and higher precipitation. Hence, some expansion of potato area into the higher parts of the catchments might be expected. More in-depth knowledge of farmer strategies in relation to frost risk on the Altiplano is needed to predict their response to the introduction of new cultivars.

To analyze frost damage, we used the average frost risk from December to March. However, a frost event in January has a different effect on yield than one in March. This could be taken into account by using a computer model that simulates the effect of frost on potato yield using, for example, a daily time scale. Moxey (1991) followed this approach to estimate the benefit of non-ice nucleation active bacteria for frost protection of potato. A model that simulates growth, development, and response to frost stress of Bolivian potato cultivars is currently under development, and will be linked to the climate surfaces. That will allow a more refined zonation, risk estimation, and ex ante impact assessment of new frost-tolerant cultivars.

This study has focused on the potential impact of breeding for potatoes with increased frost tolerance, but ignored the frost tolerant species such as *S. juzepczukii* and *S. ajanhuiri*. With a few exceptions (Rea and Vacher, 1992; Tapia and Saravia, 1997), these species have not been the subject of scientific research. Whereas they are often said to be low yielding, Tapia and Saravia (1997) report yields of 37 t/ha for *S. juzepczukii* and 22 t/ha for *S. ajanhuiri*. These native species merit more basic and adaptive research, and need to be considered when designing strategies to diminish frost risk in potato production on the Altiplano.

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Simulating the Response of Potato to Applied Nitrogen

W. Bowen[1], H. Cabrera[2], V. Barrera[3], and G. Baigorria[4]

In potato (*Solanum tuberosum*) production, nitrogen (N) is applied more frequently and in greater amounts than any other nutrient. It is also the nutrient that most often limits yield. Without added N, growing plants often show N deficiency characterized by yellow leaves, stunted growth, and lower yields. Because it is an important input, N and factors affecting its availability have been the subject of much investigation (Harris, 1992). A common objective of many of those studies has been to develop N recommendation systems to assist growers in determining the amount of N needed and the best time to apply it. Knowledge of when and how much N to apply is essential, not only because N inputs have an economic cost but N in excess of that used by the crop may have an environmental cost. The amount of N needed for crop growth and its ultimate fate are important issues regardless of whether the N source is organic matter or mineral fertilizer.

An approach often used in field experiments for estimating the amount of N to apply to potato involves measuring yield response to increasing rates of N fertilizer. Yield response is quantified by fitting a mathematical equation to the data. This equation is then used together with economic information to investigate returns to investments in fertilizer N. Although this approach has proven useful for demonstrating the concept of diminishing returns, it is nothing more than a black-box approach, which offers limited information for deriving N recommendations in another year or at another site.

Nitrogen is a dynamic and mobile nutrient, hence its effect on crop production is rarely the same from year to year. At best, equations from variable N-rate experiments describe only historical relations in the data. As such they offer little insight into the processes that must be understood to manage N inputs appropriately.

More informative approaches for making N recommendations have followed from a better understanding of the processes that affect both crop N demand and soil N supply. That has led to N recommendations based on the simple principle that the amount of additional N to be applied can be estimated by knowing the crop N requirement and the potential soil N supply. The internal N needed to obtain a specific yield sets the crop N requirement. Soil N supply is set by the properties of the soil, particularly the soil organic matter (SOM) content and other properties that affect the extent and rate of microbial decomposition. Both also depend on the vagaries of weather. For high-yielding crops in most soils, the crop N requirement will exceed the soil N supply. It is the difference between these two that approximates the amount of supplemental N needed by a growing crop.

Generally, the amount of N fertilizer to apply is calculated by estimating the soil N supply, a target yield level, and an expected fertilizer efficiency; this last because not all applied N is normally recovered by the crop (Dahnke and Johnson, 1990). To estimate each of these components, measurements of one or more of the following variables may be needed: whole plant N content required to reach a target yield, mineral N released during soil incubation, total N content of the soil,

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2 INIA, Cajamarca, Peru.
3 INIAP, Quito, Ecuador.
4 CIP, Lima, Peru.

mineral N present in the soil profile at planting, and leaf N concentration or chlorophyll content at a specific growth stage. The relation between any of these variables and the benefit of added N is usually defined in field calibration studies. Because of site-specific effects, such studies need to be conducted across a broad range of soil-crop-climate conditions. There is, however, a practical limit to the number of soil-crop-climate conditions that can be included in field studies.

An additional tool now available for evaluating N management practices and for making N recommendations is one based on computer simulation. Using dynamic simulation techniques, scientists have been able to construct computer models capable of simulating many of the major processes that control N demand and supply. When assembled within the framework of comprehensive crop-growth models, their dynamic nature makes them valuable for exploring N management options across a theoretically unlimited number of cropping practices, soil types, and weather conditions.

The purpose of this study is to illustrate how we are using a potato growth model to better understand N dynamics in potato-based cropping systems. We stress, however, that simulation models are not a substitute for standard testing and monitoring of the N status in soils and plants. Rather, they are a tool for extending the value of such measurements by facilitating a systematic analysis of how plant, soil, weather, and management factors interact to affect N dynamics. In this study, we use the SUBSTOR potato model (Ritchie et al., 1995) to systematically analyze some of these factors to demonstrate how the model can be used to gain insight into N dynamics on a site-specific basis. We will also show results from model testing in Andean conditions. The version of SUBSTOR used in this study is that released with the Decision Support System for Agrotechnology Transfer (DSSAT v3) (Jones et al., 1998).

A Comprehensive Crop Growth Model

The SUBSTOR model provides a useful tool for analyzing the quantitative effect that controlled factors (e.g., management), uncontrolled factors (e.g., weather), and site-specific soil properties have on principal components of N balance. The model is comprehensive in that it simulates the major processes associated with crop N demand and soil N supply (Table 1). The model provides a balanced approach in the level of detail used to describe soil and

Table 1. Major processes that are simulated and environmental factors that affect those processes in the N submodel of SUBSTOR-Potato (DSSAT v3).

Process simulated	Main factors influencing process
Crop N demand	
Growth	Solar radiation, temperature
Development	Photoperiod, temperature
Soil N supply	
Mineralization/immobilization	Soil temperature, soil water, C:N ratio
Nitrification	Soil temperature, soil water, soil pH, NH_4^+ concentration
Denitrification	Soil temperature, soil water, soil pH, soil C
NO_3^- leaching	Drainage
Urea hydrolysis	Soil temperature, soil water, soil pH, soil C
Uptake	Soil water, inorganic N, crop demand, root length density

plant processes. All of the processes listed in Table 1 are simulated using a daily time step. Because it is comprehensive and dynamic, the model can be used to evaluate, on a site-specific basis, many alternative management practices against the uncertainties of weather. Simulation results, when based on reliable input data, can then provide critical information for defining the best N management practices from both an economic and environmental perspective.

We have used experimental data from Ecuador and Peru to first test the performance of SUBSTOR under Andean conditions (Figure 1). In Ecuador, Clavijo (1999) showed that the model accurately simulated the response of two cultivars to N fertilizer at two sites in Carchi. In Peru, Yauri (1997) showed that SUBSTOR realistically simulated the growth of two cultivars with and without irrigation at a site in Huancayo. A comparison of simulated and observed tuber yields from the Ecuador and Peru studies is shown in Figure 1. This limited testing shows that the model realistically simulated tuber yields that ranged from 16 to 56 t/ha due to differences in weather, soils, cultivars, and management. Further testing is underway as we continue to critically evaluate the performance of SUBSTOR and search for ways to improve it as both a research and management tool.

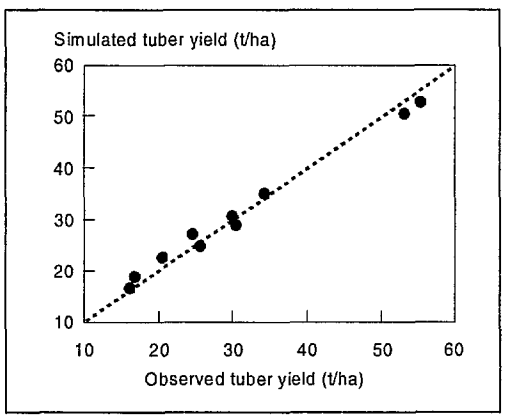

Figure 1. Relation between simulated and observed fresh weight of potato tubers for sites in Ecuador and Peru (dotted line is 1:1 line).

Components of a Systematic Analysis

A general approach for estimating the amount of N fertilizer (N_f) to apply to a crop may be based on the following calculation:

$$N_f = (N_y - N_s)/E_f$$

where N_y is crop N demand (the internal plant N required to attain the expected yield), N_s is the N supplied by the soil, and E_f is the expected efficiency or fraction of applied N the crop is expected to recover. This approach provides a useful framework for examining the main factors to be considered when managing N inputs. Within this framework, the N balance in agricultural fields can be characterized by defining three major components: N_y, N_s, and N_f. To optimize N management for a specific situation, quantitative estimates of each of these components are needed along with economic information.

Crop N demand

Crop N demand is the product of the expected yield and internal N requirement, which can be thought of as the minimum amount of plant N associated with maximum yield (Stanford and Legg, 1984). Although a growing crop may take up more than the minimum N needed, extra N (luxury consumption) does not usually result in any yield benefit. Therefore, to optimize N management and avoid its inefficient use, it is important to know the expected maximum yield and its associated internal N requirement. Maximum yield, however, is not a constant. For a single cultivar, maximum yield will vary from site to site and year to year due to the interaction of genetic traits with photoperiod, temperature, solar radiation, water, nutrient availability, and management. Many of these interactions can be captured in the SUBSTOR model.

To illustrate, Figure 2 shows how tuber yields responded differently to applied N when the SUBSTOR model was run using different weather years for a site in Huancayo, Peru. The cultivar simulated was Yungay, which was planted in mid-

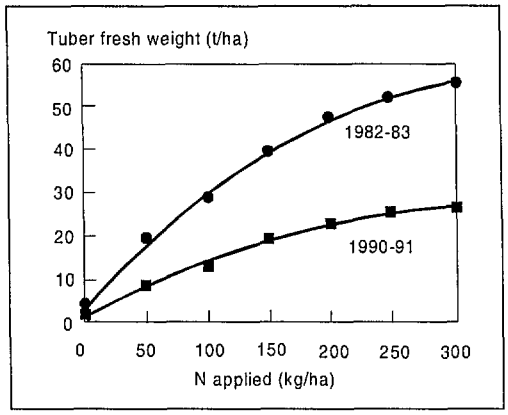

Figure 2. Simulated response of potato tuber fresh weight to applied N using daily weather data from 1982-83 or 1990-91 for a site in Huancayo, Peru.

November and harvested in early April. Whereas fresh yields reached a maximum of 55 t/ha using daily weather from 1982-83, the same amount of N in 1990-91 produced a maximum yield of only 26 t/ha. The difference in N response between seasons was attributed mostly to a less favorable distribution of rainfall during 1990-91. The simulation showed the plants suffered a significant water deficit during tuber bulking. Although yield levels varied for the two seasons, the internal N requirement remained constant at about 16 g N/kg of total dry matter (DM) (tops plus tubers), which is within the range reported by Vos (1995) for several field experiments. The simulated removal of N in fresh tubers was about 2.8 kg N/t fresh weight in each season, also within the range reported for real data by Harris (1992).

Simulation can be used as well to estimate the time course or N uptake pattern of a growing crop. With output provided on a daily basis, the model makes it possible to define the period of greatest N demand. Such information can then be used to examine how management might improve the synchrony between crop N demand and N supply. For example, the economic and yield impact of split applications of N fertilizer could be easily studied in simulations designed to vary the amount and timing of N applications.

Soil N supply

Nitrogen supplied by the soil comes mostly from two sources: 1) mineralization of soil organic N during the growing season, and 2) mineral N initially present in the soil profile at planting. Both sources should be considered when estimating the amount of supplemental N needed by a growing crop. However, the importance of initial mineral N tends to diminish in high rainfall environments where significant leaching can occur.

Since the mineralization of soil organic N is a biological process, the amount of N made available depends primarily on the level of microbial activity and the amount of carbon (C) substrate. For most mineral soils, the C:N ratio in SOM is fairly constant at 10. That ratio favors a net release of N to available mineral forms unless OM is added with C:N ratios greater than 25. At a C:N >25, there is usually a loss of plant available N as it becomes tied up through net immobilization.

The amount of mineral N present in the soil profile at planting (initial mineral N) often has a substantial impact on the need for supplemental N, particularly in less humid environments. Initial mineral N usually varies across sites and years, with the amount largely determined by management and growth of the previous crop and the residual N left from earlier applications. If rainfall is not excessive, much of the initial mineral N can remain available to a crop throughout the growing season.

The process descriptions in SUBSTOR enable capturing the interaction of these sources of available plant N with crop N demand for innumerable combinations of soil type, weather, cultivar, and management. For example, simulation could be used to examine how soil N supply might vary across years for different quantities of SOM and mineral N present at planting. Moreover, a simulation study like the one

used to derive Figure 2 would obtain somewhat different responses if SOM or initial mineral N inputs were varied.

Sources of supplemental N

In SUBSTOR, supplemental N can be added as a mineral fertilizer or as a plant residue such as green manure (GM). Algorithms dealing with the transformation of animal manure have not yet been included, although efforts to do so are underway. Nitrogen management practices that can be examined with the model include the effect of varying N rates, time of application, placement depth, and fertilizer source. These practices can be studied for their effect not only on tuber yield, but also on nitrate leaching or economic returns. Such studies can be simulated for a single growing season, or across many seasons, to quantify the impact of weather variability and its associated risk.

A simulation example that illustrates how the model might be used to estimate the yield benefit of alternative N management options is shown in Figure 3. In this example, SUBSTOR was run for 19 seasons using daily weather data from Huancayo.

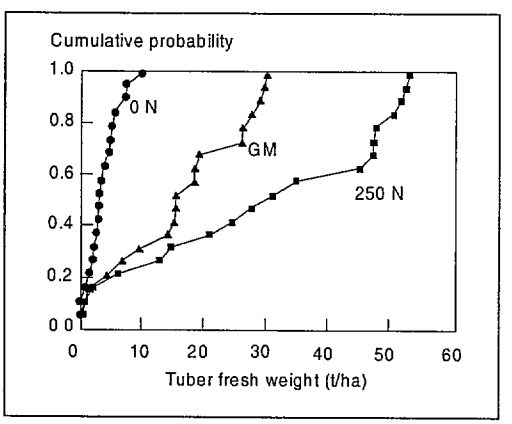

Figure 3. The cumulative probability distributions for potato tuber fresh weight resulting from simulations made across 19 years of weather from Huancayo, Peru. The N management treatments were no applied N (0 N), green manure incorporated (GM), or urea applied at 250 kg N/ha (250 N).

Once again, the cultivar simulated each season was Yungay, planted in mid-November and harvested in early April. The N management options were no external source of applied N (0 N), a legume green manure (GM) (4 t DM/ha, N content 2.5%) incorporated just before planting, and 250 kg N/ha applied as urea in two, equal split applications. The simulated tuber yields for the 19 seasons are plotted in Figure 3 as cumulative probability distributions. They clearly show the superiority of the urea treatment in increasing yield, but they also demonstrate the risk of low yields despite heavy N application. For example, because of poor rainfall distribution and subsequent drought stress, the probability of obtaining essentially no response to applied N would be about 15%, or about 1 yr in 7. But the probability of obtaining a significant response to N is much greater, with yields of 30-50 t/ha expected about 50% of the time.

With this type of information provided on a site-specific basis, decisions regarding N management can be made based on an improved awareness of both the potential and limitations of a given environment. To make a simulation even more useful, model inputs and yields could be combined with actual price and cost data to obtain similar distributions for net returns. That would better define the economic risk, which is of more interest to a farmer.

Conclusions

Nitrogen management can be improved through the insight provided by comprehensive crop simulation models such as SUBSTOR. As a continually evolving tool, such models have the potential to help researchers and farmers better understand how soil, crop, weather, and management factors interact to affect crop N demand, soil N supply, and fertilizer use efficiency on a site-specific basis. Any number of management scenarios can be examined and compared for their impact, not only on economic returns but also on the potential

for excessive leaching of nitrates. Economic and environmental (nitrate leaching) risks due to uncertain weather can also be quantified.

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Selecting Optimum Ranges of Technological Alternatives by Using Response Surface Designs in Systems Analysis

C. León-Velarde[1] and R.A. Quiroz[2]

The search for technologies that increase the productivity of a farming system or a component is one of the main objectives of agricultural researchers. The researcher is usually interested in finding maximums, i.e., highest yield, highest net income, etc. Usually, the bioeconomic outcome is dependent on several intrinsically-interrelated factors. The fact that the explanatory or independent factors are related limits the usefulness of a one-factor-at-a-time strategy to find the levels at which the dependent variable attains the maximum (Box et al., 1978). A joint, functional dependency of the dependent variable on the independent factors is thus desirable.

If all the independent factors involved represent quantitative variables, one can describe the behavior of the dependent variable as a function of the levels of the independent variables. This function is called the response surface (Cochran and Cox, 1957). When the mathematical form of the function is unknown, it may be satisfactorily approximated, within the experimental region, by a polynomial in the independent variables (Brown and Rothery, 1993). First- and second-order designs can be used to find the level at which each of the independent variables should be set to maximize the response surface (Box et al., 1978; Cochran and Cox, 1957; Leon-Velarde and Quiroz, 1994; Montgomery, 1984). In spite of its usefulness, this approach is seldom used in agriculture because it is costly and complex to implement (Wilton et al., 1974).

Systems analysis applied to agricultural field research constitutes a complementary tool to deal with complex issues. The use of simulation models enables the comparison of hypothetical situations in agricultural production systems, which are otherwise difficult to assess in the real world. A wide range of alternatives can be evaluated with simulation models designed, constructed, and validated to simulate a particular system. Despite this flexibility, the common trend in the modeling literature is to use a one-factor-at-a-time strategy (Kropff et al., 1997; Teng et al., 1997). By combining simulation models and factorial designs, response surfaces can be generated and analyzed. Critical factors and levels can be identified and ex-ante appraisal of technologies may be used to screen for most appropriate recommendations to farmers.

This paper describes how central composite, rotatable designs can be used to plan simulation studies to generate response surfaces and to determine optimum levels of the variables studied. In addition to the description of the method, an example to illustrate how to generate and analyze a simulated response surface is given.

Materials and Methods

Response surface method

The response surface method (RSM) can be represented mathematically as follows. Let Y represent the response variable and X_i the continuous independent variables that influence Y. Suppose the researcher wishes

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to find the levels of each variable at which Y is maximized. We may write the observed response as a function of X_i as shown:

$$Y = f(X_1, X_2, \ldots, X_n) + \varepsilon$$

The expected response $E(Y) = f(X_1, X_2, \ldots, X_n)$ is called the response surface. A two-dimensional graph of the response surface could be drawn on two axes, leading to contours of constant values of $E(Y)$.

In most RSM problems, the form of the relation between the response and the independent variables is unknown. Thus, the first step in RSM is to find a suitable approximation for the true functional relation between Y and X_i. Usually, a low-order polynomial can be used to describe this relation, particularly in the region described by the levels of the independent variables studied (Montgomery, 1984; Brown and Rothery, 1993).

The efficiency of the response surface fit might be improved by the use of appropriate experimental designs. Suited designs minimize the variance of the regression coefficients. First-order orthogonal designs are the simplest ones. A first-order design is orthogonal if all the off-diagonal elements of the $X'X$ matrix = 0. The class of orthogonal first-order designs includes the 2^k factorial fractions of the 2^k series in which main effects are not related to each other (Box et al., 1978; Cochran and Cox, 1957; Montgomery, 1984). The 2^k design does not afford an estimation of the experimental error unless some runs are repeated. A common method of including replication is to augment with several observations at the center (when $X_i = 0$).

The most commonly used second-order response surface design is the class of *rotatable* designs. The analysis of the fitted second-order response surface is often called the canonical analysis. The term rotatable indicates that the variance of the predicted response at some point x is a function only of the distance of the point from the design center, and not a function of the direction (Montgomery, 1984; John and Quenoville, 1977). Another property of this design is that the variance of the estimates is unchanged when the design is rotated about the center, hence the name rotatable designs.

Among the rotatable designs, the most widely used is the *central composite* design. This design consists of 2^k factorial, augmented by 2k axial points and n_0 center points (or $2^k + 2k + n_0$, where n_0 is the number of times the central point is repeated). A central composite design is made rotatable by the choice of a value "a". The value of "a" depends on the number of points in the factorial portion of the design ($P = 2^k$), i.e., $a = P^{1/4}$ (For instance, if $k = 2$ then $P = 2^k = 4$ and $a = 1.414$). The efficiency of the design, estimated as the ratio between the number of parameters to be estimated and the number of treatments, maximizes when $k = 3$, i.e., 0.67 (10 parameters and 15 treatments).

Alpaca production in the altiplano: An example

In the dry puna of the Andean Altiplano, a semiarid, tropical highland, native pastures are the only feed resource for alpaca (*Lama pacus*). The climatic variations, mainly precipitation and low temperatures, substantially affect the growth and digestibility of the grasslands. Due to heavy stocking rates, the pastures tend to be degraded, which adversely affects fiber and meat production. A physical experiment to assess the characteristics of all possible combinations of the factors in an optimum grazing management system is impossible. The cost and the time required to conduct it would be unreasonable.

A systems research approach, based on simulation, was used to address the problem (1989-1991). After a good characterization of the system, an alpaca simulation model was designed, constructed, and validated (Quiroz et al., 1990; Arce et al., 1994). This computerized model was then used to assess the levels at which pasture

growth rate (GR), pasture digestibility (D) and the stocking rate (SR) would maximize gross income. The stocking rate directly affects the pasture growth rate, and the two together modify digestibility.

A composite central, rotatable design was used to simulate an experiment to estimate the expected outcomes of changes in the levels of the independent variables deemed most relevant. The factors (X_i) included were stocking rate, pasture growth rate, and pasture digestibility. The central point was selected to mimic the management levels of the variables used by farmers (Quiroz et al., 1991) The response variables (Y_i) were yearly fiber and meat production and the annual gross income of the farm from alpaca production alone. The simulation time for each scenario was 10 yr; the average response over the period was used.

The second step consisted of simulating the time-course of the implementation of the optimal conditions encountered and the expected changes in gross income over time. A logistic model was fitted to the data to estimate the parameters describing the time changes in gross income. This exercise was of particular importance, first to assess the sustainability of the proposed changes, and second to define the milestones needed to monitor progress.

The most salient features of the grazing system simulated are summarized below (Quiroz et al., 1991).

- Type of pasture: bofedal (spring fed year-round pasture) and rainfed native pasture in the dry puna of the Altiplano.
- Surface: 80 ha of native pasture divided into 70 ha of rainfed pasture and 10 ha of bofedal.
- Initial pasture availability: rainfed pasture is 1 t dry matter (DM)/ha; bofedal is 1.5 t DM/ha.
- Grazing pattern: 3 mo on rainfed pasture (January, February, March); 9 mo in bofedal (April to December).
- Residual pasture availability: rainfed is 0.5 t DM/ha per mo; bofedal is 0.7 t DM/ha.
- The management operations were: mating in January, birth of offspring in December, weaning in September of the second year, shearing every year. Sale of products was assumed to be once a year.

The resources of land, number of divisions (paddocks), herd composition, mating, weaning, and mortality and birth rates were held constant.

Table 1 shows the variables and the levels for each variable assigned to each treatment. It also identifies the levels assigned to the factorial, axial, and central parts of the composite, rotatable design described above. The 15 treatments were coded for the respective analysis of production variables (fiber and meat). Five levels of each factor were tested in the composite central, rotatable design ($2^3 + 2(3) + 1(6)$). The central point was repeated six times. The biological response variables, meat production and fiber production, were multiplied by their farmgate prices to estimate gross income.

The analysis of the bioeconomic response was programmed in SAS (SAS, 1988) to generate the respective response surfaces.

Results and Discussion

The simulation process provided the biological information for each scenario analyzed. All the factors studied significantly influenced the response variables ($P < 0.01$) and showed a significant quadratic effect ($P < 0.01$). The coefficients of the model for fiber, meat, and gross income are shown in Table 2.

The combination of the levels of the variables studied that maximized gross income (referred to as optimum) used: stocking rate is 0.54 head/ha, pasture

Table 1. Variables, coded values, and treatments used for the application of the response surface method in a simulated study of an alpaca production system in the dry puna of the Altiplano, Peru, 1991.

Variables	Code				
	-1.682	-1.00	0.00	1.00	1.682
X_1: stocking rate (SR)	0.56	0.70	0.90	1.10	1.24
X_2: growth rate[a] (GR)	6.233	6.913	7.913	8.913	9.533
X_3: digestibility (D)[a]	62.4	63.25	65.2	67.25	68.6

Treatments: 1–8, factorial part; 9–14, axial part; 15, central part repeated six times	Code			SR (head/ha)	GR (kg DM/ha per d)	D (%)
1	-1	-1	-1	0.7	6.9	63.2
2	-1	-1	1	0.7	6.9	67.2
3	-1	1	-1	0.7	8.9	63.2
4	-1	1	1	0.7	8.9	67.2
5	1	-1	-1	1.1	6.9	63.2
6	1	-1	1	1.1	6.9	66.2
7	1	1	-1	1.1	8.9	63.2
8	1	1	1	1.1	8.9	67.2
9	-1.682	0	0	0.56	7.9	65.2
10	1.682	0	0	1.24	7.9	65.2
11	0	-1.682	0	0.9	6.2	65.2
12	0	1.682	0	0.9	9.5	65.2
13	0	0	-1.682	0.9	7.9	62.4
14	0	0	1.682	0.9	7.9	68.6
15[a]	0	0	0	0.9	7.9	65.2

[a] Weighted values correspond to pasture use, 3 mo for rainfed pasture and for 9 mo bofedal. The ranges of growth rates for rainfed pasture is from 0.57 kg to 3.93 kg DM/ha day, and for bofedal from 8.12 to 11.40 kg DM/ha day. The digestibility of rainfed ranged from 53.6 to 60.4% and of bofedal, 67.4 to 71.4%.

growth rate is 8.14 kg DM/ha per day, and digestibility is 65.9%. Since the maximum is just a point, we estimated a 95% confidence interval of the maximum and called it optimum range. If the levels of the variables are maintained within the confidence interval, the expected optimum range for gross income varied from US$2,700 to $3,000/yr.

Farmers tend to maintain stocking rates between 0.6 and 0.9 head/ha. That is understandable because they mainly market the fiber and manage the system to produce as much fiber as possible while augmenting their animal stock. If we were to maximize the objective function for fiber production, we could say farmers are already maximizing their production function. As long as the perception is that fiber is the most important product maintained, there is little hope for the adoption of technologies to improve pasture management.

Table 2. Regression coefficients to generate the response surface and variable levels that maximize the surface[a].

	Regression coefficients		
Parameters	Fiber (kg)	Meat (kg)	Income (US$)
Intercept (b_0)	167.0	2934.7	2123.30
Stocking rate (SR)	-51.6	-1178.2	-818.90
Growth rate (GR)	15.3	175.3	138.40
Digestibility (D)	3.8	59.4	43.90
SR x SR	-20.3	-324.3	-238.60
SR x GR	-4.4	17.0	0.60
GR x GR	-8.8	-392.2	-254.50
D x SR	-0.5	-33.3	-21.00
D x GR	0.8	-13.2	-6.10
D x D	-7.2	-152.9	-107.20
R^2	0.68	0.76	0.76

	Variable levels that optimize the response and maximum response obtained.		
Variable	Fiber (kg)	Meat (kg)	Income (US$)
SR	0.62	0.52	0.54
GR	8.98	8.05	8.14
D	65.93	65.96	65.93
Maximum obtained	213.70	4,040.80	2,858.90

[a] Regression coefficients according to: $$\hat{Y} = \hat{\beta}_o + \sum_{i=1}^{k} \hat{\beta}_i X_i + \sum_{i=1}^{k} \beta_{ii} X_i^2 + \sum_i \sum_j \beta_{ij} X_i X_j + \varepsilon$$

The system must be seen as a multipurpose one, instead of just a fiber-producing system. When the stock, the fiber, and the meat sold are valued, the figure changes. The findings suggest that there are different technological opportunities for increasing farmers' income that must be explored. It is clear that the fiber and meat markets should be encouraged. Recommendations in this regard are already being tested in Bolivia by the Regional Project on South American Camelids (International Fund for Agricultural Development and Instituto Interamericano de Cooperacion para la Agricultura) and in Peru by Centro de Investigacion en Recursos Naturales y el Medio Ambiente, a local nongovernmental organization.

The levels of digestibility and pasture growth rate that maximized the gross income were a little higher than the existing conditions reflected in the central treatment. Therefore, the main factor requiring change to obtain the expected maximum income is stocking rate. This needs to be worked out in relation to birth rate and mortalities.

An example of a 3-D response surface is presented in Figure 1. Shown are changes in gross income when digestibility is

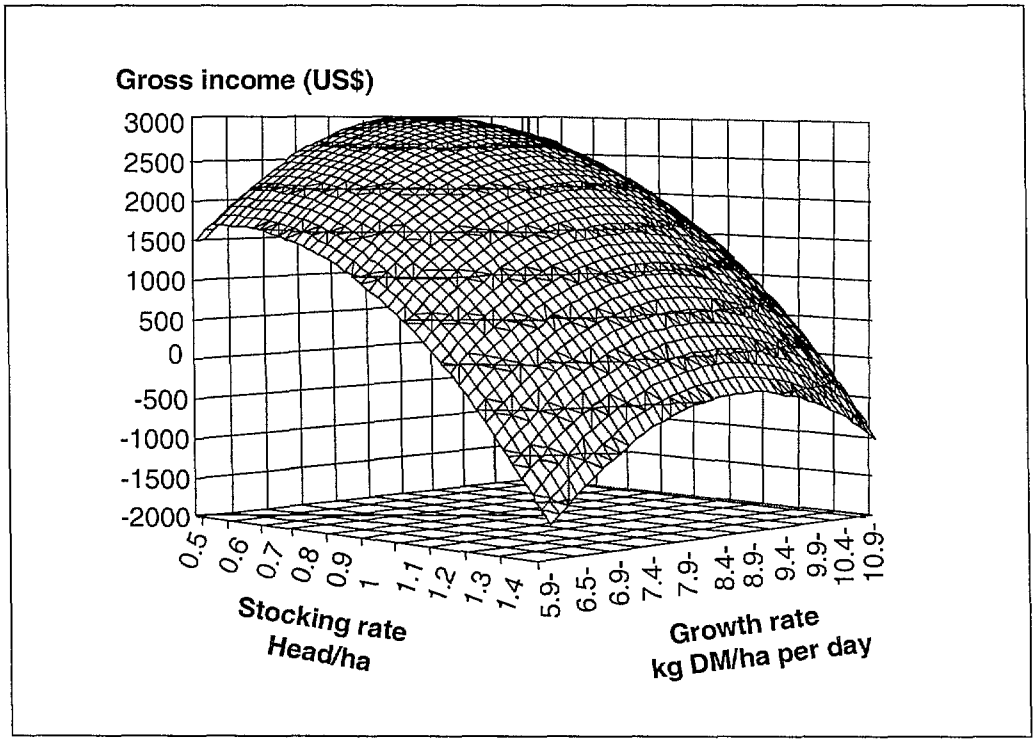

Figure 1. Response surface describing the simulated gross income of an alpaca production system as a function of changes in stocking rate and pasture growth rate at 65% pasture digestibility.

maintained constant at 65% and levels of stocking rate and pasture growth rate vary. Changes in both stocking rate and pasture growth rate are extremely sensitive. It is important to show that when the stocking rate is greater than 0.9 head/ha, income decreases sharply. As a matter of fact, stocking rates greater than 1 head/ha make the system collapse in 5-7 yr (Arce et al., 1994).

Figure 2 depicts an attempt to quantify the path of implementation of the recommended management options to maximize gross income. Three phases are identified: 1) existing, 2) adaptation, and 3) stable (León-Velarde and Quiroz, 1994). The existing phase has low productivity and an income level that appears to have been stable for many years. The adaptation phase is one in which technical changes take place. The stable phase (resilient) is one of higher production level quantified by the asymptotic value in the logistic model. According to these new sets of simulations in time, with optimum management practices the gross income of the system can reach as high as US$3,900/farm per year. It will take from 8 to 10 yr to reach the asymptotic income.

Conclusions

The paper shows how systems analysis and composite central, rotatable designs can be jointly used in agricultural systems to search for optimum ranges of technological alternatives. Our illustration was an alpaca production system. But the principle applies to any condition in agricultural research where a stochastic systems analysis tool such as a validated simulation model exists.

Regarding the alpaca system, the results showed that existing levels of income can be substantially increased. Implementing such changes, however, could take up to a decade. The simulation also showed that in

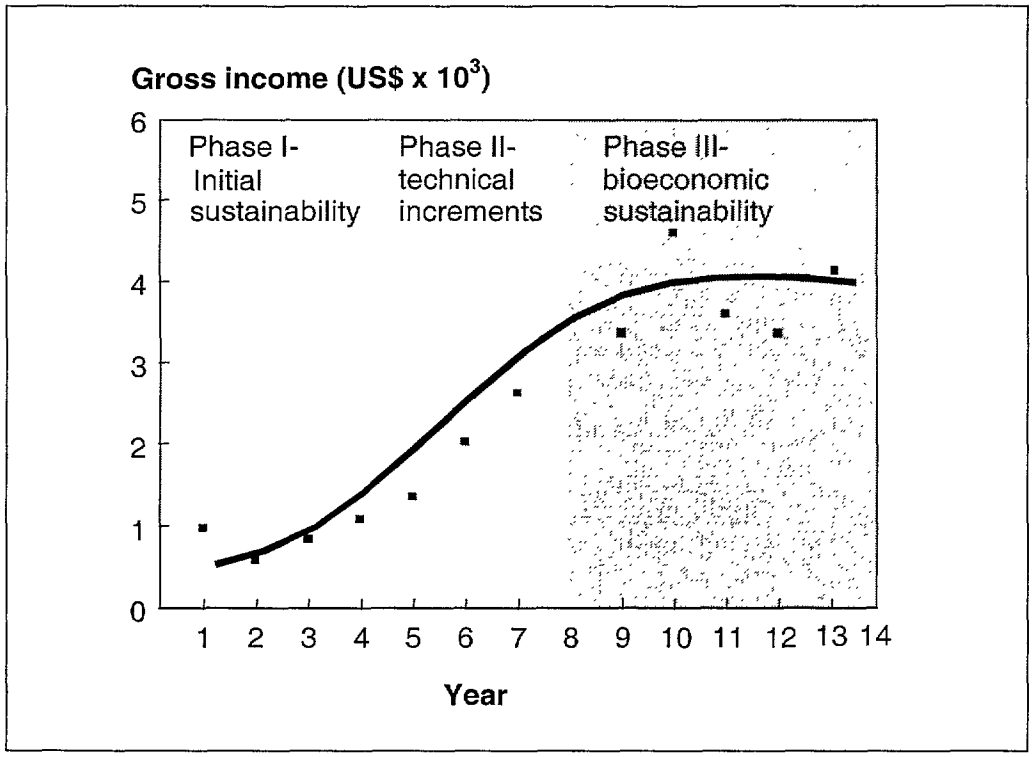

Figure 2. Simulated yearly gross income increase when the practices that maximize incomes are implemented in the alpaca system.

the medium- to long-term, the additional income generated with the changes at the farm level might be sustained.

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Mapping Aquatic and Semiarid Vegetation in the Altiplano Using Multichannel Radar Imagery

R. Quiroz[1] and S. Saatchi[2]

Remote sensing (RS) provides our first opportunity to inventory the surface resources of the earth in a systematic, repetitive manner. Remote sensing methods are becoming increasingly important for mapping land use and land cover. Some of the reasons for the increased use of RS methods are (Sabins, 1997):

- Large areas can be imaged quickly and repetitively.
- Images can be acquired with a spatial resolution that matches the degree of detail required for the survey.
- RS images eliminate the problems of surface access that often hamper ground surveys.
- Images provide a perspective that is lacking in ground surveys.
- Image interpretation is faster and less expensive than conducting ground surveys.
- Images provide an objective, permanent data set that may be interpreted for a wide range of specific land uses and land covers such as forestry, agriculture, and urban growth.

In the last 3 years, CIP has been using RS to map land use/land cover in selected research sites in the Andes. One of these is the high plateau or Altiplano at an elevation of more than 3,600 m. It is made up of a series of plains, highlands, and isolated hills extending from about 14° S latitude in Peru to 22° S latitude in Bolivia.

Fine- and coarse-resolution optical imagery, such as Landsat-Thematic Mapper and the Advanced Very High Resolution Radiometer (AVHRR), is being used to elaborate land use maps and to monitor land use/land cover changes in the Altiplano. Methods used are described elsewhere (Townshend et al., 1991; Defries and Townshend, 1994; Smith et al., 1990). Optical remote sensing in cropping areas of the Altiplano has produced various results, particularly during the cropping season. Several reasons contribute to this lack of accuracy, the most important being: (1) the area is continuously covered with clouds during the cropping period, which coincides with the rainy season; (2) the small size of the crop plots combined with the rotation pattern of crops and pasture generates large variability over small areas; and, (3) the similarity in spectral attributes (e.g., canopy architecture) of the land cover types. Some of the limitations for the successful use of optical remote sensing in the Altiplano can be circumvented by spaceborne radar data. Radar is less affected by clouds and can penetrate the vegetation layer (Saatchi, 1996; Saatchi et al., 1997).

The objective of this paper is to demonstrate the potential of spaceborne polarimetric radar in mapping land cover and land use in the Altiplano. The paper describes the most important land cover types in the cropping area of the Altiplano, the aquatic vegetation in Lake Titicaca, and the application of a maximum likelihood Bayesian procedure to classify land cover types with canopy similarities.

Material and Methods

Land cover types

The three categories of land cover types studied were aquatic vegetation, land

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vegetation, and villages. The multilevel classification system based on remote sensing (Anderson et al., 1976; Sabins, 1997) was used to select the classes. A more detailed description of aquatic and land vegetation follows.

Aquatic vegetation. Aquatic vegetation is composed of plankton and macrophytes. Within the macrophytes, there are about 15 species. The most important ones are the llachu (*Elodea potamogeton, Myriophyllum elatinoides*) and the totora (*Schoenoplectus tatora*). Macrophytes, particularly llachu and totora, occupy the shallow sector of Lake Titicaca up to 15 m deep (Collot, 1982). Llachu and totora constitute the best quality forage available to feed milk/beef cattle in the zone, with digestibility above 65% and protein contents above 10% (Quiroz et al., 1997). Totora is also used for roofing and for making reed boats. The association of llachu and totora is also of crucial importance for the subsistence of native fishes and for nesting birds. In the last 50 yr, the area of llachu and totora has been reduced by more than 50% (PELT, 1993).

Land vegetation. The agricultural zone includes potato, barley, oat, alfalfa, and quinoa, all cultivated in small plots. The crop rotation begins with potato, followed by any of the cereal crops for the next 2 or 3 yr.

Practically the entire Altiplano is a natural grassland, varying according to climate and soil. It is richest in forage in marshy areas, which yield more than 2.5 t dry matter (DM)/ha per year. The productivity of meadows, where grasses predominate, ranges from 1 to 1.6 t DM/ha. On some types of scrubland, however, production drops to between 130 and 210 kg DM/ha. The productivity of scrub or a grass-and-shrub meadow is also low, 150–210 kg DM/ha. Consequently, animal-carrying capacity varies greatly.

Grasslands are composed of different associations of plant species. They vary in size, density, growth habit, and canopy architecture according to precipitation, soil type, and altitude, among other factors.

Mixed rangeland is presented in patches all over the study area. It is an intermixture of grassland with shrub and brushland, and in some instances scattered trees. The most abundant tree is eucalyptus. Eucalyptus trees, with their thin trunks and sparse canopy, resemble shrubs more than forest. Other types of vegetation in this class include *Polylepis* sp. (queñoa), *Budleia coriacea* (kisuara), *Parasthrephya* sp., and *Baccharis sp.* (tola). In zones near the lake, yellow or inland totora is also considered as mixed rangeland vegetation.

Bofedal describes a spring fed, year-round pasture, which is characterized by a rich flora of good feed quality vital for the production of camelids. Since bofedales are the only source of year-round pasture, they are usually heavily grazed. Another peculiarity of bofedales is the roughness of the terrain. It results from soil erosion if the water is not managed correctly, trampling by the animals, and the occurrence of patches of grasses, particularly in seasonal bofedales.

Classification method

The quantitative analysis of the image was done through a supervised classification. The sequential steps are summarized below.

1. Definition of the eight land covers into which the image was to be segmented: water, llachu, totora, crops/pasture, grasslands, mixed rangeland, bofedal, and villages.
2. Selection of 25 windows of 3 x 3 pixels (or training sites) for each of the 8 land cover types listed above. The training sites were chosen on the basis of visual interpretation of the image, aided by a good knowledge of the area, plus field data.
3. Use of the training data to estimate the parameters of the classifier algorithm, and to assess the accuracy of the classifi-

cation of the automated process over the entire image.

4. Selection of another set of 25 windows, each 3 x 3 pixels, for each land cover to validate the estimated parameters (validation sites).
5. Label or classify every pixel in the image into one of the eight land cover types.
6. Produce a thematic map that summarizes the results of the classification.

A Bayesian maximum likelihood procedure was used for the automated classification procedure (Richards, 1993). Equations 1 through 4 (Table 1) describe the decision rule applied for the classification (Rao, 1973, Rignot and Chellappa, 1993). With equation 1, the pairwise squared distances between land cover types (classes) were estimated. A discriminant linear function was then calculated for each class (equation 2). Every pixel was then referenced with respect to the centroid of each class (equation 3), and then classified using the probability that a pixel X belongs to a particular class (equation 4).

The classification accuracy was calculated as the proportion of pixels correctly classified in the validation sites with the discriminant function developed for the training sites. The automated procedure was programmed in IDL (Interactive Data Language Research Systems, Inc.) where the prior probability was calculated as the number of pixels in each class of the training class over the total number of pixels in the sample.

Remote sensing scientists have access to three commercial radar satellites JERS-1 (L-HH), ERS-1 & 2 (C-VV), or RADARSAT (C-HH). (JERS, Japanese Earth Resource Satellite; ERS, Earth Resource Satellite, European Space Agency; RADARSAT, Synthetic Aperture RADAR on board a Canadian satellite.) The expected classifications with JERS-1 or RADARSAT were simulated with the corresponding channels and polarizations obtained from SIR-C data (L-HH, and C-HH).

Remote sensing data

During April and October 1994, a polarimetric shuttle imaging radar—L-, C-, and X-bands—synthetic aperture radar system (SIR-C/X-SAR) was flown on the space shuttle Endeavor during two, 10-d missions. During both missions, shuttle radar collected data over various regions in South America for deforestation, land use, biodiversity, and flooding. Data acquired in April 1994 over Lake Titicaca between Huarina and Jesus de Machaca, La Paz, Bolivia, was used for this study.

The images used in this paper are taken from orbit 110.5, with 48.1 degrees incidence angle, in multiple wavelengths (L-band, 24.0 cm; C-band, 6.0 cm) in a dual polarization mode: like-polarized (HH) and cross-polarized (HV). The image size is 32 km in range (swath) and 107 km in azimuth. The nominal resolution of the data at the 20 MHz bandwidth is approximately 12.5 m.

The images were further resampled to 25 m resolution to reduce speckle noise. The imageries were not corrected for topographic effect because a high-resolution, digital elevation model (DEM) required was not available.

Results and Discussion

Table 2 shows the backscattering coefficients in the four channels for all land cover types (Figure 1). Table 3 summarizes the classification. The main diagonal shows the percentage of pixels correctly classified and the misclassifications are shown in the off diagonal. The overall accuracy for the validation sites, as a sample of the entire image, was 88%. This is a low error rate (12%) considering the similarities of the land cover types being discriminated. The accuracy was further confirmed in the field by visually inspecting a large portion of the area mapped.

Aquatic plants were well discriminated from each other (Table 3). Twelve percent of

Table 1. Maximum likelihood decision rule for classification.

Equation 1.

$$D^2_{(i/j)} = (\bar{x}_i - \bar{x}_j)^t * \Gamma^{-1} * (\bar{x}_i - \bar{x}_j) - 2 * Ln\text{Prior}_j$$

Equation 2.

$$\text{Constant} = -0.5 * x_j^{\,t} * \Gamma^{-1} * x_j + Ln\text{Prior}_j$$

$$\text{Coefficient vector} = \Gamma^{-1} * x_j$$

Equation 3.

$$D^2{}_i(x) = (x - x_j)^t * \Gamma^{-1} * (x - x_j) - 2 * Ln\text{Prior}_j$$

Equation 4.

$$\Pr(j/x) = \exp^{(-0.5 * D_j^2(x))} \Big/ \sum_k \exp^{(-0.5 * D_k^2(x))}$$

Where,

$D^2_{(i/j)}$ = squared distance between land-covers i and j

x_i = mean value of class i

x_j = mean value of class j

Γ = variance covariance matrix

Prior_j = prior probability for class j

Ln = natural logorithm

Pr (j/x) = probability that a pixel at a location X belongs to a class j

$D_j^2(x)$ = distance between the pixel at location X and the centroid of the class j

exp = exponential function

k = a class where the observation in the pixel at location X is not included in the calculation

totora pixels were misclassified as crops. Totora plants are expected to have backscattering attributes similar to annual crops as they mature. A multitemporal spectral analysis is then required to clearly differentiate them from crops.

The backscattering of the crop/pasture class was lower than expected because the image used was taken in mid-April, which coincides with harvest. This implies that the backscattering was mainly the response to the crop residue remaining in the fields and the alfalfa fields, which were still green. Crop residues can contain 20-30% water, depending on rains. The main misclassification of the crop/pasture class was as totora.

Both the training and the testing areas for grasslands were selected in the pastoral systems of Jesus de Machaca. This zone is

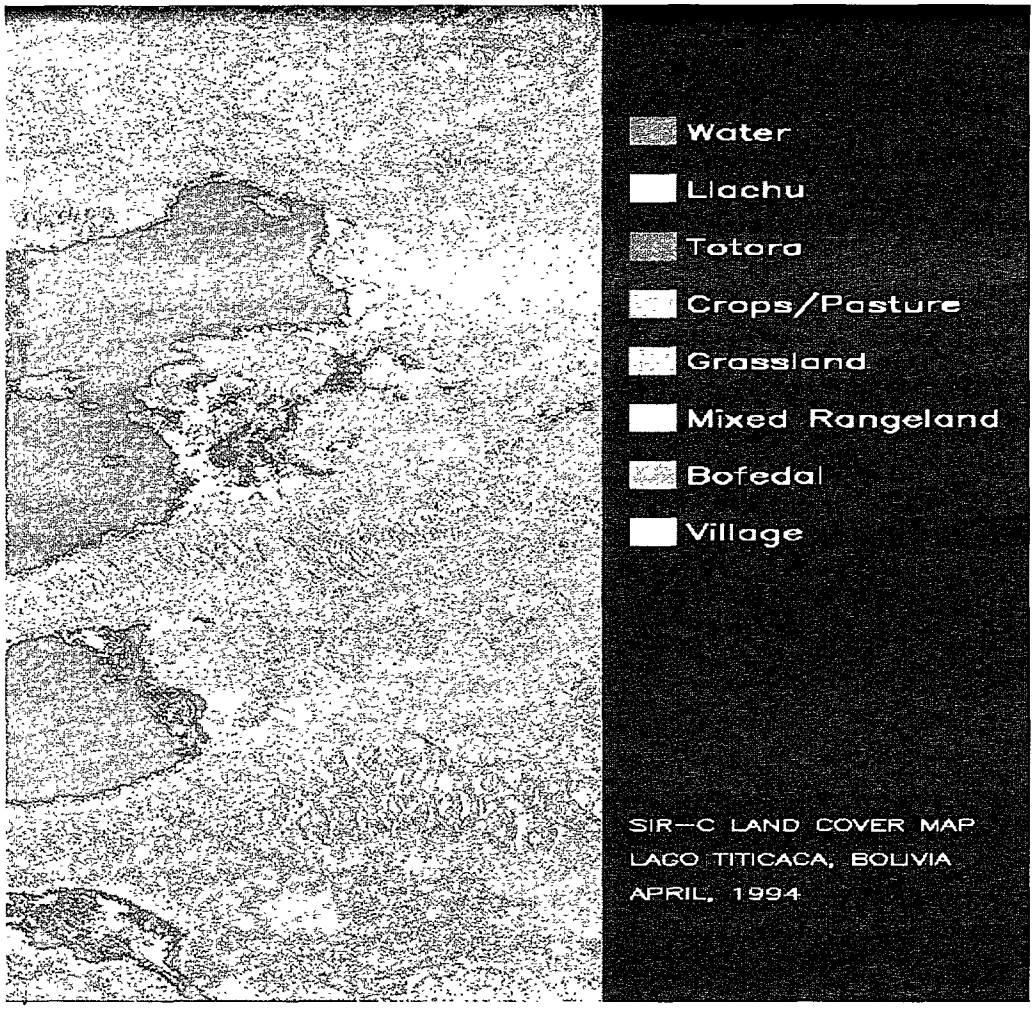

Figure 1. Thematic map produced by maximum likelihood classification.

classified as dry, arid puna (GS/OAS, 1996). Low-density vegetation with patches of bare soil is typical of this zone. The LHH backscattering (Table 2) corresponds to patches of bunch grasses, locally known as *pajonales*, and roughness variation. The low water content of both soil and plants in the semiarid zone was reflected in low responses in the C-band. The misclassification of 8% of the pixels in this class as mixed rangeland is not surprising. There is a fuzzy boundary between the spectral characteristics of these two classes.

The strong double-bounce scattering resulting from the mixed rangeland differentiates this land cover from the other three classes within the land vegetation. The presence of taller trunks in vegetation such as brush, scrub, or trees was evidenced by the magnitude of the strong LHH signal (Table 2). On the other hand, the volume of LHV scattering was typical of shrubs, scrub, or trees containing a low-density canopy, e.g., eucalyptus trees growing in the Altiplano.

Bofedales showed the highest error in the classification, with 16% of pixels classified as grassland. There are at least two reasons for this misclassification. First, bofedales are small and associated with

Table 2. Backscatter statistics (dB) of training sites for land-cover type classes at L-Band and C-Band frequencies.

Class	σ^0, HH	S_x	σ^0, HV	S_x
L-Band				
Water	-33.00	1.00	-38.61	0.38
Llachu	-25.37	0.40	-36.49	0.37
Totora	-11.98	0.39	-21.67	0.32
Crops	-16.58	0.58	-22.55	0.46
Grasslands	-20.49	0.38	-28.94	0.37
Mixed rangelands	-9.97	0.86	-22.40	0.47
Bofedal	-23.09	0.58	-32.99	0.40
Village	-3.35	0.43	-14.40	0.36
C-Band				
Water	-39.92	0.08	-25.93	0.22
Llachu	-11.18	0.55	-18.69	0.37
Totora	-10.52	0.87	-14.23	0.31
Crops	-18.46	0.70	-17.23	0.33
Grasslands	-24.40	0.78	-22.22	0.27
Mixed rangelands	-20.00	0.98	-20.37	0.18
Bofedal	-17.53	0.58	-19.04	0.26
Village	-6.85	0.57	-12.43	0.34

S_x = standard error of the mean; σ^0 = Backscattering, dB.

patches of dryland pastures or rangeland of good quality, due to their closeness to water and natural fertilization by grazing animals. Second, grasslands in the lower lands present higher soil moisture than neighboring lands. These high-producing grasslands are called seasonal bofedales. A more accurate differentiation between permanent and seasonal bofedales requires a multitemporal analysis.

Villages were a separate class. The effect of corner reflectors and metal roofing, in both urban areas and widely dispersed communities, were clearly distinguishable in all four channels used (LHH, LHV, CHH, and CHV). Areas with pronounced topography showed similar backscattering to the village class. This problem could not be corrected due to the lack of a high-resolution DEM for the area.

No single channel or pairs of channels separated all land vegetation classes accurately. Therefore, the information contained in all four channels had to be combined. All four channels combined resulted in a good (89% accuracy) classification of the land cover types. The resulting map containing a level II land cover classification (Sabins, 1997) of the study area is shown in Figure 1.

The simulation of JERS-1 and RADARSAT classifications resulted in less than 45% accuracy. Neither of the two sources of commercial radar data alone produced an adequate classification of the most important land cover types in the Altiplano. By combining the LHH and CHH bands—mimicking the combination of JERS-1 and RADARSAT data—the accuracy of classification increased to around 78%.

Table 3. Confusion matrix of land-cover types derived from the Bayesian classifier.

From class	Water	Llachu	Totora	Crops	Grasslands	Mixed rangelands	Bofedal	Village	
Water	100	0	0	0	0	0	0	0	
Llachu	0	92	0	0	0	0	8	0	
Totora	4	0	80	12	0	0	4	0	
Crops/pasture	0	0	12	84	0	0	4	0	
Grasslands	0	0	0	0	92	8	0	0	
Mixed rangelands	0	0	0	0	8	88	4	0	
Bofedal	0	4	0	0	16	0	80	0	
Village	0	0	0	0	0	0	0	100	
									Total Error
Error Rate	0	8	20	16	8	12	20	0	11

Conclusions

Space borne polarimetric radar data were used to map aquatic and semiarid vegetation in the Altiplano. L- and C-bands and two polarization modes (like-polarized bands HH and cross-polarized bands HV) were used to classify eight land cover classes. A thematic map was produced with a classification accuracy of 89%. This accuracy might be improved if the image is first corrected for the topographic effect, which requires a high-resolution DEM. Some of the classes require a multitemporal analysis, including at least two seasons, to be completely spectrally separated. The HV bands contributed more to the discrimination than the HH bands.

The results provide new possibilities for monitoring land use changes in semiarid conditions. Despite the fact that most vegetation presented similar spectral attributes, particularly for optical RS, radar imagery proved a good alternative for separating even very similar classes such as grasslands and mixed rangeland. The capability of monitoring cropping systems during the rainy season gives radar RS a clear advantage over optical sensing. Furthermore, different classes of aquatic vegetation, specifically llachu and totora, can be easily differentiated.

An additional finding was that imagery from the two contemporary commercial radar satellites produced low expected accuracy for the classification of land cover types when used alone. When combined, however, data from JERS-1 and RADARSAT satellites increase the classification to an acceptable 78% accuracy.

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A Process-Based Model (WEPP) for Simulating Soil Erosion in the Andes

W. Bowen[1], G. Baigorria[2], V. Barrera[3], J. Cordova[3], P. Muck[4], and R. Pastor[5]

Soil erosion by water represents a major threat to the long-term productivity of hillside agriculture in the Andes. To help combat this threat, researchers need a quantitative understanding of the hydrologic and physical processes that drive soil loss. They also need to understand how these processes interact with land use and management to either diminish or increase soil loss. This understanding, however, is not easily obtained in a cultural and physical environment as diverse and complex as the Andes, particularly given the paucity of experiments and data needed to quantify soil erosion for the myriad land-use systems in the region.

To better understand soil erosion and its impact in the Andes, we have begun a multi-institutional and multidisciplinary effort based on a systems research approach. This approach is designed to take advantage of existing simulation models, using existing experimental data to the extent possible for model calibration and model testing. New experiments and other data collection activities will be pursued as this approach helps us to identify gaps in available data sets and possibly inaccuracies in process descriptions incorporated in present models. With time, we expect the iterative process of experimentation and model evaluation to increase our understanding of the major processes that cause soil erosion. We also expect the systems research approach to result in improved simulation models that can be used to help predict how conservation measures—or the lack of them—might affect soil productivity on a site-specific basis.

A process-based simulation model we have begun to evaluate under Andean conditions is one recently developed by the Water Erosion Prediction Project (WEPP) of the U.S. Department of Agriculture (Flanangen and Nearing, 1995). The WEPP model mathematically describes the processes of soil particle detachment, transport, and deposition due to hydrologic and mechanical forces acting on a hillslope profile. It is considered to possess state-of-the-art knowledge of erosion science, and has become an important analytical tool for global change studies (Favis-Mortlock et al., 1996).

The purpose of this study is to provide a first approximation of the capability of the WEPP model for simulating soil loss in an Andean environment. We will do this by comparing model predictions of runoff and soil loss to data measured from fallow runoff plots during a 154-d study in the eastern Andes of Peru.

Materials and Methods

Model description

The WEPP erosion model is a continuous simulation computer program that calculates runoff and erosion on a daily basis. Erosion processes may be simulated at the level of a hillslope profile or at the level of a small watershed. Our evaluation, however, is restricted to the hillslope profile version (v 98.4). The major inputs for running the hillslope profile version need to be specified in four data files: weather, slope, soil, and management.

1 IFDC/CIP, Lima, Peru
2 CIP, Lima, Peru.
3 INIAP, Quito, Ecuador.
4 UNC, Cajamarca, Peru.
5 UNALM, Lima, Peru.

The weather file requires daily values for precipitation, maximum and minimum temperature, and solar radiation. In addition to rainfall amount, the model requires three variables related to rainfall intensity that are used to compute rainfall excess rates and thus runoff. These are (1) rainfall duration, (2) the ratio of time to peak rainfall intensity to rainfall duration, and (3) the ratio of maximum peak intensity to average intensity.

With the WEPP model, a user can simulate differences in soil types or management along the length of a hillslope through the use of overland flow elements (OFE). An OFE is a specified section of the hillslope with a region of homogeneous soils and management. Up to 10 OFEs can be defined for one hillslope of a given width. The number of OFEs to include in a simulation is specified in the slope file, along with the length and slope characteristics of each OFE.

The soil file contains information on the physical characteristics of the surface soil and subsoil for each OFE. The surface soil parameters required are the effective hydraulic conductivity (Green and Ampt effective conductivity), interrill erodibility (sheet erosion mostly caused by raindrop impact), rill erodibility (small eroded channels), critical shear stress (rill detachment threshold parameter), and albedo (fraction of solar radiation reflected back to the atmosphere). For each soil layer, the inputs required are cation exchange capacity (CEC) and percentages of sand, clay, organic matter (OM), and rock fragments. Up to eight soil layers to a maximum profile depth of 1.8 m may be defined in the soil file.

The management file contains information needed to define initial conditions, tillage practices, plant growth parameters, and residue management and crop management. It is the file with the largest number of parameters.

Runoff plot study

Measurements of runoff and soil loss were obtained from a runoff plot study conducted during the first 6 mo of 1991 in San Ramon, Peru (Pastor, 1992). In this study, 30 runoff plots, each 10 m long and 4 m wide, were set up on slopes of 30, 35, 40, 45, 50, and 60%. At each of the six slope sites, five plots with the following management systems were installed: (1) clean fallow, (2) natural grass vegetation, (3) sweetpotato (*Ipomoea batatas*) planted in rows along the contour with hilling, (4) sweetpotato planted in rows along the contour without hilling, and (5) sweetpotato planted up and down the slope with hilling. Treatments were not replicated, meaning there was only one set of observations for each unique combination of slope and management system. There were also fairly large differences in the infiltration properties of the soils (Entisols) across slope sites. Infiltrometer measurements in the field showed infiltration was 21.0 mm/hr on the 30-35% slopes, 12.4 mm/hr on the 40-45% slopes, 215.0 mm/hr on the 50% slope, and 104.7 mm/hr on the 60% slope.

Runoff and soil losses were measured after each rainfall from 21 Jan to 24 Jun 1991. There were 62 rainfall events during this 154-d period, each producing measurable runoff and soil loss. The total rainfall for the period was 1,053 mm. Total runoff and soil loss measured for all treatments and slopes are shown in Table 1 (note the sweetpotato contour treatment represents the mean of plots with and without hilling). The greatest runoff and soil loss occurred from the clean fallow plots. Any discernible impact of slope on runoff and soil loss apparently was masked by the differences in soil infiltration properties across slopes. The 50% slope, because of more rapid infiltration, actually produced less runoff and soil loss than the 30-45% slopes.

Model analysis

Our analysis of the WEPP model in this initial study focuses on measured and simulated data obtained from the clean fallow plots only. Soil is often left bare

Table 1. Runoff and soil loss measured for four different management systems at six locations with different slopes in San Ramon, Peru, from 21 January to 24 June 1991 (Pastor, 1992).

	Slope (%)						
Treatments	30	35	40	45	50	60	Treatment mean
	Runoff (mm)						
Natural vegetation	42.18	41.57	38.25	52.84	25.77	27.77	**38.06**
Sweetpotato/contour[a]	30.95	26.24	26.29	29.36	21.83	29.67	**27.39**
Sweetpotato/up-down[b]	59.10	44.69	38.52	33.53	23.39	34.58	**38.97**
Clean fallow	62.85	50.99	43.40	60.05	48.38	41.30	**51.16**
Slope mean	**48.77**	**40.87**	**36.62**	**43.95**	**29.84**	**33.33**	**38.90**
	Soil loss (mg ha^{-1})						
Natural vegetation	0.44	0.48	1.10	0.86	0.45	0.79	**0.69**
Sweetpotato/contour[a]	0.61	0.80	0.98	1.42	0.65	1.06	**0.92**
Sweetpotato/up-down[b]	2.42	3.33	3.21	4.01	1.82	3.96	**3.13**
Clean fallow	14.88	13.03	11.38	7.74	3.12	8.39	**9.76**
Slope mean	**4.58**	**4.41**	**4.17**	**3.51**	**1.51**	**3.55**	**3.62**

[a] Sweetpotato planted in rows along the contour.
[b] Sweetpotato planted in rows up and down the slope.

between crops, thus it is important to quantify the vulnerability of exposed soil to the erosive forces of natural rainfall. Also, we thought it better to first parameterize and evaluate the performance of the model for bare soil where there would be no expected interaction between residue cover and plant growth. If the model cannot be shown to simulate soil loss realistically from bare soil, then it would not be expected to do so for other management systems.

Our analysis of WEPP in this study is also restricted to results averaged across slopes. There was insufficient information about the on-site soil properties to parameterize the WEPP model for each slope site. Therefore, we evaluate the performance of the model by averaging both measured and simulated data across slopes. That is, WEPP model input files were set up to simulate by slope, but the simulated output values were averaged across slopes before comparing them to measured data, which were also averaged across slopes.

For evaluating model performance, we followed the suggestion of Nearing et al. (1994) to compare the frequency distributions of the measured and simulated events rather than make event-by-event comparisons. Although the WEPP model should eventually be evaluated by comparing outcomes on an event-by-event basis, such a comparison is not valid in this study. The reason is that critical input parameters for soil properties and rainfall intensity were not measured on site and could only be approximated.

Model inputs

The weather file for simulating erosion from the clean fallow plots was assembled using daily rainfall recorded in pluviometers at the experimental site. Daily temperature and solar radiation values were obtained from the CIP-San Ramon weather station located about 1 km from the experimental site. Rainfall intensity was not recorded at the site, so we estimated values for the duration and intensity parameters

using statistical relations derived from recorded values at the CIP-San Ramon weather station.

Slope input files were assembled for each of the six slopes by specifying one OFE with a slope length of 10 m and a plot width of 4 m. Soil input files were made identical for each of the slope sites. Soil profile parameters for soil depth, texture, OM, CEC, and rock fragments were based on measurements taken from a nearby site (La Torre, 1985). Surface soil parameters were estimated using either empirical relations described in the WEPP User Summary (Flanagan and Livingston, 1995) or by calibrating simulated runoff and soil loss to measured data from only the 30% slope. Input values for surface soil parameters were 7.0 mm/h for effective hydraulic conductivity, 2.0 x 10^6 kg s/m^4 interrill erodibility, 0.002 s/m for rill erodibility, and 4.0 N/m^2 for critical shear stress. The management input files were also made identical for each slope with parameters set to simulate bare soil.

Results and Discussion

One of the most notable discrepancies between WEPP model simulations and measured data was in the number of rainfall events that resulted in runoff and soil loss. Whereas field measurements showed that each of the 62 rainfall events produced some runoff and soil loss, although often in only small amounts (Figures 1A and 1B), the WEPP model produced runoff and soil loss values for only 16 of the events. Closer analysis revealed that the model failed to pick up the less intense or smaller rainfall events that produced measured runoff values of less than 1 mm or soil loss values of < .1 t/ha.

The failure of the model to simulate the smaller events was judged not significant as the measured data clearly showed that any substantial soil loss only occurred when rainfall exceeded 10 mm (Figure 1B) or runoff exceeded 1 mm (Figure 1C). Furthermore, we were able to demonstrate in a sensitivity analysis that the model would reproduce more of the measured runoff and soil loss events by adjusting the rainfall intensity parameters of specific rainfall events. Thus, if the on-site rainfall duration and intensity parameters had been known with more certainty, the model output may have more accurately reflected the observed number of events.

The cumulative frequency distributions for runoff and soil loss measured during all 62 events are provided in Figure 2, expressed as the probability that any one event will exceed a given runoff or soil loss

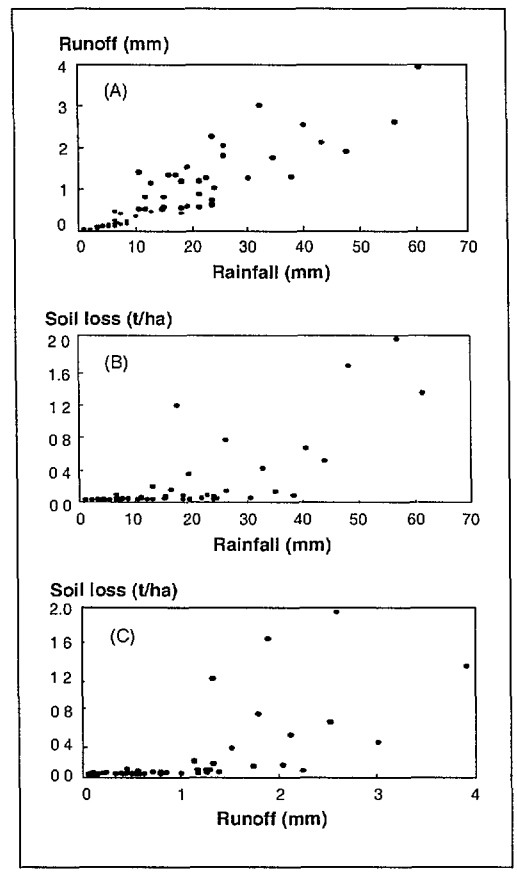

Figure 1. Measured data from fallow plots showing the relations between (A) rainfall and runoff, (B) rainfall and soil loss, and (C) runoff and soil loss. Runoff and soil loss values represent the mean across slopes for each event.

amount. These distributions represent the same data presented in Figure 1. Here, however, the highly skewed nature of the data is more apparent; relatively few events produced most of the runoff and soil loss. For example, only 4 of the 62 events resulted in a combined soil loss of 6.0 t/ha, whereas the cumulative soil loss from all events amounted to 9.8 t/ha.

The cumulative frequency distributions for simulated runoff and soil loss are also shown in Figure 2. These were calculated using the simulated output for the 16 events reproduced by the model together with zero values for the other 46 events not reproduced by the model. For that reason the simulated distributions indicate that most of the events would not have produced runoff exceeding 1 mm or soil loss exceeding 0.1 t/ha, values similar to those indicated by the measured distributions. When these values were exceeded, the simulated distribution of events similarly reflected the measured distribution.

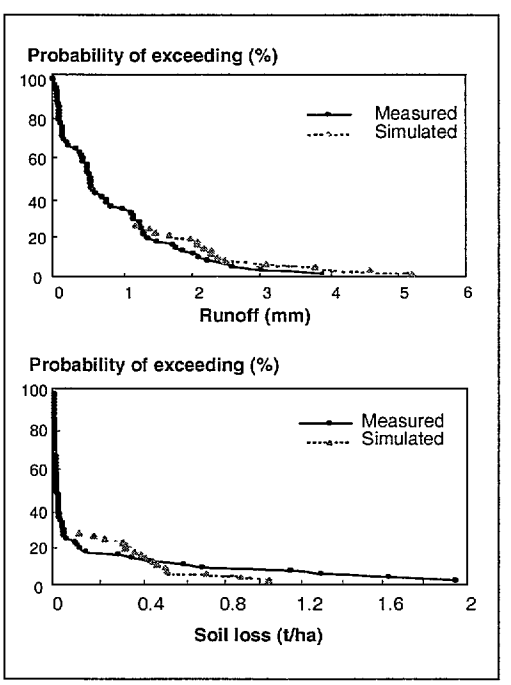

Figure 2. Measured and simulated cumulative frequency distributions showing the probability of exceeding a given runoff or soil loss from fallow plots.

For runoff, the simulated distribution was shifted to the right of the measured distribution, indicating the model tended to overpredict runoff. For soil loss, the model tended to overpredict small values (distribution shifted to the right), but underpredict large values (distribution shifted to the left). This same trend in overpredicting small values and underpredicting large values is common when evaluating many erosion models with measured data. Nearing (1998) attributes the trend to limitations in capturing the random component of measured erosion data with a deterministic model. Although measured and simulated distributions were somewhat similar, the model underestimated the 154-d totals for runoff and soil loss. We attribute that to the failure of the model to reproduce all events. The total measured runoff was 51.2 mm compared with 40.4 mm for the simulation. The total measured soil loss was 9.8 t/ha compared with 7.6 t/ha for the simulation.

In addressing some of the uncertainty regarding input parameters, we found both runoff and soil loss to be quite sensitive to rainfall and surface soil parameters. To illustrate, Figure 3 shows how runoff and soil loss would vary with the duration or intensity of a 61-mm rainfall event for two soils with different effective hydraulic conductivity values. The 61-mm rainfall was the largest recorded during the runoff plot study. In general terms, the model indicates that the difference in soil loss between a 4- or 6-h event could be as much as 20 t/ha. Likewise, an 8-h event might result in no soil loss on a soil with good infiltration properties, but erode more than 10 t/ha if infiltration is poor. The measured soil loss for this event was 1.3 t/ha. Clearly, it is important to have reliable estimates of parameters like rainfall intensity and effective hydraulic conductivity if the model is to provide realistic estimates of runoff and soil loss.

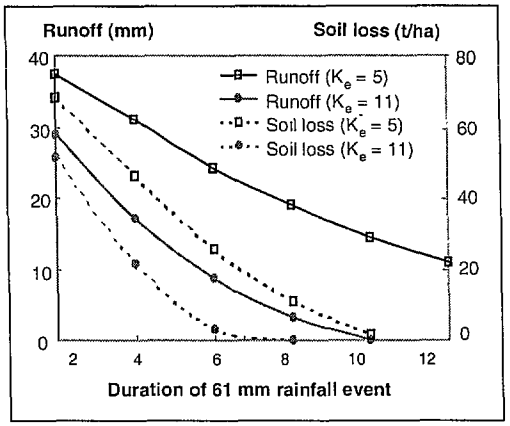

Figure 3. Sensitivity of simulated runoff and soil loss due to variation in the duration of a 61 mm rainfall event for two soils with different effective hydraulic conductivity values (K_e).

Conclusions

This initial analysis of the WEPP erosion model has shown that it can be an effective tool for studying the hydrologic and erosion processes that drive soil loss in the Andes. The model should be particularly valuable for focusing on the quantitative relations and interactions between soil, weather, topography, slope, and management factors that determine runoff, soil loss, and deposition on a site-specific basis. Nevertheless, we must caution that this study should not be seen as a validation of the WEPP model for Andean conditions. More rigorous testing of model assumptions is needed. That will require more complete experimental data sets than the one used in this study.

The results presented in this study represent our first attempt at working with the WEPP model and collating the type of measured data needed to parameterize and evaluate the model. The runoff plot study used in this analysis was certainly not ideal for model testing as shown by the lack of some on-site measurements needed to parameterize the model. It did at least start us on the road toward a better understanding of model assumptions and data input needs. As part of an ongoing regional effort, we are gathering experimental data from other historical runoff plot studies in the Andes. We will continue to evaluate the WEPP model with these data. As the need and opportunity arise, we will also conduct new experiments using the WEPP model to help us focus on improved understanding of processes.

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Ecoregional Research: A Vision from the Andes

In response to growing interest among scientists and donors in natural resource management and sustainable development, the CGIAR initiated ecoregional research programs beginning in 1992. The CGIAR defines the ecoregional approach as:

> "The main role of the ecoregional approach is to contribute to the goal of increasing sustainability of agricultural production by providing: first, a process that identifies the **right research content** due to its holistic and forward looking approaches to research; second, a **mechanism for partnership**, among relevant actors with complementary functions, that contributes to achieving their common and individual institutional goals through applied and strategic research on the foundations of sustainable production systems; and, third, a mechanism that develops, tests, and supports **effective research paradigms** for the sustainable improvement of productivity." (The eco-regional approach to research in the CIGAR. TAC, CGIAR, Rome Italy. 1993, p. 4.)

Ecoregional Research Agenda in the Andes

CONDESAN, the Consortium for the Sustainable Development of the Andean Ecoregion, carries out ecoregional research in the Andes in the context of the CGIAR approach. Operating under the umbrella of CIP, CONDESAN is a consortium of more than 75 associated groups, including universities, NGOs, communities, and local government agencies. CIP's natural resource management program develops methodological tools for use in meeting the research and development objectives of CONDESAN whose ecoregional approach contains three objectives.

- Sustainable natural resource management.
- Improved rural incomes and employment.
- Increased community input and control of the landscape.

To meet these objectives, energy is invested in both research programs and benchmark integrated research/development programs. The former are developing much needed tools for improved natural resource management and monitoring, participatory methodologies, and productive technologies, whereas the latter are working at the frontier of increasing agricultural productivity, resource use, and community control. In almost all cases, the activities are inter-disciplinary, multi-institutional, and strive to develop a participatory agenda.

The research agenda for the Andes is a work in progress, initiated with a series of Andean-wide project planning by objective (PPO) exercises. In the broadest terms, the Consortium is focusing on four "cross-Andean" research components.

1. Soil and water management. Methodologies for the evaluation and rehabilitation of natural resource —GIS, remote sensing, ex-ante and ex-post watershed modeling, and promoting community management of natural resources.

2. Agrobiodiversity in Andean roots and tubers and pasture species. Identifying micro-centers of genetic diversity; characterizing clones; improving agronomic and postharvest technologies; and understanding marketing pathways.

3. Improved farming systems for the Andes: From producer to consumer

- Production systems research. Modeling (crop and animal production, chemical leaching, soil erosion, and water run-off); resource management (soil biology, drip/sprinkle irrigation, pesticides/health); commodity research.

- Agroindustries and Marketing research. Development of new products; identifying bottlenecks and new opportunities.

4. Policy research. Modeling trade-offs between productivity, profit, and environmental impact; using government policy to promote Andean development; and promoting private investment in the rural Andes.

These research activities primarily take place in the field at "research sites," where both the energy and funding originates from the research agenda. Several examples are:

- San Gabriel (Ecuador): Tradeoffs project.
- Lake Titicaca fringe (Peru/Bolivia): Remote sensing project.
- San Antonio/Rio Recio/Rio Guadalajara (Colombia): Ex-ante analysis of watershed management project.
- Pensilvania (Colombia): Joining entrepreneurs and local and national government authorities in investing in the hillsides.
- San Jose de Minas (Ecuador), Sucse (Peru), and San Juan de Miel (Bolivia): Developing the local arracacha industry: methodologies for working with cottage industries.

Two companion themes are part of the cross-Andean portfolio: developing human resources and communications. In addition to conducting workshops, in the case of human resources, CONDESAN is working to improve postgraduate education in agricultural production and natural resource management. With respect to communication, INFOANDINA is the Consortium's information network with nearly 500 participants. It is focusing on improving communications between Consortium members, providing access to the "gray literature," and conducting forums on key development issues.

Research and Development Agenda: Work at the Benchmark Sites

A crucial component of the ecoregional approach is "effective research paradigms" and the concept of the benchmark site. For us, a benchmark site is neither a pilot, "integrated rural development program," nor a point along some heroic Andean transect, but rather, a place where sustainable development becomes operational. It is here where the three goals of the Andean Program come together: (1) sustainable natural resource management; (2) rural poverty alleviation; and (3) community empowerment. Each benchmark site represents a small number of communities that share a common resource base and have an interrelated set of management and development challenges (usually 10,000-100,000 ha). These benchmark sites have been selected based on three criteria.

1. The site selected represents a "typical" location within an important Andean ecology (e.g., the green Andes, semi-arid inter-Andean valleys, the high plains). A good database already exists at the site.

2. Local organizations are willing to collaborate to address an important productivity/natural resource management issue. This normally requires building a multidisciplinary and multi-institutional team, with a shared research/development agenda.

3. The benchmark sites are in different stages of development. Some have solidified teams with a second round of funding; others are still forming and debating their research agenda. Ideally, the team develops an integrated funding proposal, funding from one or several sources are secured, and the research/development activities begin. Over time, the "round table" of team members is strengthened and new research and development activities are designed. Descriptive titles and themes for the benchmark site projects are shown below.

Benchmark site projects.

Location	Themes	Comments
Pueblo Llano and Gavindia, Merida, Venezuela	Intensifying potato production	Motor for and menace to sustainable development in Alto Merida
La Selva de Florencia, Manizales, Colombia	Managing the Florencia bioreserve and buffer zone	Developing profitable alternatives in the humid cloud forest
Rio El Angel, Carchi, Ecuador	Phase 1: Characterizing the watershed with special emphasis on the potato-pasture zone Phase 2: Building a sense of commonwealth in the watershed and promoting rural prosperity	Managing a new irrigation canal in Rio El Angel
La Encanada, Cajarmaca, Peru	Phase 1: Using GIS tools to help characterize the watershed Phase 2: Building a micro-watershed management plan	From landscape interventions to increasing incomes
Manazo, Puno, Peru	Intensifying production in a new irrigation district	From water management to marketing Andean products
Aroma, La Paz, Bolivia	Intensifying livestock production in the semi-arid Andes	Landscape and risk management
Cochabamba, Bolivia	- Andean roots and tubers in Candelaria - Cochabambina water forum	From prospecting to profit Clarifying the debate

The Future

Although not yet fully realized, the expectation is that the cross-Andean methodologies, research findings, and discussions will increase the effectiveness of the benchmark teams, and that the benchmark successes will serve to focus the cross-Andean themes. The future has a threefold thrust.

- Research activities will result in new and user-friendly tools for natural resource management, better participatory methodologies, and improved technologies.
- The Consortium will grow stronger as the model of shared-risk, shared-benefit, multi-institutional teams has greater success.
- The ability to have a real impact on sustainable rural development in the Andes will increase as the synergism of the cross-Andean methodology and in-depth benchmark site research activities take off.

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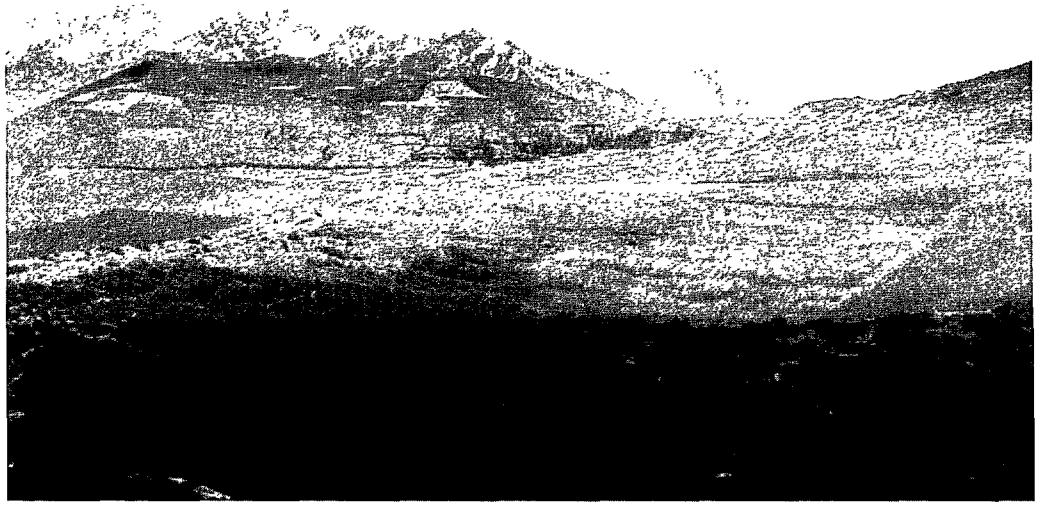

A cultivated mountainside near Cusco, Peru.

Research on Andean Roots and Tubers

Impact on a Changing World

413

Reappraisal of Edible Canna as a High-Value Starch Crop in Vietnam

M. Hermann[1], N.K. Quynh[2], D. Peters[3]

Edible canna (*Canna edulis* Ker-Gawler) or Queensland arrowroot is a vegetatively propagated root crop from the Andes. Abundant archaeological canna remains found in the Pacific littoral in Ecuador and Peru predate most other food crops in this area (Piperno and Pearsall, 1998). That suggests canna was a fairly common staple in prehistoric times, but was successively diminished by the introduction of other crops, notably by maize from meso-America and by Old World crops in the wake of the Spanish conquest. In the Andean highlands, canna continues to be grown as a subsistence crop or, to a lesser extent, as a cash crop for occasional ritual use. However, it is of no economic significance and is largely unknown in its native range.

Production advantages of canna include high N-use efficiency, high yields and harvest indices (Hermann et al., 1997), shading tolerance, outstanding drought tolerance and water-use efficiency (Jureit, 1997), and the absence of pest and disease and replant problems. A severe constraint to its wider use is its long duration to full productivity.

Similar in texture and taste to sweetpotato (*Ipomoea batatas*), the starchy canna rhizome is actually a palatable food, but it has an unattractive brown color and is rather fibrous. More important, canna must be boiled or steamed for several hours to soften root tissue sufficiently for it to be consumed. That constrains its use not only in urban areas but also in poor, rural highland communities where fuel wood is scarce. Thus, there is little scope for canna to regain some of its previous importance as a food for direct consumption.

Yet the ease with which canna starch can be extracted using makeshift equipment has not escaped the attention of rural people in the search for wheat flour substitutes. Canna has the largest starch granules known. They quickly settle out of a suspension of grated rhizome tissue. In the northern Andes, cottage industries have sprung up to extract canna starch, albeit of questionable hygiene and low productivity. Although the starch is highly valued locally, it is limited to certain bakery products to which it confers a spongy and light texture not achieved with alternative raw materials (Hermann, 1994).

Canna production in the Andes is dwarfed by the crop's use in tropical Asia, particularly in Vietnam and China. It spread there in past centuries presumably because of the ornamental value of its flowers. Because of its highly localized importance, and generally restricted role as pig feed and famine food, its presence in backyard gardens has rarely been noted. In recent decades, however, canna starch production in Vietnam, almost exclusively for transparent noodles, has become a major agricultural operation. This paper examines the principal features of canna use in Vietnam based on rapid appraisals in 1992 and 1995, and research from 1996 to 1998. The information provided fills a gap in the agricultural and food science literature, and identifies priorities for further research and breeding efforts.

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3 CIP, Hanoi, Vietnam.

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Canna production

Elderly rural informants invariably state that the use of canna as pig feed has a long tradition in Vietnam. In the 1950s and 1960s, when rice harvests were as low as 2 t/ha, canna rhizomes also entered the human diet to a considerable degree. In some areas, canna was produced to a much larger extent than today. At the time, some starch was extracted and used rather unspecifically as a thickener. Beginning in the late 1960s and early 1970s, the principal use of canna starch for the manufacture of cellophane noodles emerged and has since fueled the expansion of canna production.

Canna is grown in all mountainous provinces and also in some low-lying areas. According to official estimates, some 20,000 ha of canna are cropped in northern Vietnam. In the five leading canna-producing districts of Tanh Hoa Province (Red River Delta) alone, 2,930 ha were registered in 1998. Recent evidence suggests that from 4,000 to 5,000 ha are grown in the South, principally in the provinces of Dong Nai, Song Be, Tay Ninh, Gia Lai, and Lam Dong. Other roots and tubers used for starch in Vietnam include cassava (*Manihot esculenta*) for a range of secondary processed products such as maltose and fermentation products, and kudzu (*Pueraria lobata*), a tuberous legume yielding a highly prized starch used in a traditional soft drink.

In northern Vietnam, canna is cropped principally in the highlands (300-1,200 m) of Hoa Binh and Son La provinces, which border Laos and China, and in the Red River Delta at sea level. Cropping is strictly seasonal, beginning at the onset of rains and lasting for 10-12 mo. Propagation is by apical rhizome sections that are either immediately replanted or stored for 2-3 mo to allow for staggered harvesting.

In the rice-dominated cropping systems of the Red River Delta, canna is mostly relegated to the least fertile and unirrigated uplands such as river dams, backyards, and other areas that do not compete with food production. Occasionally, canna is grown on more fertile land after a winter vegetable crop. Under high N fertilization, yields can exceed 80 t/ha in 8-9 mo. Usually, however, yields are under 40 t/ha and reflect marginal inputs.

In the highlands, most canna comes from agroforestry systems or shifting cultivation. In agroforestry systems, which may involve steep slopes, shading can exceed 50% and the crop is not fertilized. No plowing is practiced. Production is therefore extensive with no external inputs and low yields.

In Vietnam, as in other parts of Asia, edible canna shows little variability and belongs to a broad-leaved morphotype. Fully expanded leaves assume a near-horizontal orientation as opposed to the erect leaf habit of most Andean cultivars. Another special feature of Asian starch canna is its hypogaeic rhizome compared with the more common rhizome position at or above the soil surface in Andean material. Vietnamese canna is reported by farmers to be seed-sterile, and indeed we never found sexual seed in mature fields. All six accessions examined were found to be triploid (2n = 27), which suggests they originated in the northern Andes, where such material is common. That is corroborated by randomly amplified polymorphic DNA analysis, which places Vietnamese canna next to triploid Colombian cultivars (Hermann, 1999).

Starch extraction

Some canna starch is extracted in the highlands, but the bulk of the harvest is trucked to processing villages in the Red River Delta about 100-200 km away. Processing of the rhizomes into starch and then into noodles takes place in a number of highly specialized villages. Many of them add domestic rhizomes to those imported from the highlands. Some villages specialize in starch extraction, others in noodle making, and still others provide processing equipment such as drying racks, baskets,

graters, and noodle cutters. Several of these functions may even coexist in a given village.

The economics of canna production and processing are little understood, but production in the lowlands, i.e., near the processing sites, and noodle-making seem to be particularly profitable. Farmgate prices for canna between 1990 and 1995 were slightly higher than for cassava and double that of sweetpotato, although cassava and sweetpotato have much higher dry matter (DM) contents. Canna rhizome, starch, and noodle prices fluctuate seasonally suggesting corresponding profit variation.

Starch processors require the rhizomes to be free from the adventitious roots that firmly anchor the canna rhizome in the soil and remain attached to it after harvest. The soil and small stones they trap can damage grater surfaces. Up to 20 person hr are needed to remove the roots from 1 t of canna rhizomes.

Vietnamese starch processors use mostly engine-driven drum graters. They are locally made and consist of a hardwood cylinder, 20-25 cm diam and 30-40 cm long, with longitudinal rows of nails providing an abrasive surface. Only wealthier households own such graters and rent them out to other processors, moving grater and engine around on wheelbarrows. Figure 1 provides a schematic of a typical, family-owned rural starch factory. The pulp generated by the grater is collected in buckets and poured onto a cloth suspended (immersed) in stationary water tanks. The pulp is then moved across the cloth and kneaded to release the starch (Figure 2), which settles to the bottom of the tank. The

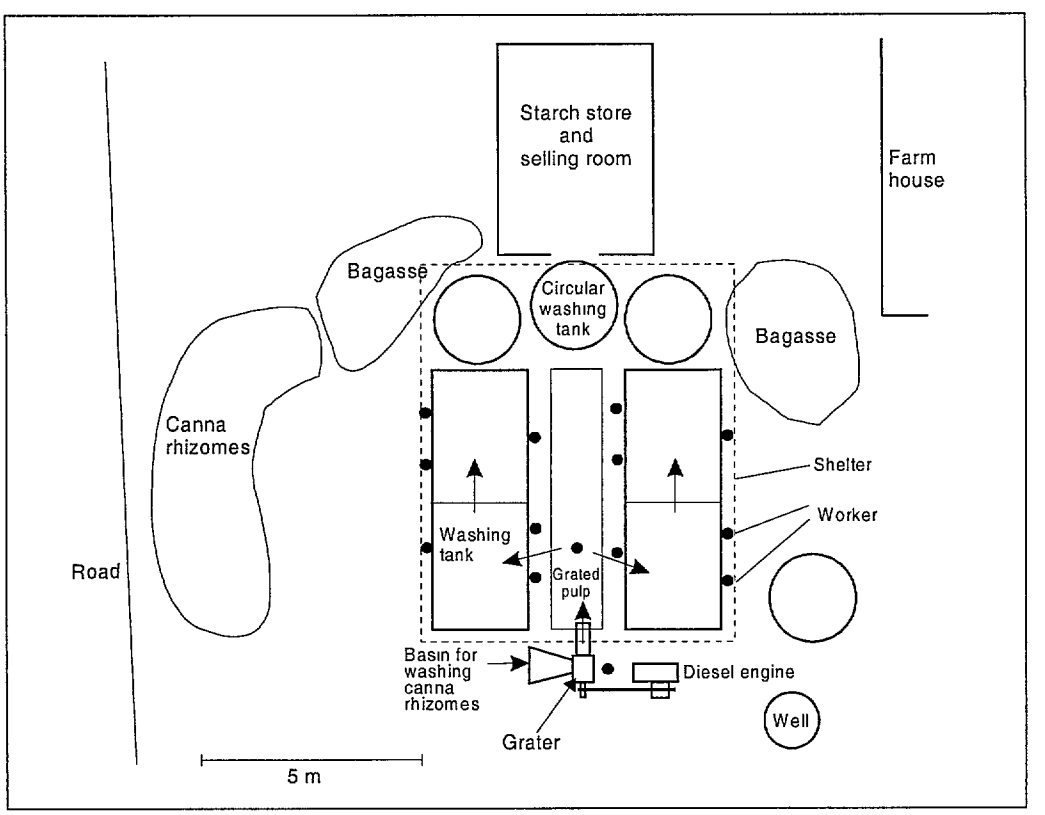

Figure 1. Schematic of canna starch factory in Moc Chau, Vietnam.

Figure 2. Rural women workers washing canna pulp in Moc Chau starch factory, Son La province, northern Vietnam, 1995.

remaining fiber may be passed on to workers at another tank (Figure 1) who repeat this process to extract additional starch and the fiber is finally discharged.

The starch sediment accumulating in the rectangular tanks is shovelled into circular washing tanks and is given a number of washes by stirring it in clean water. After each wash, the starch is allowed to settle for an hour or so and a lighter, brown slurry on top of the firm starch cake is scraped off. Once supernatant water of the final washing is siphoned off, any free water remaining on the starch sediment is soaked up with hygroscopic materials. Bags filled with ash, or bricks that have been dried over a heat source and then cooled, are commonly used. The final water content of the starch as it comes out of the sedimentation tank is 46.5-49.0% (wet wt basis).

The farmer-extracted starch in Vietnam ranges from between 10 and 15% of fresh rhizome weight (Table 1), with three out of four observations being between 10 and 11%. That is roughly equivalent to half of rhizome DM. Actual starch yields are about three-fourths of total extractable starch, which includes starch released from process residue by treatment in a food blender. Extraction efficiency across production zones is thus much better than in other tuber crops (having smaller granules with lower sedimentation rates) but there is room for improvement.

Noteworthy are the high concentrations of soluble solids (shown to be sugars by Ripperton, 1927), as revealed by the high refractometric index. This indicates that wastewater must have high values of biological oxygen demand and illustrates its polluting potential. Table 1 does not suggest differences between Vietnam and the Andes in canna DM content, extraction efficiency, or total extractable starch, but no firm conclusions can be drawn from these preliminary data.

Traditionally, all starch has been dried in the open. Otherwise it quickly deteriorates

Table 1. Parameters of starch extraction from canna rhizomes in Vietnam and Andes (in % of rhizome fresh matter unless otherwise specified).

Locality	Cultivar	Soluble solids ° Brix	Dry matter	Farmer starch[b]	Laboratory starch[c]	Extractable starch[d]	Extraction efficiency (%)[e]
				% rhizome fresh matter[a]			
Vietnam							
Hai Hau, Nam Ha, sea level, 20°14′ N	MH1400	5.0	22.5	10.1	3.8	13.9	73
Hai Hau, Nam Ha, sea level, 20°14′ N	MH1401	-	21.0				
Tu Ly, Hoa Binh, 300 m, 20°53′ N	MH1402	6.2	26.7	10.8	4.3	15.1	72
Tu Ly, Hoa Binh, 300 m, 20°53′ N	MH1403	-	27.1				
Moc Chau, Son La, 1000 m, 20°50′ N	MH1170	4.5	24.7	10.9	6.3	17.2	63
Moc Chau, Son La, 1000 m, 20°50′ N	MH1171	4.9	22.5	14.5	4.4	18.9	77
Andes							
Briceño, Colombia, 2050 m, 1°37′ N	MHIF1335	6.4[f]	23.8	11.3	4.7	16.0	71
Las Delicias, Colombia, 1800 m, 1°57′ N	MHIF1344	9.1[f]	22.1	9.0	2.0	11.0	82
Patate, Ecuador, 2350 m, 1°19′ S	MH1173	5.5	23.8	13.4	6.0	19.4	75

[a] All starch contents are expressed as starch with 20% humidity (wet weight basis)
[b] Starch extracted by farmer
[c] Starch extracted from process residue
[d] Extractable starch is the sum of farmer and laboratory starch and approximates the potential starch yield achievable with better extraction equipment.
[e] Ratio farmer/total starch
[f] calculated by difference

due to fermentation. Since the 1990s, however, most starch has been stored as wet starch until sale or further processing (which can be months ahead) by keeping it in anaerobic conditions. To that end, the starch cake is firmly pushed into polyethylene bags, containing an inner layer of foil and an outer layer of woven plastic. This practice obviates the need for large areas for starch drying and prevents airborne contamination. Table 2 gives retail prices for carbohydrate commodities on the Hanoi markets and shows the high relative value of canna starch.

In villages where hundreds of families engage in starch extraction, the disposal of residue and wastewater poses serious

Table 2. Commodity retail prices for carbohydrate products, Hanoi, December 1995.

Commodity	Comments	Price (dong/kg)
Canna noodles	From Huu Hoa	7500-8000
Canna starch	From Duong Lieu	7500
Rice noodles	From Huu Hoa	6000
Cassava starch	From Duong Lieu	3500
Cassava flour	'From the mountains'	2500
Wheat flour	From Australia	6000
Indica rice		4000
Japonica rice	Sticky rice	8000
White sugar		6500-6800
Brown sugar		5500
Potatoes		2500-4000

US$1 = Dong 10,800.

problems. Wastewater, which is rich in organic material, especially sugars, is discharged without treatment into streams and bad odors emanate from fermenting extraction residue.

Although extraction residue is used in various ways, its abundance makes it more of a liability than an asset. Some of the fiber-rich residue is returned to fields as mulch or is fed to pigs, either plain or mixed with rice bran. During peak processing, more residue is produced than can be consumed as feed and needs to be dried. It is spread out on all available surfaces in the villages, including walls and sidewalks. Larger processing units have also been known to ferment residue, a process that might add to its nutritional value. The light, brown slurry scraped off settled starch makes a good feed, especially if cooked with other components.

Noodle making

A small proportion of canna starch is destined for unspecific household uses or processed into minor products such as candies, cakes, and rice papers. Overwhelmingly, however, canna starch is processed into noodles.

Of the two techniques for making canna noodles in Vietnam, traditional extrusion is the older, but is practiced on a small scale. It involves forcing a freshly gelatinized and highly viscous starch paste through the perforations of a metal plate forming the bottom of an open-topped box. The noodles are directly released onto a drying rack. As with other extrusion noodles, they are round, but are unacceptably thick (1.8-2.0 mm diam) to most consumers. That is because of the large die diameter chosen to keep the extrusion force sufficiently low for manual operation.

Steam-sheeting, the technique used for well over 95% of canna noodle production, is apparently derived from rice noodle making for which a similar process is used. First, wet starch is slurried into a solution of fully gelatinized starch, which acts as a matrix keeping the starch granules in suspension and accounts for 5-10% of the starch in the resultant batter. This batter is then applied to a steam-heated textile membrane (Figure 3) and gelatinizes into translucent gel sheets. These are then transferred onto concave bamboo racks and are stretched by a factor of 2.5 into a rectangular shape (Figure 4). After preliminary drying to 55-58% moisture, the sheets assume a rubbery, nonsticky texture and

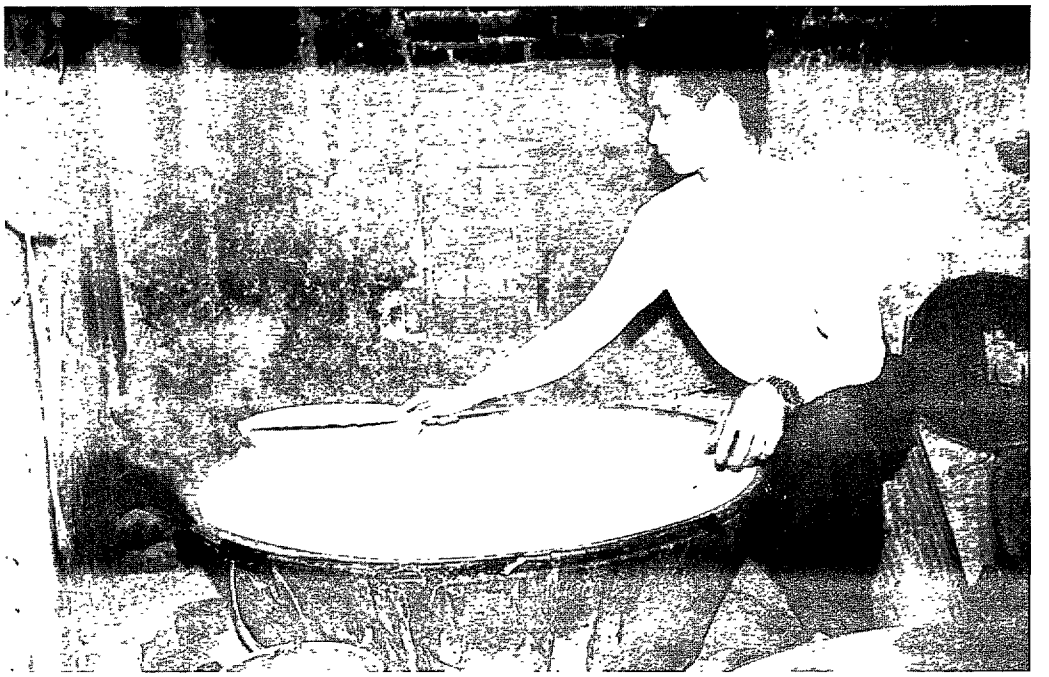

Figure 3. Canna noodle production in Huu Hoa village, Hanoi, Thantri District, 1995. Man applying starch batter to steam-heated textile membrane.

Figure 4. Woman stretching hot gel to the limits of a bamboo rack.

can be easily handled for subsequent cutting into noodles. Two persons can produce 150 sheets/day or the equivalent of 160 kg of dry noodles (retail value US$110.00).

Typically, a guillotine is used to cut the noodles (Figure 5). It moves a stack of folded gel sheets incrementally toward a vertically moving knife that cuts off the noodles. This machine, originally developed for manual operation, has been semiautomated since 1993. A watchlike mechanism attached to the cutter and powered by an electric motor moves the gel stack and the cutting knife in a coordinated fashion. Automated cutting has greatly increased productivity but requires relatively high investment and thus has not completely replaced manual operation. The machine's capacity is 400 kg of noodles/day per operator compared with 100 kg/day per operator with manual operation. Drying of the noodles to 18-21% final moisture takes place in a confined space (Figure 6).

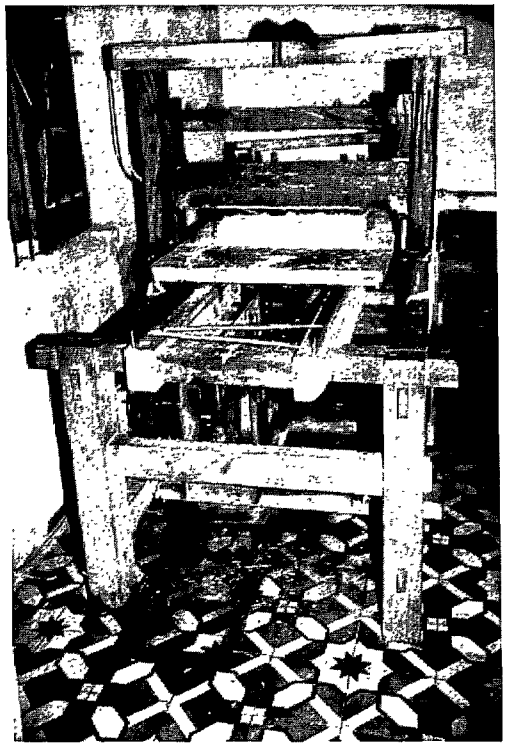

Figure 5. Semiautomated noodle cutter.

Canna noodles belong to the class of cellophane or glass noodles with a glossy, transparent appearance. They are rectangular and are 0.8 mm thick. Bland and slippery, they add texture to a variety of Vietnamese dishes, especially to soups and stir-fried dishes. They are regarded as a luxury item and reserved for celebrations. Glass noodles are traditionally produced from mungbean (*Vigna radiata*) starch, which continues to be a superior raw material (Lii and Chang, 1981). However, Vietnamese canna noodles exhibit sufficiently high tensile strength to satisfy even demanding consumers. They stay firm and lose a minimum of solids during cooking. Being less wasteful and less costly to extract, canna starch has totally replaced mungbean starch as the raw material for glass noodle production.

Attempts to substitute canna starch with less costly sweetpotato starch have had mixed success because noodles made from pure sweetpotato starch are unacceptable to consumers. A proportion of 70% canna

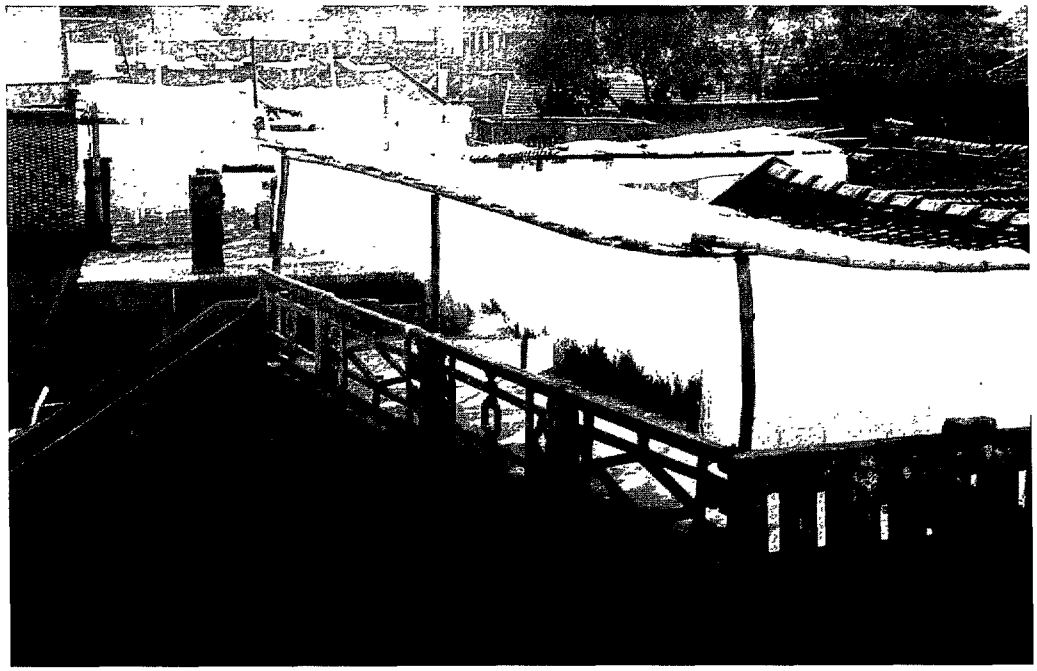

Figure 6. Final drying of noodles on roofs.

starch mixed with sweetpotato starch is deemed appropriate to retain the aspect and consistency of canna noodles (Lan and Huy, 1999).

Discussion and Conclusions

Declining direct consumption of canna in Vietnam and in the Andes is contrary to the occasionally stated view that canna is a promising staple for the poor in montane tropics. Future research and development should focus on canna as a source for starch with functional properties that make it a possible substitute for mungbean starch in glass noodle production, not only in Vietnam but also in other Asian countries. There is mounting evidence for canna starch also being functionally similar to potato starch in shared end products, high peak viscosity, high amylose content, large granule size, crystallinity, and amount of covalently bound phosphorus (Hermann, 1994; Hulleman, 1995; Inatsu et al., 1983; Tu and Tscheuschner, 1981).

Canna and common commercial starches, however, are currently unequal competitors. For example, potato starch is being developed aggressively for a myriad of uses and novel products. In contrast, canna is scientifically neglected. Advanced technologies for its production and processing are unknown and the cultivars used have not been bred for specific uses.

The price competition from other starches, mainly from cassava and sweetpotato, will restrict canna starch use in the medium term to very specific applications. At current prices, it seems unlikely that new markets will open up for canna starch. Efforts should therefore be undertaken to reduce production costs. The Vietnamese retail price of dry canna starch was the equivalent of US$0.70/kg in December 1995. At that price, European high-grade potato starch may well be a threat to the Vietnamese canna starch industry. Opportunities for reducing production cost include:

- increasing extraction efficiency,
- increasing rhizome starch content and starch yield, and
- increasing labor productivity of starch extraction.

Current extraction efficiency ranges from 63 to 77% of total extractable starch. Improved grating surfaces are likely to succeed in releasing more starch from the fibrous rhizome tissue.

The increase of starch content will reduce shipping costs per unit DM and potentially increase starch yields. That will require varietal selection or breeding using Andean material, which is sexually fertile and has greater variability than Asian cultivars (Hermann et al., 1997). Breeding would also have to address the high residual sugar content, which exists at the expense of starch yields and incurs environmental costs as increased organic load in wastewater. Further research is also needed to identify germplasm with improved processing characteristics (extractable starch, oxidative browning).

Increased labor productivity, and probably higher starch quality, could be achieved by using rotary strainers to separate starch milk from fibrous residue. That would replace the onerous task of manual batchwise separation. Such intermediate technology could be produced domestically using blueprints from existing equipment. Stationary paddle washers, which were used to clean canna rhizomes earlier this century in Australia, could also help to reduce processing costs. Alternative technology includes rotating drum washers currently used in small cassava operations in South America. Such equipment would obviate the need for the very labor-intensive removal of adventitious roots.

Other than in wheat-derived pasta with its nonstarch components (especially gluten), the quality of starch noodles depends solely on the functional properties

of the starch itself (Pagani, 1986). Hot canna gels have minimal adhesiveness and outstandingly high elasticity. That, in combination with the productivity of steam-sheeting, explains the wide adoption of this method in Vietnam and its apparent superiority over manual extrusion methods, which are so widely used in the manufacture of sweetpotato noodles in China. Also, hot canna gels are translucent. They do not need to be immersed in water or subjected to other cooling treatments following extrusion to produce the vitreous aspect and desired consistency required for other raw materials.

An assessment of the potential of edible canna, if conducted a few decades ago, would have concluded it was no more than an ethnobotanical curiosity, hardly worthy of promotion and conservation. However, canna use in Vietnam shows how product development can provide novel perspectives for the use of a seemingly obsolete crop. It demonstrates the unpredictability of future germplasm use and illustrates the need to conserve germplasm with no apparent value. Current use patterns of minor crops should not be taken for granted; they may well change over time.

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Compositional Diversity of the Yacon Storage Root

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Yacon is a little-known, nonstarchy Andean root crop, which is eaten raw and functions as fruit in traditional food systems. It belongs to the Asteraceae (sunflower family) and is vegetatively propagated. Botanically, the crop has been referred to until recently as *Polymnia sonchifolia* Poepp. & Endl., but the binomial *Smallanthus sonchifolius* (Poepp. & Endl.) H. Robinson is gaining acceptance among taxonomists (Grau and Rea, 1997).

Yacon is a very productive crop with root dry matter (DM) yields in soils of moderate fertility exceeding 10 t/ha in 6-8 mo. The dark-skinned roots vary from spherical to oblong and weigh from 100 g to 1 kg. The concentration of a yellow orange pigment responsible for yacon's light flesh color varies by genotype. Defining organoleptic attributes of the yacon root are a succulent, tender crunchiness, which approaches that of a watery radish or apple, and a mildly resinous but pleasantly sweet taste.

Smallholders in the Andes cultivate yacon fairly commonly for subsistence. Rarely, however, do the roots reach rural fairs, and reliable production estimates for the crop are not available. Typically, only a few plants or rows are cultivated in field corners or backyard gardens and, through piecemeal harvest, provide a continuous supply year-round. The lack of urban demand for this root is poorly understood, but constraints may include the root's short shelf life of a few days and a lack of consumer familiarity.

The bulk of yacon DM has previously been shown to consist of free sugars and fructans of low polymerization, i.e., fructo-oligosaccharides (FOS) (Ohyama et al., 1990, Wei et al., 1991). FOS consist of short chains of fructose units linked by (2→1) ß-glucosidic bonds. They carry a single D-glucosyl unit at the non-reducing end of the chain (1→2)-α as in sucrose.

The nutritional significance of the sweet-tasting FOS is that the human small intestine has no enzyme to hydrolyze the glucosidic bonds. Therefore, FOS are considered indigestible and serve as dietetic sweeteners. Health benefits are also claimed for fructans. They have been shown to stimulate the growth of bifidobacteria in the human colon, to suppress putrefactive pathogens, and to reduce serum cholesterol concentrations. They are thus increasingly added to pastry, confectionery, and dairy products (Campbell et al., 1997).

There is limited information on the chemical composition of yacon and it mostly comes from one cultivar, presumably Ecuadorian, grown under temperate conditions in Japan. The object of this study was to determine the chemical composition of the yacon root and its variation in a germplasm sample taken from throughout the crop's geographic range in a tropical highland environment. Yacon chemical composition in relation to product development and nutrient removal by harvested roots is examined. This study intends to contribute to the increased use of the biodiversity of this neglected Andean crop in its native range.

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Materials and Methods

Field cultivation

Ten yacon accessions, for which attributes are given in Table 1, were grown in natural soil in an open-sided, insect-proof, quarantine greenhouse in the Tumbaco Valley near Quito, Ecuador, under thermic and light conditions close to the surrounding equatorial environment at 2,500 m altitude. Monthly mean temperatures varied from 14.6°C to 16.0°C, with average daily minimums ranging from 4 to 8°C and maximums from 23 to 29°C. Monthly sunshine was 110-230 h. Before planting, samples taken from the sandy soil had a pH of 7.2-7.5. Nitrogen content of the soil ranged from 22 to 30 µg/ml soil (low), P content 80-200 µg/ml (high), and K content 0.29-0.68 meq/100 ml soil (medium to high). Three to four plots per accession were used in a completely randomized design.

Pre-rooted apical cuttings were planted on 12 Aug 1995, at a spacing of 1 m x 0.7 m. Mineral fertilizers at the rate of 50 kg N/ha and 100 kg K/ha were applied 4 wk after planting, at which time the plants were hilled up. Plots were weeded at 2 and 4 mo after planting. Furrow irrigation was provided as needed.

Chemical composition determination

When all accessions had become senescent (8 mo after planting), 2 plants/plot were harvested, yielding 20-50 roots with root fresh wt of 6-10 kg. Harvested roots were speedily delivered to the laboratory, where they were peeled and chopped into 1-1.5 cm cubes. The cubes were thoroughly mixed and a sample of 1-2 kg was taken for subsequent analysis. One-third of the sample was used to extract juice with a kitchen extractor for determining the refractometric index (°Brix). The remaining root cubes were immediately frozen and subsequently freeze-dried. Dried samples were ground to the consistency of flour and stored at –80°C until analysis. All values obtained for freeze-dried material were corrected to a fresh wt basis.

Moisture content (MC) was determined for fresh and freeze-dried root material by vacuum oven drying for 24 h at 70°C, fat by Soxhlet extraction using petroleum ether as solvent, protein as Kjeldahl N x 6.25, and

Table 1. Geographical attributes and mitotic chromosome number of yacon clones used in this study.

Accession[a]	Year collected	Country	Province	Locality	Altitude (m)	Latitude	Longitude	Mitotic chromosomes
ASL 136	1992	Peru	Cajamarca	Chota	2,900	06°33'S	78°38'W	87
AW 5075	1991	Peru	Cajamarca	Cancan	2,600	07°11'S	78°19'W	58
ARB5027	1991	Peru	Lima	Tintín	3,200	12°20'S	75°47'W	58
ARB5073	1991	Peru	Cajamarca	Sucre	2,600	06°56'S	78°08'W	58
ARB5074	1991	Peru	Cajamarca	Sucre	2,600	06°56'S	78°08'W	58
ECU1243	1984	Ecuador	Azuay	Cumbe	2,560	03°10'S	78°09'W	58
HN1013	1992	Argentina	Jujuy	Bárcena	1,900	23°58'S	65°26'W	58
MHG919	1991	Bolivia	Cochabamba	Pairumani	2,600	17°25'S	66°20'W	58
MHG923	1991	Bolivia	Cochabamba	Paracti	2,100	17°10'S	65°55'W	58
MHG927	1991	Bolivia	Cochabamba	Locotal	1,800	17°10'S	65°45'W	58

[a] Accession ECU1243 is maintained by Instituto Nacional de Investigaciones Agropecuarias, Quito, Ecuador; all other accessions are kept in the CIP genebank.

ash (minerals) by incineration at 550°C for 4 h. Potassium and Ca were determined by flame spectrophotometry, P spectrophotometrically (molybdovanadate method). Crude fiber was determined on defatted samples using the Fibertec system (Tecator A.B., Högenäs, Sweden). We calculated total carbohydrates as total DM less protein, fat, and ash.

Free sucrose, glucose, and fructose were extracted with water at 70°C for 30 min and determined with a high performance anion exchange chromatograph (HPAEC). Fructans were determined indirectly by a novel method adapted from Hoebregs (1997). This method relies on the acid hydrolysis of the sample, followed by HPAEC determination of the released sugars as was done for free sugars.

Hydrolysis depolymerizes fructans and sucrose into its component sugars, glucose and fructose. By determining the glucose and fructose content before hydrolysis (G_{free}, F_{free}) and after hydrolysis (G_{total}, F_{total}), and considering the loss of water in the hydrolysis of sucrose, we can calculate glucose and fructose released from fructans as

$$G_{Fructans} = G_{total} - G_{free} - S/1.9 \text{ and}$$

$$F_{Fructans} = F_{total} - F_{free} - S/1.9$$

where G = glucose, F = fructose, and S = sucrose. The average degree of polymerization (DP) of fructans is then

$$DP = F_{Fructans} / G_{Fructans} + 1$$

and the quantity of fructans originally present in the sample becomes

$$\text{Fructans} = C\,(F_{Fructans} + G_{Fructans})$$

where C is a constant correcting for water gained for each glucosidic bond during polymerization:

$$C = [180 + 162\,(DP - 1)] / 180 \cdot DP.$$

The caloric value per 100 g edible portion was calculated using a formula adapted from Merrill and Watt (1973), namely: kcal = (3.36 x % protein) + (3.60 x % [total carbohydrates – fructans]) + (8.37 x % fat). This formula assumes that no fructans are metabolized in humans. A handheld Atago refractometer was used to determine °Brix at 18°C. Duncan's multiple range test and Pearson correlation coefficients were calculated using SAS procedures GLM and CORR, respectively. Principal component analysis was done with NTSYS-pc, v. 1.80 (SAS, 1989; Rohlf, 1992).

Results

Chemical composition of yacon relative to root fresh matter (FM) is shown in Table 2. Composite factors relative to root DM are shown in Table 3. For all 10 accessions low values and narrow ranges of DM (98-136 g/kg) and carbohydrate content (89-127 g/kg) were found, especially when accession AW5075 was excluded. Carbohydrates accounted for 91-94% of DM. Discounting the outlying accession AW5075, the accessions also had narrow ranges for fructans (50-89 g/kg FM, 52-66% DM) and total free sugars (18-31 g/kg FM, 14-29% DM). By contrast, AW5075 had a much reduced fructan content (31 g/kg FM, 32% DM) and correspondingly high free sugar content (42 g/kg FM, 43% DM). This accession matured precociously and, when harvested, had started developing new sprouts.

Accession ASL136 had the highest values for DM, total carbohydrates, fructans, and °Brix. This accession from Peru is also distinguished by its dodecaploid nature (9A + 3B = 2n = 87; A = 7, B = 8) from the other material (Table 1), which has been shown by Salgado (1996) to be octoploid (6A + 2B = 2n = 58). In a recent field trial of 24 Peruvian accessions, ASL136 ranked among the highest in DM content and yield (C. Arbizu, CIP, Lima, Peru, 1999, pers. comm.) thus underscoring

Table 2. Chemical composition of 10 yacon accessions per 1 kg of root fresh matter.

Variable	Range	Mean	C.V.	Accessions[a]									
			(%)	ASL136	AW5075	ARB5027	ARB5073	ARB5074	ECU1243	HN1013	MHG919	MHG923	MHG927
Dry matter (g)	98-136	115	8	136 a	98 d	114 bc	115 bc	109 cd	111 bc	109 cd	118 bc	123 b	120 bc
Total carbohydrates (g)	89-127	106	8	127 a	89 d	104 bc	105 bc	100 cd	102 bcd	100 cd	111 bc	114 b	112 bc
Fructans (g)	31-89	62	23	89 a	31 d	62 bc	61 bc	50 c	59 bc	58 bc	68 b	74 b	72 b
DP	3.6-4.3	3.9	6	4.2 a	4.3 a	3.8 bcd	3.6 e	3.6 de	4.2 a	3.7 cde	3.9 bc	4.0 b	3.9 bc
Total free sugars (g)	18-42	26	27	19 cd	42 a	27 bc	26 bcd	31 b	24 bcd	24 bcd	22 cd	20 cd	18 d
Free glucose (g)	2.3-5.9	3.4	32	2.8 d	2.3 d	2.8 d	4.5 b	5.9 a	2.4 d	4.0 bc	3.0 d	3.3 cd	2.8 d
Free fructose (g)	3.9-21.1	8.5	58	4.6 c	21.1 a	9.4 bc	7.5 bc	9.3 bc	11.4 b	6.6 bc	5.6 c	3.9 c	4.3 c
Free sucrose (g)	10-19	14	18	12 cd	19 a	15 bc	14 bcd	16 ab	10 d	13 bcd	13 bcd	12 bcd	11 d
°Brix	9.0-12.6	10.7	9	12.6 a	9.0 c	10.6 abc	10.6 abc	9.9 bc	10.7 abc	10.2 bc	10.8 abc	11.8 ab	11.1 abc
F_{tot}/G_{tot} ratio	1.95-2.86	2.38	12	2.64 b	2.84 ab	2.36 c	2.07 d	1.95 d	2.86 a	2.14 cd	2.35 c	2.34 c	2.37 c
Protein (g)	2.7-4.9	3.7	19	3.3 de	3.5 cde	4.7 ab	4.9 a	3.7 cde	4.3 abc	3.8 bcd	2.7 e	2.7 e	3.7 cde
Fiber (g)	3.1-4.1	3.6	8	3.6 abc	3.5 bcd	3.3 cd	3.7 abc	3.8 ab	4.1 a	3.4 bcd	3.1 d	3.6 abc	4.0 a
Fat (mg)	112-464	244	43	191 cde	289 bc	171 de	311 b	464 a	234 bcd	331 b	118 de	194 cde	112 e
Energy (kcal)	148-224	174	12	148 c	224 a	170 bc	177 bc	197 ab	168 bc	165 bc	163 c	155 c	156 c
Ash (mg)	4,275-6,014	5,027	10	5,630 ab	4,881 abc	5,071 abc	4,931 abc	4,357 bc	5,369 abc	5,015 abc	4,275 c	6,014 a	4,944 abc
Calcium (mg)	56-131	87	25	68 def	84 bcde	94 bc	92 bcd	103 b	131 a	76 cdef	61 ef	101 b	56 f
Phosphorus (mg)	182-309	240	17	291 abc	197 d	240 abcd	245 abcd	204 d	302 ab	232 bcd	182 d	309 a	224 cd
Potassium (mg)	1,843-2,946	2,282	15	2,859 ab	1,969 c	2,267 bc	1,999 c	1,843 c	2,361 abc	2,327 abc	2,065 c	2,946 a	2,382 abc

[a] Means followed by a common letter are not significantly different at $P < 0.05$ by DMRT.

Table 3. Carbohydrate composition of 10 yacon accessions relative to root dry matter (%).

Accession	Total Carbohydrates	Fructans	Total free sugars	Free glucose	Free fructose	Free sucrose
ASL136	93	66	14	2.0	3.4	8.5
AW5075	91	32	43	2.3	21.6	19.5
ARB5027	91	54	24	2.5	8.3	13.3
ARB5073	91	53	22	3.9	6.4	12.0
ARB5074	92	46	29	5.4	8.7	14.7
ECU1243	91	52	23	2.1	11.1	9.4
HN1013	92	53	22	3.8	6.1	12.1
MHG919	94	58	19	2.6	4.9	11.3
MHG923	93	60	16	2.7	3.2	10.1
MHG927	93	60	15	2.3	3.6	9.1

its production potential. At a root production of 50 t/ha, which underestimates yield potential of yacon under reasonable soil fertility, ASL136 would have yielded 4.5 t fructans/ha. From the same root production, fructose and sucrose totaling 5.8 t/ha could have been obtained through hydrolysis of fructans and from free sugars (calculations not shown).

Free glucose and fructose were among the most variable root parameters; with C.V. 32% for free glucose and C.V. 58% for free fructose. There was a significant and highly negative correlation between fructans and free fructose (-0.88, Table 4) indicating the interrelation of these metabolites in depolymerization. Interestingly, free fructose was positively correlated to DP (0.42), which suggests that polymer elongation increased with the size of the fructose pool.

Conversely, high glucose concentrations are associated with lower DPs (r = -0.68), perhaps because they increase the number of fructan molecules *competing* for free fructose. Although there were significant differences of DP between accessions, the range was narrow 3.6-4.3 (C.V. = 6%). The ratio of total fructose to glucose (F_{tot}/G_{tot}) indicates that in a syrup obtained after acid hydrolysis of yacon root carbohydrates, fructose would be present at a concentration 2-3 times greater than glucose (Table 2).

As shown in Table 4, °Brix was highly and positively correlated with fructan content (r = 0.84) and DM (r = 0.86), which suggests that refractometric measurements provide convenient and quick assessments of these important variables. Free fructose, sucrose, and total free sugars are noted for their inverse correlation with the refractometric index as well as fructans. That implies accessions high in fructans are low in free sugars. Noncarbohydrate compounds are omitted from Table 4, since they were only weakly correlated among themselves and with carbohydrate variables.

As Table 2 shows, yacon is a poor source of protein (2.7-4.9 g/kg FM). It is also low in lipids (112-464 mg/kg FM), but has moderate levels of fiber (3.1-4.1 g/kg FM). It is a good source of K (1.8-2.9 g/kg FM), a little less than half of its total mineral content. Food energy ranged from 148 to 224 kcal/kg FM and is several times lower than for comparable foods.

Using the variables shown in Table 2, a principal component analysis (PCA) was computed. The first component explained 54% of total variation; the second accounted for 20%. PCA did not reveal any

Table 4. Pearson correlation coefficients[a] of chemical variables of yacon root fresh matter.

Variables	Dry matter	Free glucose	Free fructose	Free sucrose	Total sugars	Fructans	°Brix	DP[b]
Dry matter	1							
Free glucose	-.13	1						
Free frucose	-.77 a	-.16	1					
Free sucrose	-.58 a	.13	.75 a	1				
Total sugars	-.76 a	.08	.94 a	.91 a	1			
.Fructans	.95 a	-.14	-.88 a	-.75 a	-.90 a	1		
°Brix	.86 a	-.20	-.69 a	-.57 a	-.71 a	.84 a	1	
DP	-.04	-.68 a	.42 a	.03	.20	-.07	.01	1

[a] Computed across repetitions: n = 36; a = significant at $P < 0.01$.

[b] Degree of polymerization.

geographically defined clusters of accessions (Figure 1). That suggests yacon chemical diversity is not partitioned into geographical subgroups, which would allow the search for special characteristics in germplasm from certain areas. Carbohydrate variables were highly correlated with the first and second principal components (data not shown). Thus, these variables contribute more than others in differentiating yacon clones by chemical characteristics.

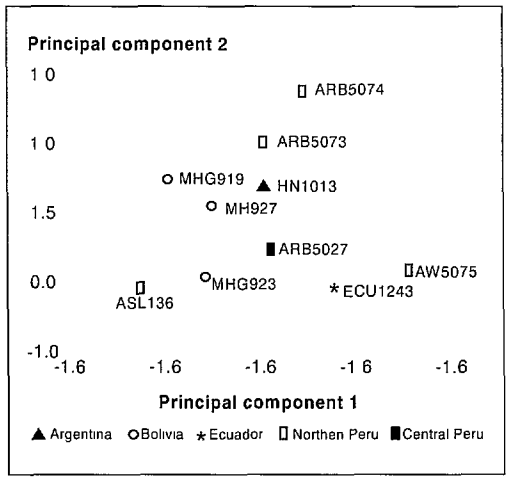

Figure 1. Principal component analysis on compositional data of 10 yacon accessions.

Discussion and Conclusions

The yacon accessions used in this study were collected between 1984 and 1992 during multicrop missions or as chance collections (Table 1). Thus they were not the result of a systematic collection effort aimed at capturing maximum yacon diversity. Northern Peru, with four accessions, and Cochabamba Department, Bolivia, with three accessions, are likely to be over-represented in the sample. The collection sites, however, describe an area that is congruent with the distribution of the species, which stretches from Ecuador to northern Argentina. Also, the accessions come from widely differing ecologies and a considerable altitudinal range. Therefore, samples do encompass a reasonably large part of yacon diversity, permitting conclusions about compositional diversity from the data obtained.

Although claims for high inulin content in yacon continue to be made, most prominently in the often cited *Lost Crops of the Incas* (NRC, 1989), the consistently low DP in 10 yacon accessions (3.6-4.3) shows that yacon fructans are of low molecular weight. This is in agreement with Ohyama et al. (1990). Yacon fructans are therefore different from the inulins in chicory (*Cichorium intybus*) with a DP range of

7-12 and individual fructan chains up to 80 fructose units long (Van Waes et al., 1998). High molecular weight inulin also accounts for most of the carbohydrates in Jerusalem artichoke (*Helianthus tuberosus*) (Praznik and Beck, 1987; Wei et al., 1991). Yacon also differs from Jerusalem artichoke in that it has significant fructose and glucose contents. Fructose accounts for 3-22% of root DM, glucose for 2-5% (Table 3).

In the calculation of food energy (148-224 kcal/kg FM), we have assumed that fructans behave as dietary fiber in the intestinal tract (Quemener et al., 1994) and make no caloric contribution during digestion. Fructans are unlikely to be broken down to a significant extent by stomach acidity, but some degradation occurs in the colon due to bacterial fermentation (Silva, 1996). Therefore, our food energy values somewhat underestimate true caloric values. In any case, food energy of yacon is very low and fully justifies the root's reputation as a low-caloric diet food.

The data do not support the notion of chemical differentiation of yacon along geographic gradients (Figure 1). Overall, there was little compositional diversity in the 10 yacon accessions. Carbohydrate variation due to physiological factors (e.g., plant age) and postharvest conditions (e.g., storage duration) appear to have much more practical relevance than genetic differences. For example, Ohyama et al. (1990) observed fructans to be reduced to 20% of DM after storage for 3 mo "under cold conditions." Also, Wei et al. (1991) report decreasing fructans and increasing fructose after storage. Considerable compositional changes also occur during the traditional *soleado* treatment after harvest. It involves spreading the harvested roots in an unshaded place for a week or so. That results in increased root sweetness and a concomitant rise in °Brix (Hermann, unpublished data), which, apart from respirative water loss, is most likely due to the incremental de-polymerization of fructans.

Highest DM and fructan yields (accession ASL136) were associated with dodecaploidy compared with octoploidy in the other accessions. This provides a pointer for identifying superior germplasm and for breeding yacon.

Based on Table 2, nutrient removal from the field per t root FM can be calculated as 0.4-0.8 kg N, 0.2-0.3 kg P, and 1.8-2.9 kg K. These data allow an approximation of minimal fertilizer requirements for yacon. The ranges for nutrient removal per 100 kg soluble carbohydrate produced (fructans and free sugars) are 0.5-0.9 kg N, 0.2-0.4 kg P, and 2.3-3.2 kg K. These figures identify yacon as not only high in N-use efficiency but also demanding in its K requirements.

Despite its high fructan productivity, yacon is unlikely to become a source of purified dietetic sweeteners or fructose products in the near future. That is because of several factors including 1) lack of suitable extraction technology and industrial scale production, 2) competition from very low priced, high-fructose syrups from corn starch, and 3) protectionism of sugar markets.

It is more likely that processed yacon products requiring little or no refining could be targeted as a natural or low-calorie food to a health-conscious clientele. Entrepreneurial farmers in Brazil and Japan have already seized this opportunity and are producing a number of processed yacon products for niche markets (Grau and Rea, 1997; Kakihara et al., 1997). One such product consists of air-dried tuber slices, which resemble dried apples. Current research at CIP examines processing parameters bearing on final product quality.

Another potentially interesting product is unrefined yacon syrup. It could be marketed as a dietetic sweetener the consistency of honey and possibly priced at the same level. Yacon syrup-making in rural Andean settings could find much

inspiration from makeshift technology developed in the early days of maple syrup production. The challenge for yacon product development is to design research interventions that will allow Andean farmers to retain some of the value added through processing.

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Training

Training activities at CIP over 1997-98 focused on responding to programmatic changes as well as to our various stakeholders' interests. At the regional level, special efforts were made to strengthen knowledge for accelerating enhancement in improved varieties of resistance against late blight, bacterial wilt, viruses, and pests. Another area that received special training attention was the use of technologies aimed toward sustainable production, such as improved potato propagation and crop management practices.

CIP uses a dynamic, participatory training method. This combines exposure to recently developed advanced techniques with hands-on experience emphasizing procedures that are directly applicable to working conditions in developing countries. The method enhances active participation and information exchange and aims to expand the capabilities of partner organizations and strengthen collaboration with them. Such a methodology allows faster research progress, identifies those elements that need further work at the national level, and gives the opportunity to solve constraints of common interest. We present below an overview of group and individual training, and close with our vision for training in the future.

Group training activities included courses, workshops, conferences, and symposia conducted both at headquarters and in-country. Strong emphasis was also given to individualized training, an effective way to continue developing the research skills of collaborators and partners throughout the developing world. Over 1,000 research scientists and development agents across the globe were trained during 1997-98 in activities organized and conducted by CIP. Another 911 persons participated in 27 CIP-facilitated training events in Peru (Table 1).

Table 1. All group training activities and participants during 1997-98.

Course focus	Activities	Participants
Potato	18	372
Sweetpotato	18	474
Andean roots and tubers	3	50
Natural resources management	6	123
Total	**45**	**1,019**
CIP-facilitated activities		
CONDESAN	2	23
Other Peru-based	25	888
Total	**27**	**911**

Potato

Training courses and workshops in potato addressed six subject matter areas. Courses in these areas varied in content according to specific needs. The course theme, numbers of participants, activities, and the countries represented are shown in Table 2.

Courses on **improved potato propagation techniques and sanitary control** are in continuous demand because there is an urgent and constant need to produce higher quality seed of newly developed genetic materials that have improved productivity and resistance to pests and diseases. The program content of these activities includes agronomic aspects, formal and informal seed systems, sanitary control procedures, seed storage and marketing, and organizational aspects of seed programs. All topics are from the perspective of an integrated seed potato industry.

The major focus in **potato germplasm management** courses is to train scientists and help them develop research activities that use biotechnological techniques to accelerate breeding progress for improved resistance to pests and diseases. This involves equipping scientists from developing countries to use advanced laboratory techniques in their own countries.

Training materials, such as a specialized manual, videos, and other publications, were developed for supporting training activities in those locations having the highest potential for adopting **true potato seed** as an alternative to traditional potato propagation. Mainly, the techniques and methods used in TPS production and use are addressed.

Training activities in **integrated pest management** provide information on the latest developments in control and management of the principal potato pests using IPM

Table 2. Group training activities on potato-related subjects.

Course	Activities	Participants	Countries represented
Potato propagation systems and techniques	4	43	Argentina, Bolivia, Colombia, Ecuador, Ethiopia, Guatemala, Kenya, Nicaragua, Peru, Venezuela,
Potato germplasm conservation	2	34	Kenya
True potato seed (TPS)	3	63	Bangladesh, Egypt, India, Nepal, Peru, Sri Lanka, Thailand
Integrated pest management (IPM)	4	112	Argentina, Bolivia, Colombia, Ecuador, Guatemala, Peru
Integrated management of late blight	5	120	Argentina, Bolivia, Chile, Colombia, Panama, Peru, Venezuela, USA,
Total	**18**	**372**	
CIP-facilitated group training in Peru			
Natural resources management	5	88	
Postharvest and marketing	3	63	
IPM	6	310	
Seed production	11	472	
Total	**25**	**888**	

techniques. Training is based on sharing experiences from pilot locations in key potato-producing areas endemically affected by the most serious pests.

The **integrated management of late blight** courses combine a wide range of components to reduce the effects of this devastating disease. Training emphasizes current biotechnological tools for the use and enhancement of potato germplasm and conventional breeding needs as a means to search for resistance that could improve crop performance in areas regularly threatened by the disease. In 1997-98, pilot testing began of the farmer field school (FFS) approach, new to Latin America but used widely in Asia. Among other benefits identified by farmer participants was an improved understanding of the principles involved in disease progression and management. This success has led to research into how farmers' new knowledge helps them to reduce losses and increase profits.

Sweetpotato

Subjects covered by the training program on sweetpotato included germplasm management, breeding and production, integrated pest management, and postharvest and marketing. The number of activities and participants' countries are shown in Table 3.

Germplasm management training focused on taxonomy, biodiversity, propagation, and conservation of sweetpotato germplasm. Special attention was given to the morphological identification of genotypes, maintenance of genebanks (in situ and in vitro), and rapid multiplication of clonal material.

The objective of **breeding and production** courses was to train selected farmers on sweetpotato seed production, with an emphasis on the practical knowledge and skills needed in seed and participatory research procedures to select and evaluate new, improved varieties. The courses covered growth physiology, climate, soil and nutrient requirements, genetic resources, morphological characterization, breeding and selection approaches, evaluation and variety release procedures, management of cropping systems, pests and diseases of sweetpotato, tissue culture and micropropagation techniques, production methods, and postharvest management.

A program of **training of trainers** (TOT) was initiated in Indonesia at the request of

Table 3. Group training activities on sweetpotato-related subjects.

Course	Activities	Participants	Countries represented
Germplasm management	3	93	Cameroon, Dem. Rep. of the Congo, Ethiopia, Ghana, Indonesia, Kenya, Madagascar, Malawi, Malaysia, Mozambique, Myanmar, Nigeria, Philippines, Rwanda, Senegal, Tanzania, Thailand, Zambia
Breeding and production	12	338	Bangladesh, Burundi, China, Ethiopia, Indonesia, Kenya, Malawi, Malaysia, Mozambique, Philippines, Rwanda, Tanzania, Uganda, Zambia
Integrated pest management	1	11	Zambia
Postharvest and marketing	2	32	China, Ethiopia, Kenya, Malawi, Uganda, Zambia, Zimbabwe
Total	**18**	**474**	

several NGOs and in collaboration with several development agencies operating locally. The participants planned the implementation of sweetpotato farmer field schools in six districts of Java, with a goal of introducing sweetpotato production technology into an FFS program.

The integrated pest management courses emphasized management of sweetpotato weevil, fresh and dry storage, and maintenance and multiplication of planting material, as well as planning, implementing, monitoring, and preparing follow-up and evaluation of IPM program activities at the field level. In turn, CIP gained information from participants on the importance and constraints in sweetpotato production in their country, and obtained feedback from participants on the practicality of suggested management strategies. Successful IPM experiences in some countries are used to illustrate the potential of a particular control strategy.

The general aim of **postharvest and marketing** training was to develop the skills of NARS researchers in agricultural marketing research. This involved familiarizing participants with standard methods for analyzing agricultural marketing in developing countries, providing hands-on instruction in these methods in both classroom and field and offering feedback about on-going and proposed marketing research by specialists and institutions, including the organizing CG centers and NARS in the region. Briefings were given on funding opportunities for market-oriented research. Participants practiced developing concept notes for research projects.

Andean Root and Tuber Crops

Fifty scientists from Andean countries received training in germplasm characterization of Andean root and tuber crops (ARTC), production, and postharvest and processing (Table 4).

Participants of Bolivia and Ecuador attended a course on germplasm characterization, which was conducted in Peru. The goal was to train scientists in the techniques needed to identify duplicates within ARTC germplasm collections. Twenty-five national scientists from Peru, Bolivia, Ecuador, Brazil, and Colombia participated in a course on the production of Andean root and tuber crops. A new training manual especially developed for production of ARTC was used in this course.

Twenty-one participants from Bolivia, Colombia, Ecuador, and Peru attended an international workshop on Andean food crops held in Lima, Peru. The participants represented different projects operating in the Andes. Workshop discussion results were used for coordinating future research and development efforts in Andean food products, within the framework of CONDESAN, the Consortium for the Sustainable Development of the Andean Region.

Natural Resources Management

A first course on watershed management was organized by CIP in Peru, in collabora-

Table 4. Training activities on Andean root and tuber crop-related subjects.

Course	Activities	Participants	Countries represented
Germplasm conservation	1	4	Bolivia, Ecuador, Peru
Andean root and tubers production	1	25	Bolivia, Brazil, Colombia, Ecuador
Postharvest and processing	1	21	Bolivia, Colombia Ecuador, Peru
Total	**3**	**50**	

tion with several local organizations. These local organizations actively participate in projects related to the conservation and sustainable improvement of agriculture in Andean watersheds. The course program emphasized relationships between biological and social sciences in the context of watershed management. Other course topics included soil and water management, conservation and use of biodiversity, ecological zoning, climatology, GIS, and industrialization potential of agricultural products. Five short courses were organized for Latin American countries on simulation modeling and one in Uganda for supporting research activities (Table 5).

Individualized Training

National scientists from Africa, Asia, and Latin America received training at CIP laboratories and facilities at Lima headquarters and CIP's regional office in Nairobi, Kenya (Table 6). Training subjects featured were potato seed production, micropropagation and tissue culture techniques, advanced methods for virus characterization, antisera production and detection techniques, as well as biotechnological training concentrating on methods such as RFLP, AFLP, RAPD, and genetic manipulation in potato.

International and Intercenter Collaboration in Training

There are several excellent examples of international and intercenter cooperation in our training over 1997-98. A regional workshop for the conservation and utilization of sweetpotato, cassava, and yam in Sub-Saharan Africa (SSA) took place in Kenya. The system-wide genetic resources program comprising CIP, IITA, IPGRI, and the National Network of PRAPACE and SARRNET sponsored this workshop. Forty-eight national scientists participated. Two courses on postharvest and marketing of sweetpotato were conducted in Kenya and Uganda in collaboration with ICRAF, ILRI, ICRISAT, and IFPRI. This was a short training course on methods for analyzing agriculture markets in SSA and was attended by 23 participants from this part of Africa. Participants were familiarized with standard marketing analysis procedures and received hands-on instruction on market oriented research. In 1997, CIP staff gave lectures on the potato and sweetpotato related issues at an IITA-organized regional course on product and market development for roots and tuber crops.

In conjunction with national collaborators, a workshop on root processing technology took place in Chengdu, in the Peoples Republic of China. Forty-seven participants received a solid foundation in the knowledge of starch structure, properties, and application. The program included visits to starch and noodle factories in Sichuan to assess adoption of Sichuan Academy of Agricultural Sciences-CIP project results and for planning future research needs.

Collaboration with regional networks in Sub-Saharan Africa resulted in a course on

Table 5. Group training activities on natural resources management.

Course	Activities	Participants	Countries represented
Watershed management	1	14	Argentina, Bolivia, Chile, Ecuador, Peru
Simulation modeling	5	109	Bolivia, Brazil, Chile, Colombia, Ecuador, Guatemala, Mexico, Nicaragua, Peru , Uganda
Total	**6**	**123**	

Table 6. Individual training.

Subject	Participants	Countries represented	Venue
IPM	5	Colombia, Ethiopia, Indonesia, Peru	HQ(4), SSA(1)
Virology	3	Argentine, Senegal, Thailand	HQ(2), SSA(1)
Germplasm management and molecular techniques	18	Angola, Argentina, Bolivia, Brazil, Chile, Korea, Peru, Zaire	HQ(18)
Pathology	13	Argentina, Bolivia, Chile, Ecuador, Peru, Syria	HQ(12), SSA(1)
Breeding	5	Ethiopia, Iran, Korea, Peru, Uganda	HQ(4), SSA(1)
Potato propagation	15	Angola, Brazil, Iran, Kenya, Peru, Senegal, Syria, Vietnam	HQ(4), SSA(11)
Natural resources	2	Argentina, Peru	HQ(2)
Communications	2	Argentina, Peru	HQ(2)
Total	**63**		

HQ = Headquarters in Peru; SSA = Sub-Saharan Africa (CIP Regional Office and KARI).

food dehydration by solar drying and sweetpotato flour processing. Nine participants from Kenya, Tanzania, and Uganda attended this course held in Uganda.

CIP collaborated in the organization of two national courses in Ecuador and one in Peru on soil management with 81 participants from various development agencies. Also, CIP staff collaborated on two courses on management of natural resources organized in Uganda and Vietnam D.R. in which 120 national personnel from different research and extension organizations participated.

The Future: Developing a Vision for Training

In 1998, a highly participatory process set the basis for CIP's training program strategy. In this Training Vision, CIP's program is seen as a mechanism to efficiently overcome current constraints and effectively identify emerging opportunities. Fulfilling this vision will (1) enable CIP to streamline research priorities to meet clients' needs, (2) enhance capabilities for faster and better collaborative technology development, (3) facilitate community-level adaptation of improved technologies, and (4) create a bridge between current and future partners throughout the developing world.

CIP's training program will be a vehicle for interaction, input, and collaboration with a wide range of partners enabling the Center to achieve its mandate for potato, sweetpotato, Andean root and tuber crops, and mountain natural resources. It will be inextricably linked with the research agenda and will respond to partners' needs for enhanced research skills and methods. It will provide effective mechanisms for the introduction of technologies to achieve sustainable improvements in the productivity and utilization of CIP's mandate crops, and in the management of natural resources in the developing world. The program will create an international network of highly capable research scientists able to conduct independent studies, to offer skills training to others, and to collaborate effectively in the CIP global community of interest.

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Acronyms and Abbreviations

ADFA	average of diseased foliage area
AFLP	amplified fragment length polymorphism
ARTC	Andean root and tuber crops
ASAR	Asociación de Servicios Artesanales y Rurales (Bolivia)
AUDPC	area under the disease progress curve
BU	blight unit
CAPS	cleaved amplified polymorphic sequence
CEC	Cation exchange capacity
CIAT	Centro Internacional de Agricultura Tropical (Colombia)
CIMMYT	International Maize and Wheat Improvement Center (Mexico)
CONDESAN	Consortium for the Sustainable Development of the Andean Ecoregion
CPRI	Central Potato Research Institute (India)
CPRO	Centre for Plant Breeding and Reproduction Research (Netherlands)
CpTI	cowpea trypsin inhibitor
CMD	cassava mosaic virus disease
DEM	digital elevation model
DNA	deoxyribonucleic acid
ELISA	enzyme-linked immunosorbent assay
ESARC	East and Southern Africa Regional Centre (Kampala, Uganda)
FAO	Food and Agriculture Organization of the United Nations
FFS	farmer field school
FMV	feathery mottle virus
FORTIPAPA	Fortalecimiento de la Investigación y Producción de Semilla de Papa en el Ecuador
FU	fungicide unit
GXE	genotype by environment
GIS	geographic information systems
GUS	b-glucuronidase
Gpi	glucose-6-phosphate isomerase
h.a.i.	hours after inoculation
HDP	high demand and production growth
HH	like polarized
HV	cross polarized
IARC	international agricultural research center
ICAR	Indian Council of Agricultural Research
ICRAF	International Centre for Research in Agroforestry
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
IFAS	immunofluorescence antibody staining
IFAD	International Fund for Agricultural Development

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IFPRI	International Food Policy Research Institute (USA)
IITA	International Institute of Tropical Agriculture (Nigeria)
IMPACT	International model for policy analysis of agricultural commodities and trade (IFPRI)
INERA	national potato and sweetpotato programs of the national agricultural research institute of D.R. of the Congo
INFOANDINA	CONDESAN information network
INIAP	Instituto Nacional Autónomo de Investigaciones Agropecuarias (Ecuador)
INIA	Instituto Nacional de Investigación Agraria (Peru)
INRA	Institut National de la Recherche Agronomique (France)
INTA	Institute Nacional de Tecnología Agropecuaria (Argentina)
IPGRI	International Plant Genetic Resources Institute (Italy)
IPM	integrated pest management
IRRI	International Rice Research Institute
ISO	International Organization for Standardization
KARI	Kenya Agricultural Research Institute
LB	late blight
LMF	leafminer fly
MENA	Middle East and North Africa (CIP region)
MERCOSUR	Southern Common Market
NAFTA	North American Free Trade Association
NARO	National Agricultural Research Organization (Uganda)
NARS	national agricultural research systems
NASH	nucleic acid spot hybridization
NCM	nitrocellulose membrane
NGO	nongovernmental organization
N/m^2	Newtons/m^2 (1 kg m per second squared)
OFE	overland flow element
OM	organic matter
pep	peptidase
PAGE	polyacrylamide gel electrophoresis
PARC	Pakistan Agricultural Research Center
PCR	polymerase chain reaction
PI	proteinase inhibitor
PICTIPAPA	Programa Internacional Cooperativo del Tizon Tardio de la Papa (Mexico)
PPO	project planning by objective
PRAPACE	Programme Régional de l'Amélioration de la Culture de la Pomme de Terre et de la Patate Douce en Afrique Centrale et de l'Est (CIP network)
PRECODEPA	Programa Regional Cooperativo de Papa (CIP network in Central America and the Caribbean)
PROINPA	Proyecto de Investigación de la Papa, National Potato Research Program (Bolivia)
PSTVd	potato spindle tuber viroid
PVY	potato virus Y
QTL	quantitative trait loci
RAPD	randomly amplified polymorphic DNA
rDNA	ribosomal DNA
RFLP	restriction fragment length polymorphism
RKN	root-knot nematode
RRA	rapid rural appraisal
SAAS	Shandong Academy of Agricultural Science (China)

SAPPRAD	Southeast Asian Program for Potato Research and Development
SARRNET	Southern Africa Root Crop Research Network
SBTI	soybean trypsin inhibitor
SCRI	Scottish Crop Research Institute
SDS	sodium dodecyl sulfate
SEINPA	Semilla e Investigacion en Papa (Peru)
SKTI	soybean kunitz trypsin inhibitor
SLW	silverleaf whitefly
SPCFV	sweetpotato chlorotic fleck virus
SPCSV	sweetpotato chlorotic stunt virus (see SPSVV)
SPFMV	sweetpotato feathery mottle virus
SPMSV	sweetpotato mild speckling virus
SPLV	sweetpotato latent virus
SPMMV	sweetpotato mild mottle virus
SPSVV	sweetpotato sunken vein virus
SPVD	sweetpotato virus disease
SWP	sweetpotato whitefly
SSR	simple sequence repeats
t	metric ton (1000 kg/2,200 lbs.)
TAC	Technical Advisory Committee of the CGIAR
TPS	true potato seed
UNICEF	United Nations International Children's Emergency Fund
UPGMA	unweighted pair group method with arithmetic mean algorithm
UPWARD	Users' Perspective with Agricultural Research and Development (CIP network)
WEPP	Water Erosion Prediction Project