BIBLIOGRAPHIC DATA SHEET

1. CONTROL NUMBER	2. SUBJECT CLASSIFICATION (695)
PN-AAJ-076	AH10-0210-0000

3. TITLE AND SUBTITLE (240)

Developments in the control of nematode pests of potatoes; report of the Second Planning Conference, Lima, Peru, 1978

4. PERSONAL AUTHORS (100)

5. CORPORATE AUTHORS (101)

CIP

6. DOCUMENT DATE (110)	7. NUMBER OF PAGES (120)	8. ARC NUMBER (170)
1978	200p.	633.491.I61

9. REFERENCE ORGANIZATION (130)

CIP

10. SUPPLEMENTARY NOTES (500)

11. ABSTRACT (950)

12. DESCRIPTORS (920)

Potatoes
Parasitic diseases
Root knot
Resistance
Pest control
Viral diseases
Nematoda
Disease vectors
Hybridization

13. PROJECT NUMBER (150)

931097300

14. CONTRACT NO.(140)	15. CONTRACT TYPE (140)
AID/ta-G-1492	

16. TYPE OF DOCUMENT (160)

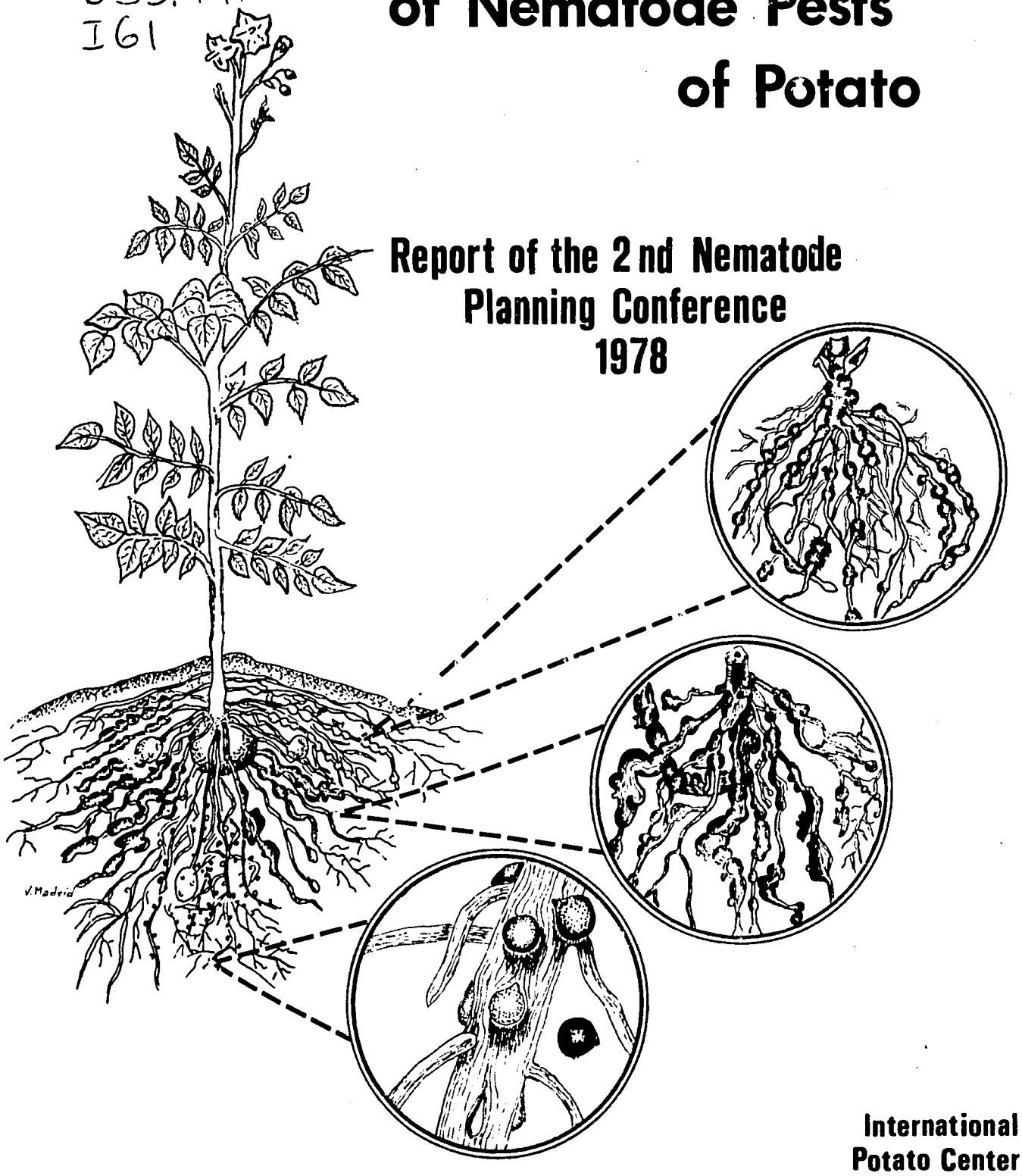
AID 590-7 (10-79)

PN-AAJ-076

Developments in the Control of Nematode Pests of Potato

633.491
I61

Report of the 2nd Nematode Planning Conference 1978



International
Potato Center
Lima Peru

Participants in the Planning Conference shown in front of CIP headquarters in Lima, Peru were (left to right): Drs. A.S. Seshadri, R. D. Winslow, A. F. Van Der Wal, B. B. Brodie, O. Page, H. Mendoza, H. J. Jensen, R. Tarte, C. P. Madamba, M. M. de Scurrah, J. Franco and P. Jatala.

INTERNATIONAL POTATO CENTER

REPORT OF THE

PLANNING CONFERENCE

ON THE

DEVELOPMENTS IN THE CONTROL OF

NEMATODE PESTS OF POTATOES II

Held at CIP - Lima, Perú

November 13-17, 1978

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PLANNING CONFERENCE ON DEVELOPMENTS IN THE

CONTROL OF NEMATODE PESTS OF POTATOES II

A G E N D A

Monday, November 13

	Chairman, morning session. Dr. O. T. Page Director of Research
08:30	Welcome and opening remarks. Dr. R. L. Sawyer Director General
09:00	Tour of CIP research facilities. Dr. P. Jatala
10:00	An overview of the important nematode pests of potatoes. Dr. R. D. Winslow
10:30	Coffee
10:45	Quinquennial Review Mission Report on Nematode Pathogens. Dr. O. T. Page
11:00	Summary of research progress on potato cyst nematode. Dr. M. de Scurrah and Dr. J. Franco
12:00	Lunch

Monday afternoon

	Chairman, afternoon session. Dr. R. D. Winslow
13:30	Summary of research progress on root-knot nematode. Dr. P. Jatala
14:15	Summary of research progress on the false root-knot nematode. Dr. P. Jatala
14:45	Coffee
15:00	Progress on cyst nematode research in The Netherlands. Dr. A. van der Wal
15:30	Progress in Cornell root-knot nematode and cyst nematode contracts. Dr. B. B. Brodie

POTATO CYST NEMATODE

Tuesday, November 14

	Chairman, morning session. Dr. B.B. Brodie
08:30	Breeding for resistance to the potato cyst nematode. Dr. M. de Scurrah and Dr. A. van der Wal
09:30	Identification of resistance and tolerance to potato cyst nematodes and their practical implications. Dr. R. Tarte
10:00	International cyst nematode trials. Dr. J. Franco

10:30	Coffee
10:45	Discussion on means of control of the potato cyst nematode: Practical implications of integrated control measures.
11:30	Formulation of preliminary recommendations.
12:00	Lunch

POTATO ROOT-KNOT NEMATODE

Tuesday afternoon

	Chairman, afternoon session. Dr. C. P. Madamba
13:30	Breeding for resistance to the root-knot nematode. Dr. H. Mendoza
14:15	Identification of resistance and tolerance to the root-knot nematodes and their practical implications. Dr. C. P. Madamba
14:45	International root-knot nematode trials. Dr. P. Jatala
15:00	Coffee
15:15	Discussion on means of control of the root-knot nematode: Practical implications of integrated control measures.
15:45	Formulation of preliminary recommendations.

FALSE ROOT-KNOT AND OTHER NEMATODES

Wednesday, November 15

	Chairman, morning session. Dr. A. S. Seshadri
08:30	*Nacobbus aberrans*: Importance and Control. Dr. P. Jatala
09:15	*Pratylenchus species*: Importance and Control. Dr. H. J. Jensen
10:00	Coffee
10:15	Other nematode pests: Importance and Control. Dr. R. D. Winslow
11:00	Interrelationships of nematodes and other organisms in disease complexes. Dr. H. J. Jensen
12:00	Lunch

BIOLOGICAL INTERACTIONS AND CONTROL

Wednesday afternoon

	Chairman, afternoon session. Dr. A. van der Wal
13:30	Interaction studies at CIP. Dr. P. Jatala

14:00	Nematode Virus Vectors Dr. R. A. C. Jones
14:30	Biological and cultural control of potato nematodes. (Discussion). Dr. P. Jatala and Dr. A. van der Wal
15:00	Chemical control of potato nematodes. Dr. A. S. Seshadri
15:30	Coffee
15:45	Integrated pest management in controlling potato nematodes. Dr. B. B. Brodie

FORMULATION OF RECOMMENDATIONS

Thursday, November 16

A committee of three will formulate recommendations arising from presentations and discussions during the first three days of the Conference.

Participants not involved in developing recommendations will have the opportunity for discussions with CIP staff or to visit CIP facilities in Huancayo.

GENERAL DISCUSSION OF IMPORTANT NEMATODE PESTS OF POTATOES: APPROVAL OF RECOMMENDATIONS

Friday, November 17

	Chairman Dr. O. T. Page
08:30	General Discussion of Important Nematode Parasites of Potatoes. a) Assessing importance of specific nematodes. b) Communication of information on control of nematodes to regional research scientists. c) Integration of field trials.
10:00	Coffee

APPROVAL OF RECOMMENDATIONS

10:15	Final discussions and approval of recommendations.
12:00	Lunch

Friday afternoon

13:30	Continuing discussion and approval of recommendations.

RECOMMENDATIONS

1. General Recommendations

In reviewing the progress CIP nematologists have made, we recognize that many basic problems have been successfully solved. In the coming 5 years the greater part of the institutes efforts in nematology should be directed to the incorporation of resistant sources into advanced material and the release of this material for regional evaluation. At the same time we recommend the further development of screening methods to improve screening capacity.

We further recommend a higher level of specialization within the Department. The main areas of interest are:

(1) breeding (incorporation of resistance to various nematodes into advanced material);

(2) development of methodology and large scale screening for resistance; and

(3) nematological research that complements CIP's nematode control program.

Apart from these three, CIP's nematologists should consider their contribution to integrated pest management.

2. Potato Cyst Nematode

2.1 Screening for Resistance

21.1 Some high levels of resistance to potato cyst nematodes have been found but we RECOMMEND that further search be made because the genetic base is too small.

21.2 We RECOMMEND initial screening to be reduced to only Huancayo (P_4A) and Otuzco (P_5A) populations. Once resistance has been found to these pathotypes screening against other pathotypes must be done.

21.3 We RECOMMEND studies be initiated on intermediate levels of resistance, for example zero population density change, to determine the field usability of this type of resistance.

2.2 Breeding for Resistance

We RECOMMEND that ALL CURRENTLY AVAILABLE RESISTANT CLONES AND THOSE IDENTIFIED LATER BE TRANSFERRED IMMEDIATELY INTO ADVANCED MATERIAL even if they have resistance to a single pathotype. CIP scientists should monitor the resistances once they have been introduced into the field.

2.3 Tolerance

Because of the expected usefulness of tolerance in areas of high population densities and diverse or unknown pathotypes, we RECOMMEND development of screening methods to detect tolerance (contract). We further RECOMMEND that the search for sources of tolerance continues at CIP according to currently available techniques initially in advanced material.

2.4 Pathotypes

Previous work on pathotype identification at CIP has provided an excellent insight into the present pathotypes situation. Therefore, we RECOMMEND that further identification of pathotypes be limited to the present CIP collection of populations. We further RECOMMEND that new collections be made only in relation to the introduction and performance of new resistant cultivars.

3. Root-Knot Nematodes

3.1 Screening for Resistance

Rapid progress has been made in detecting high levels of resistance to root-knot nematodes. We RECOMMEND that available sources of resistance be transferred into advanced material immediately. We also RECOMMEND that no search for additional sources of resistance be made at the present. However, we RECOMMEND that this high level of resistance be evaluated against other species of *Meloidogyne* either in cooperation with the International Meloidogyne Project or at other institutions.

3.2 Breeding for Resistance

We RECOMMEND that the current level of emphasis on combining root-knot resistance and bacterial wilt resistance with other desirable traits be continued.

3.3 Pathotypes (Races)

Because of the work on identification of races of Meloidogyne spp. is being carried out by the International Meloidogyne Project, we RECOMMEND that any work on races of these nematodes done by CIP be related to introduction and performance of resistant varieties.

4. False Root-Knot Nematodes

4.1 Screening for Resistance

Resistance to Nacobbus has been identified by scientists in Bolivia and has been studied at CIP. We DO NOT RECOMMEND a large scale screening program be initiated by CIP until standardized screening procedures are developed. We RECOMMEND studies on the life cycle of the pathogen be narrowed to the production of inoculum and conditions necessary for infection by this nematode to develop such screening methods. Research on screening for resistance to this nematode should be coordinated with scientists in Andean countries.

4.2 Breeding for Resistance

After development of suitable screening techniques, we RECOMMEND a program on breeding for resistance be initiated. Because false root-knot, potato cyst and root-knot nematodes often occur together, we RECOMMEND combining resistance to these nematodes, if possible.

4.3 Host Range

There is insufficient data on host range to aid in judgements on cropping systems. Consequently, we RECOMMEND that studies on host range among cultivated varieties should be initiated only after screening techniques have been developed.

4.4 Species Identification

Sufficient knowledge of the taxonomic status of false root-knot nematodes has been gained to support CIP's resistance breeding program. However, we do recognize possible existence of variants in this nematode species,but these variants have no practical implication until resistant varieties have been introduced.

4.5 Dispersal

We recognize the substantial improvement of knowledge on means of dispersal of this nematode, and therefore, RECOMMEND that research on means of dispersal be terminated within one year.

5. Root Lesion Nematodes

Although additional information has become available indicating economic losses caused by Pratylenchus on potatoes,we DO NOT RECOMMEND any research on Pratylenchus by CIP, at this time. However, if more evidence becomes available, the problem with Pratylenchus should be reconsidered.

6. Interaction Studies

We recognize the important advances made by CIP in establishing positive interactions of potato nematodes and other diseases of potato. The demonstration of a positive interaction of root-knot nematodes and bacterial wilt is sufficient to support combining resistances to these two organisms. Any further studies into the details of this interaction are academic. Therefore, we RECOMMEND that such detailed studies be terminated.

Although interactions of Globodera spp. with bacterial wilt have been demonstrated, we do not believe that there is sufficient evidence of their coexistence to warrant combining these resistances.

The existence of interaction of Pratylenchus spp. with bacterial wilt is a matter of speculation. Until further knowledge is available on the importance of Pratylenchus spp. in potato culture, this possible interaction should not be investigated.

7. Virus Transmission

We recognize that certain nematode species are capable of trans-

mitting potato viruses. A few examples of economically important transmission have been reported; however, only transmission of tobacco rattle virus is of economic importance on a global basis. At present, we DO NOT RECOMMEND that CIP nematologists investigate virus transmission by nematodes. However, CIP nematologists should be alert to major changes in this situation and review their program accordingly.

The demonstration of coexistence of root-knot, false root-knot and cyst nematodes is sufficient to support limited investigations on interactions in yield density effects caused by these nematodes on potatoes.

8. Chemical Control

Certain chemicals are effective against potato cyst nematodes. However, because of the increasing cost of such chemicals they are probably not economical for many parts of the world. We DO NOT RECOMMEND that CIP initiates research on nematicides. However, we RECOMMEND that CIP nematologists keep informed of developments in chemical control especially those chemicals related to plant protection, for example seed treatment, rather than soil disinfection. We further RECOMMEND that if a chemical management specialist joins the CIP staff, nematologists act in an advisory capacity and encourage evaluation of nematicides that provide protection against potato cyst nematodes, in view of their own responsibility.

9. Biological Control

Evidence of biological control appears in the literature; however, success in the field has been lacking. Recent developments on fungal parasites of root-knot and cyst nematodes seems promising. Because of these interesting results we RECOMMEND field evaluation of possible biological control agents on a limited basis.

10. Nematode Management Studies

The search for nematode management systems should be in relation to potato production practices in the developing countries. Major constraints are located in lack of extension services. We recognize the fact that crop rotation has in general a limited effect on population density control, that effects of chemicals are limited to just one season per application, and at present resistance is not yet available on a large scale. Therefore, we RECOMMEND that only a limited amount of time be spent on management approach to nematode control.

AN OVERVIEW OF THE IMPORTANT NEMATODE PESTS OF POTATO

R. D. Winslow

The Crop-Origins and Early Development

According to Simmonds (1969), when and where the potato was first domesticated is not known with certainty, but it must have been several thousand years ago, probably in the general vicinity of Lake Titicaca on the Peru-Bolivian border. In the process the wild diploids with small bitter tubers containing poisonous alkaloids were converted to autotetraploids with larger edible tubers. Some of these tubers were brought to Europe, probably not by Sir Walter Raleigh but by Spaniards, and the first European crops were grown in Spain c. 1570. The crop was not treated seriously in Europe (except in Ireland) for almost 200 years, but thereafter became an important source of cheap human food. Introduced to Ireland c. 1590, the potato rapidly became the main, virtually the sole, food crop of the Irish peasantry. When blight, *Phytophthora infestans*, spread to Europe from Central America in the 1840's - the "hungry forties" - and wiped out the crop, it caused hardship and civil unrest in Europe generally, but was much more serious in Ireland, causing widespread famine and death. Many of the survivors migrated, mainly to North America, thus establishing the strong Irish-American connection. To this day Ireland's national holiday (St. Patrick's Day, 17th March) is more rapturously celebrated in New York than in Dublin.

Crop Importance

The 1977 world potato crop comprised almost 300 million tons prepared from some 20 million hectares (FAO Yearbook for 1977, Vol. 31, pp 100-111). Almost 90% of the crop was produced in Eurasia, with the remaining 10% mainly in the Americas (Table 1). Main producer nations were the USSR, China and Poland (Table 2) but these were not among the most efficient producers, which were headed by Switzerland, the Netherlands and Israel (Table 3), three small countries with advanced technologies, but otherwise with relatively little in common, the first being noted for its mountains, the second for its flatness and the third for its deserts.

Table 1

WORLD POTATO CROP 1977 FAO YEARBOOK VOL. 31

	AREA		YIELD	PRODUCTION	
	million ha	(%)	t/ha	million ton	(%)
USSR	7.07	(33.7)	11.8	83.4	(28.5)
EUROPE *	6.11	(29.2)	18.7	114.5	(39.1)
ASIA*	5.45	(26.0)	11.2	60.9	(20.8)
S AMERICA	0.98	(4.7)	9.5	9.3	(3.2)
N & C AMERICA	0.74	(3.5)	26.2	19.4	(6.6)
AFRICA	0.56	(2.7)	7.8	4.4	(1.5)
OCEANIA	0.04	(0.2)	23.0	1.0	(0.3)
WORLD	20.95		14.0	292.9	

* excluding USSR.

Table 2

MAIN POTATO GROWING NATIONS FAO YEARBOOK

	AREA (%)	TONNAGE (%)
USSR	33.7	28.5
CHINA	18.6	14.2
POLAND	11.5	14.1
INDIA	3.0	2.5
GERMANY E	2.7	3.4
U S A	2.6	5.5
GERMANY W	1.9	3.8
FRANCE	1.4	2.8
U K	1.1	2.3

Table 3

NATIONS WITH HIGHEST POTATO YIELDS (TON/HA)*

Switzerland	37.8	Belgium-Lux	28.5
Netherlands	33.8	U K	28.4
Israel	32.6	Germany W	28.4
New Zealand	29.9	Sweden	28.2
U S A	29.2	France	27.5

* FAO Yearbook 1977, Vol. 31, Table 19 p 110-1.

Nematode Importance

As an indication of the relative importance of potato nematodes, we may compare the number of publications on potato nematodes with the number of publications on all plant and free-living nematodes cited in recent volumes of Helminthological Abstracts. Volumes 29-46 (from 1960, when regular quarterly issues started, to 1977, last complete volume) were chosen for this study (Table 4). About one in 12 of all publications on plant-parasitic and free-living nematodes is devoted to potato nematode problems. Further analysis of the data (Table 5) indicates that some 70% of all papers on potato nematodes are concerned with the cyst nematodes, Globodera spp, confirming the general impression that these are by far the most important nematodes. Ditylenchus and Meloidogyne spp. appear next in importance, followed by Pratylenchus and trichodorids. Of the minor genera, Tylenchorhynchus is the most frequently mentioned (1% of all potato nematode papers), but two others, Belonolaimus and Nacobbus, are locally important in Florida and Peru-Bolivia, respectively.

Cyst Nematodes, Globodera rostochiensis and G. pallida

The potato cyst nematodes are believed to have evolved along with their principal hosts, potatoes, in the Andes, probably in Peru or Bolivia, although Brucher (1960) suggested that the mountains of north Argentina, where the pests occur in inaccessible places, may be their original home. The nematodes were introduced to Europe, probably in mid or late 19th century on South American potatoes imported for breeding purposes. They have spread throughout Europe and to Asia (Israel, Lebanon, India, Japan), north and south Africa, Canary Islands, Cyprus, Iceland, north and central America, New Zealand, etc.

Considerable advances have been made in the nomenclature and pathotyping of potato cyst nematodes. A decade ago three British pathotypes of Heterodera rostochiensis were recognized: pathotype A, non-aggressive to resistance derived from Solanum andigena, had a gold-coloured stage in the process of cyst formation: pathotypes B and E, aggressive to such resistance, had no such stage, (Guile, 1970). Webley (1970) found other differences, e. g. a small but consistent difference in stylet length in the hatched larva, whilst workers at Rothamsted (Jones, 1968) found that attempts to hybridize A with B or E met with little or no success. These and other data led eventually to the description of British pathotypes B and E as a separate species, H. pallida, Stone 1973. The situation in the Netherlands was different, where many golden-cyst populations were found aggressive to resistance from S. andigena. Eventually Dutch, German and British workers collaborated to recognize 8 pathotypes (5 rostochiensis, 3 pallida) and 8 differential host plants by which the pathotypes could be distinguished (Kort et al, 1978). Additional path-

Table 4

No. OF PAPERS CITED IN HELM ABS 1960-77

	1960-65	1966-71	1972-77	1960-77
* All 'plant'	3136	5382	9163	17681
Potato	265	398	807	1470
" %	8	7	9	8

* Includes some free-living and entomophilic

Table 5

POTATO NEMATODE PAPERS IN HELM ABS 1960-77

% DISTRIBUTION AMONG NEMATODE GROUPS

	1960-65	66-71	72-77	1960-77
Cyst nematodes	76	72	69	71
Ditylenchus	8	9	10	9
Meloidogyne	6	8	6	7
Pratylenchus	5	4	3	4
Trichodorus	-	2	5	4
Other named gg	3	3	4	3
Unnamed	2	3	2	2

otypes of H. pallida have been found in S. America (Canto Saenz & Mayer de Scurrah, 1978) and England (Fuller et al, 1977), however, requiring additional differential host plants. Meantime, a further change in nomenclature occurred, with the elevation to generic rank of the subgenus Globodera, to which the potato cyst nematodes and related species belong (Mulvey and Stone, 1976). G. rostochiensis is the more widely distributed of the two species, G. pallida being rare or absent in many countries. Exceptions are northern England, and northern Peru-southern Colombia, where G. pallida predominates.

The cyst dimensions given in the C. I. H. descriptions of the two species (Stone, 1973) suggest that they are partially separable by sieving. Presumably width, not length, is the important dimension, i. e. the one that decides the minimum aperture through which the cyst will pass. Width is given as 0.382 $\pm$ 0.061 mm for G. rostochiensis and 0.534 $\pm$ 0.066 for G. pallida. Assuming width distribution is near normal, then 95% of G. rostochiensis cysts have widths between 0.260 and 0.504 mm, and 95% of G. pallida cysts have widths between 0.402 and 0.666 mm. Therefore, in a mixture of the two type populations, most cysts below 0.4 mm in width are G. rostochiensis, most cysts above 0.5 mm in width are G. pallida, and cysts between 0.4 and 0.5 mm are a mixture. Body dimensions, however, are known to vary greatly in some plant nematodes, e. g. Ditylenchus spp., and are often regarded as unreliable for diagnostic purposes.

Breeding for resistance has continued, but the vast majority of resistant varieties produced to date are resistant to Ro 1 only; out of 133 officially registered varieties in the German Federal Republic, 40 are resistant to Ro 1, with only a few of them having any additional resistance. Producing commercial varieties with complete or near complete resistance to all or most pathotypes will probably be a long slow task, if not impossible, and interim varieties with partial (80% - 90%, say) resistance may be desirable. Accurately assessing such resistance is proving difficult, however, as indeed is defining it. Whereas complete resisters to Ro 1 derived from Solanum andigena act as traps and consistently diminish nematode level, partial resisters behave as inefficient hosts either multiplying the nematodes less quickly, or supporting a lower final (ceiling) population density, or both.

A novel method of assessing or comparing host efficiencies is to grow the plants under test in moistened sand in closed containers in the dark, inoculating them with the appropriate nematodes after root formation has started (Foot, 1977). A measure of sterilization may be necessary, and the containers should not be completely air-tight. Thus light, temperature and moisture may be standardized. Although the anaemic top growth soon atrophies, roots continue to grow amazingly well for some months, long enough to complete a nematode generation. Whether this method

will replace the more conventional glasshouse or outdoor pot testing remains to be seen. In any case the ultimate test must be in the field, in different soil types where possible.

Assessment of partial resistance is closely linked with nematode population dynamics, especially population increase, which depends on a number of factors, including nematode species and/or pathotype, initial density, soil type and fertility, potato cultivar, geographical location and season. Population decrease in the absence of host crops may be comparatively independent of initial nematode density, but is strongly affected by climatic factors, decline being much faster in hot countries than in cold. Decline may also be affected by nematode species, soil factors and non-host grown. In short, population dynamics may vary greatly between and within countries, but a knowledge of them is so essential in controlling nematode infestations that they should be studied in each country, district and soil type situation. Methods for detecting and measuring populations have been outlined by Southey (1974). To illustrate the effects of two factors on nematode infestation increase, I have assembled multiplication data from untreated plots in some forty tests on chemical control of potato cyst nematodes by Whitehead & co-workers in England, 1972-76 (Table 6). Where initial infestation level was 25 e/g soil or less, multiplication in peaty soils (50 x) was much greater than in mineral soils (less than 20 x). Where soil type and initial infestation level greatly influenced multiplication rate.

Great advances have been made in chemical control of cyst nematodes in soil, especially with systemic nematicides in cool climates such as the U. K., where soil fumigants have been generally ineffective, leaving disappointingly high post-crop infestation levels. Whitehead and co-workers, inter alia, have shown that the oximecarbamates aldicarb and oxamyl are very effective in promoting yields and restricting nematode multiplication (Tables 7 - 9). When treated at similar rates, aldicarb was marginally more effective but it may be the more hazardous to man, and European colleagues have expressed concern about its use on ware potatoes because of possible harmful residues (Mathis, 1977). Generally, systemic nematicides only control nematodes in the soil layer (top 15-20 cm) into which they are incorporated; nematodes may be numerous below 20 cm and in dry seasons may damage the deeper roots seeking water and thus reduce yield. Nevertheless these nematicides have been generally welcomed around the world, where they may replace or augment soil fumigants. Systemics are regarded as useful additional tools in the campaign to eradicate G. rostochiensis from Long Island by the end of 1980 (Sand, 1976). Foliar and seed-piece treatments to protect potatoes growing in infested soil have met with varying degrees of success; and various chemicals such as Rindite, formalin and hypochlorites were deemed successful in freeing tubers from adherent cysts.

Table 6

PCN MULTIPLICATION ON SUSCEPTIBLE POTATOES IN ENGLAND
(FROM WHITEHEAD AND CO-WORKERS 1972-76)

Initial e/g soil	Peaty Loam	Sandy Loam	Silt Loam	Sandy Clay	All sites
≤ 25	50 (6)	19 (5)	17 (4)		31 (15)
26 - 50	32 (3)		10 (6)		18 (9)
50 >	4 (6)	3 (6)	6 (2)	3 (2)	4 (16)
All levels	28 (15)	10 (11)	12 (12)	3 (2)	17 (40)

Figures in brackets are the numbers of experimental sites involved.

Table 7

SYSTEMIC NEMATICIDES - EFFECTS ON POTATO YIELDS IN
PCN SOILS IN ENGLAND. (WHITEHEAD & CO-WORKERS)

No. of sites	Pre-crop e/g soil	Crop Yield (Ton/Ha) untreated	treated	increase
6	- 50 (12-46)	20 (12-38)	42 (29-55)	22 (12-31)
5	50-100 (50-99)	31 (11-52)	50 (34-72)	19 (9-25)
6	100- (113-506)	21 (5-41)	37 (20-59)	16 (9-21)

Table 8

ALDICARE CONTROL OF PCN, AS (LIVE) EGGS/G SOIL
IN 4 SOIL TYPES IN ENGLAND

Soil Type	No. of sites	% Control Mean	Range
Peaty Loam	15	78	39 - 98
Sandy Loam	7	92	85 - 94
Silt Loam	9	77	26 - 97
Sandy Clay	3	84	73 - 90
All Sites	34	81	26 - 98

(From Whitehead and Co-Workers 1972-76)

Table 9

OXAMYL CONTROL OF PCN, AS (LIVE) EGGS/G SOIL
IN 3 SOIL TYPES IN ENGLAND

Soil Type	No. of Sites	% Control Mean	Range
Peaty Loam	13	73	30 - 97
Sandy Loam	8	90	81 - 97
Silt Loam	9	75	29 - 94
All Sites	30	78	29 - 97

(From Whitehead and Co-Workers 1972-76)

In a series of recent papers, Evans, Trudgill and others looked at the effect of various factors on pathogenicity of potato cyst nematodes on susceptible and resistant potatoes and concluded that early poor growth of heavily infested plants was associated with decreased rates of nutrient uptake. Recent studies on the involvement of potato cyst nematodes in disease complexes involved various fungi including species of Verticillium, Colletotrichum and Phoma. Data on damage assessment or economic losses at national level are tentative because they vary from season to season, and indirect losses may far outweigh the direct losses, for example the cost of the Long Island campaign. At the other extreme, direct losses in parts of the Andes, although globally insignificant, may be all-important locally, especially as there is no satisfactory control measure at present, and alternative crop choice is limited (Mai, 1977). Whitehead (1975) put losses in England at £ 10m, while Koliopanus (1976) estimated losses in Greece at 2-3 m dollars. Seinhorst (1974) and Brown (1961) have suggested equations for yield loss due to cyst nematodes, Brown's simpler expression (-1 ton/ha for each 8 egg/g soil) being easy to understand, but probably applying only locally.

Other aspects of plant-nematode relationships studied recently are the ultrastructure of nematode-induced syncytia (transfer cells) and the biochemical interchanges between nematode and susceptible or resistant plant.

Ditylenchus spp.

Two species of Ditylenchus are known to attack potatoes, D. destructor, the potato tuber or potato rot nematode, and D. dipsaci, the stem nematode. Although the volume of literature (Table 5) suggests that these nematodes are next in importance to the cyst nematodes, closer examination indicates that virtually all the recent literature is from the USSR, where these nematodes seem to be serious, widespread pests. Few people outside Russia are currently investigating them and, since they will feature in a later paper, I propose to leave them for the present.

Meloidogyne spp., Root-knot Nematodes

Several members of this genus are known to attack potatoes. The four most frequently encountered are M. hapla, M. incognita, M. incognita acrita and M. javanica. M. hapla, the northern root-knot nematode, has the most northerly geographical range, including Canada, northern USA, northern Europe and north Japan, but has been recorded on potatoes in warmer climates, including Pakistan and Rhodesia. M. incognita, the most frequently recorded species, attacks potatoes in many countries, including sourthern USA, South America, southern Europe, Africa, USSR, India, Australia. M. incognita acrita is found on potatoes in southern USA, South America,

southern Europe and Africa. M. javanica is important in southern Africa, but attacks potatoes in other countries, including India and Australia. Other species occasionally encountered, mainly in Africa, are M. arenaria, M. acronea, M. africana, M. ethiopica and M. thamesi. The diagnostic symptoms of Meloidogyne attack on potatoes are the galls found on roots and tubers. The galls differ considerably in size, depending on the potato cultivar, nematode species, climatic conditions and stage of growth. The galling, mainly an enlargement of plant cortex, is probably not essential in nematode nutrition, which is supplied by the giant transfer cells. Possibly the gall offers some protection unsaleable through unsightly tuber galling.

Species of Meloidogyne are often involved in disease complexes with other pathogens (Armstrong et al., 1976) frequently with synergistic effects, but they are quite capable of causing huge crop losses without help (Sitterley and Fassuliotis, 1965; Koen, 1966; Table 10). Breeding for resistance is progressing in many countries, and rotation (despite wide host-ranges), soil amendments and nematicides (fumigant and non-fumigant), and seed disinfestation can all play a role in control of these pests.

Pratylenchus spp. (Lesion Nematodes)

These nematodes cause damage to potatoes either alone or in disease complexes with other pathogen, especially Verticillium spp. The species most frequently encountered is P. penetrans found on potatoes in Europe, Canada and throughout most of the United States, being replaced in the southern U.S. by P. brachyurus, P. scribneri and P. zeae. Species found on potatoes elsewhere include P. crenatus (Canada), P. brachyurus (Southern Africa, Australia), P. thornei (Israel), P. coffeae (Japan) P. scribneri and P. andinus (S. America). Most species show definite soil-type preferences (P. penetrans, for example, favors light loams or sandy soils), and this restricts their distribution. When associated with wilt fungi such as Verticillium they may intensify the wilt, thus causing early death of the crop. A more direct form of damage is the "pimpling" (small raised areas) on tubers caused by P. brachyurus. Control by fumigant and non-fumigant nematicides is usually successful, where warranted, the beneficial effects of a treatment sometimes lasting two to three years. The wide host ranges of some species, notably P. penetrans, may make control by crop rotation difficult, and the use of enemy crops such as Tagetes is not normally an economic proposition. Seed disinfestation with hot water or chemicals is feasible. Some resistance or tolerance is known in existing varieties.

Table 10

ECONOMICS OF MELOIDOGYNE SPP

(MAINLY M. JAVANICA) ON POTATO IN S.AFRICA*

Year	Crop	Profit: £ sterling/ha			Crop
1	Peanut	97	92	57	Potato
2	Peanut	95	92	40	Potato
3	Cotton	55	53	2	Potato
	EDB	- 46	0	0	No EDB
4	Potato	310	151	0	Potato
Total		511	388	99	

* From Koen H 1966: Nematologica 12, 109-112.

Trichodorus and Paratrichodorus (Stubbly-root Nematodes)

Although these migratory root ectoparasites can directly damage crops by preventing normal root development, their main importance is as vectors of tobacco rattle virus (TRV) which causes spraying or corky ringspot disease. Symptoms in the tubers are internal bands or arcs of corky tissue which are virtually inedible. Despite this obvious association of the disease with tubers, seed transmission to new areas may be rare, unless the right combination of virus strain inthe seed potatoes and nematode population in the new site occurs. (Hoof, 1968).

P. pachydermus is the species most commonly found associated with potatoes in Europe followed by T. primitivus. Other European species include T. cylindricus, T. similis, T. viruliferus, T. sparsus, P. teres and P. nanus. P. pachydermus and P. teres have also been found in USA, but the common species there seems to be P. christiei, with P. allius, P. porosus and T. proximus also present. P. christiei occurs in S. America, P. porosus in Japan, and P. minor in Israel. Most of the above species can trasmit TRV. Many species have a severely restricted distribution because of a marked preference for very sandy soils; T. primitivus is an exception and can thrive in medium-heavy soils (Reepmeyer, 1973). Trichodorids tend to lie deeply in soil, at or below plough depth. Consequently chemical treatments, especially with systemics, have given very variable results. Host ranges tend to be wide, with many crops and weeds being hosts of vector and virus. Widespread use of asparagus, an enemy crop, is impractical. Field resistance, mainly to the virus, is known in some existing varieties.

Other Nematodes

Species of Belonolaimus, Criconemoides, Longidorus and Nacobbus are locally important pests. Other genera of minor or unproven importance include Helicotylenchus and other spirals, Tylenchorhynchus, Tylenchulus, Rotylenchulus and Xiphinema.

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QUINQUENNIAL REVIEW MISSION REPORT ON NEMATODE PATHOGENS

O. T. Page

The purpose of my presentation is to provide a background of the recommendations made by the Technical Advisory Committee Quinquennial Review Mission in December, 1976. Their recommendations reflect and agree with those proposed by the seven participants at the first Planning Conference on Nematode Control Strategy held at CIP in February, 1974.

The value of these recommendations in guiding nematode research at CIP can best be judged by progress to be reported following my presentation. Progress will be summarized on cyst, root-knot and false root-knot nematode research at CIP as well as in Contracts in Wageningen, the Netherlands and at Cornell University.

SUMMARY OF RECOMMENDATIONS

The Nematology Planning Conference was held to examine priorities and recommend a program of research for the next five years. The following criteria were used to establish priorities.

1. Nematode distribution and present world-wide economic importance.
2. Predicted economic importance in relation to expanded geographic range of potato production.
3. International applicability of research results.
4. Probability of success of research projects.

The potato cyst nematode, root-knot nematodes, false root-knot nematode, and root lesion nematodes were considered at the conference. Based on the above criteria the following research objectives listed in order of priority, were identified and recommended.

1. Potato Cyst Nematode

   Because of their widespread occurrence in many potato growing regions of the world, the potato cyst nematodes (*Heterodera rostochiensis* and *H. pallida*) are the most important nematode pests of potato. Thus, potato cyst nematode should be given the highest priority in the nematology research program. Lines of research program. Lines of

research which would have the greatest impact on world potato production are listed below in order of priority.

A. Breeding for resistance. Concentrate mainly on native potato cultivars and at the same time search for resistance in wild species. (3-5 years).

B. Pathotype identification. Concentrate on the populations occurring in the Andes of Peru, Bolivia, Ecuador, Colombia, Venezuela, and perhaps Argentina and Chile. (3-5 years).

C. Search for tolerance. Field evaluations of native cultivars with inheritance studies on prospective tolerant lines. (3-5 years).

2. Root-knot Nematodes

The root-knot nematodes (*Meloidogyne* spp.) are widely distributed in the warm climates of the world. The successful adaptation of potato to warmer climates will undoubtly increase the importance of root-knot nematodes as pathogens of potatoes. To minimize the effects of root-knot nematodes on potato production in warmer climates, the following lines of research are recommended.

A. Breeding for resistance. Concentrate on the native potato cultivars as source of resistance and include wild species only if it becomes apparent no resistant genes are present in native cultivars. (3-5 years).

B. Combining root-knot resistance with bacterial wilt resistance. Because of the interactions of these two pathogens on other solanacearous plants, interaction on potato is probable in climates where both pathogens co-exist. (4-5 years).

3. False Root-knot Nematodes

The false root-knot nematode (*Nacobbus* sp.) is a destructive pest of potato in the Andean region of Peru and Bolivia. At present its distribution and economic importance in other countries are not known. Very little is known about the false root-knot nematode, particularly as it relates to potatoes. The following areas of research are recommended to ascertain the importance of false root-knot nematodes to potato production in the developing world.

A. Species identification. Positive identification of species of *Nacobbus* that attacks potato. (1-3 years).

B. Life cycle and reproductive capacity. The reproductive potential of this nematode under various climatic conditions is to be established. (2-3 years).

C. Host range. Information is needed on the number and identity of plant species on which this nematode can survive. (2-4 years for major crops; 3-5 years for wild weed species).

D. Survival and dispersal. Because of important international implication, knowledge on how this nematode survives and spreads is of utmost importance. (2-3 years).

E. Host resistance. On a limited basis, the native cultivars should be evaluated for resistance. (5 years).

4. Root Lesion Nematodes

At least nine species of root lesion nematodes (*Pratylenchus* spp.) attack potatoes. Since these vary greatly in their soil and temperature requirements, root lesion nematodes represent a potential threat to potato production throughout the world. At the present, it is recommended that CIP should not initiate a research program on root lesion nematodes. In the event root lesion nematodes become economically important internationally, CIP should be aware of current research on root lesion nematodes and possibly support such research through contract projects. Current research on root lesion nematodes which have the greatest international applicability are as follows:

A. Host resistance. Useful resistance to *P. penetrans* has been found in potato cyst nematode resistant varieties derived from *S. tuberosum* subsp. *andigena* (No research recommended).

B. Resistant cover crops. Certain cover crops resistant to *P. penetrans* have been identified. (No research recommended).

5. Interaction of Nematodes and Other Organisms

Since nematodes are, for the most part, debilitating parasites, they often predispose the plant to attack by other organisms or increase the severity of other diseases. Also, certain species of nematode, root-knot nematodes, and root-lesion nematodes are reported to increase the severity of *Verticillium* wilt of potato. There are no reported interactions involving the false root-knot nematode which is obviously due to the lack of extensive studies of this nematode.

Investigations of possible interactions of nematode and other organisms should be of lower priority research until more is known about the control of the major nematode pests of potatoes.

However, obvious interactions should not be overlooked and the economic importance of such interactions should be determined in cooperation with scientists from other disciplines at CIP. However, judgement must be exercised to distinguish between possible interactions.

CONCLUSIONS AND RECOMMENDATIONS OF THE TAC QUINQUENNIAL REVIEW MISSION

December 5 - 18, 1976

I. Although in principle, the concentration of this Thrust on the development of resistant varieties is justified, other possibilities of reducing harmful nematodes should not be overlooked. The nematologists of the Center must be able to advise the Regional Research staff on crop rotation in areas with heavy nematode infestations. They should also be acquainted with recent control developments in chemical control, in particular with systemic nematicides and be able on request to advise on chemical control or refer to appropriate sources.

II. CIP is to be commended for recognizing and reporting a wider pathotype range of Heterodera cysts than was previously known. As justified, within budget constraints, surveys by national collaborators should be encouraged to evaluate the full spectrum of Heterodera pathotypes in all regions.

III. Tolerant potato varieties should not be used in areas with relatively low infestations of Heterodera; as contrary to resistant varieties, they build up the cyst population in the soil to a higher level than do non-tolerant varieties.

IV. The germplasm collection should not only be tested on resistance to Heterodera spp. and the root-knot nematode, Meloidogyne incognita acrita, but also to other Meloidogyne species. If such species are not present in Peru, clones resistant to M. incognita acrita should be sent to other regions where such species are indigenous.

V. As the false root-knot nematode, Nacobbus spp., is still rather unknown but locally causes severe damage, every possible care should be taken to prevent the spreading of this pest with seed potatoes. Careful study should be made of its biology, host range, distribution pattern and reproductive potential.

VI. In accordance with the 1974 Planning Conference recommendations, for the time being root lesion nematodes (Pratylenchus spp.)and nematode vectors of viruses should not be studied. If in the future they appear to do more harm than at present anticipated the question may by reopened.

VII. The total number of scientists in this Thrust seems rather on the high side, and the Panel suports the proposed reduction in the manpower resources applied to this Thrust and recommends CIP to utilize the posts released for essential strengthening of other Thrusts, e.g., virology.

SUMMARY OF RESEARCH PROGRESS ON POTATO CYST NEMATODE, *Globodera* spp.

M. M. de Scurrah and J. Franco

The aim of the research on potato cyst-nematodes *Globodera* spp. is to provide National Programs and farmers in developing countries with potential potato varieties or breeding material resistant or tolerant to the cyst-nematodes.

The most important nematode pest of the potato in temperate and sub-tropical regions are the potato cyst-nematodes with their two species: *Globodera rostochiensis* and *G. pallida*. The latter is more prevalent in the Andean region and it may be, at the present time, in most world potato growing areas. Within each of these species several pathotypes (races) have been identified. The major emphasis in CIP is concentrated on screening and breeding for resistance.

In order to accomplish this end, it is necessary to do further research on the population behaviour of potato cyst-nematodes and their management under natural conditions. Considering these points the whole research progress on P.C.N. will be covered under three aspects: Potato Cyst-Nematode Populations, Screening and Breeding for Resistance, and Management.

1. Potato Cyst-Nematode Populations

In accordance with the recommendations given during the First Planning Conference on Nematode Control, held at CIP, Lima, Peru, in 1974, the identification, distribution and classification of pathotypes of P.C.N. in the Andes has been carried out. Research has been done to improve techniques which allow a better handling and processing of nematode populations. Further populations in the Andean countries and elsewhere have been collected. The total number of populations in CIP's collection are summarized in Table 1. All these populations are being maintained and utilized for further taxonomic and behavioural studies.

It has been found that variation of characters used for identification of P.C.N. species are due to both intrinsic genetic variation and the influence of external factors such as, density of nematodes in the roots, temperature, daylength and the techniques used to prepare the specimen to be measured. Among these the least altered

Table 1

POTATO CYST NEMATODE COLLECTION

COUNTRY	N°OF SAMPLES	COUNTRY	N°OF SAMPLES
CHILE	3	ENGLAND	4
ARGENTINA	4	GERMANY	5
URUGUAY	2	HOLLAND	6
BOLIVIA	35	DENMARK	1
PERU	112	ICELAND	8
ECUADOR	16	SPAIN	2
COLOMBIA	11	ITALY	2
VENEZUELA	2	CYPRUS	1
PANAMA	6	GREECE	3
COSTA RICA	2	MALTA	1
MEXICO	3	INDIA	12
UNITED STATES	4	JAPAN	3
CANADA	1	NEW ZEALAND	1
NEWFOUNDLAND	1	SOUTH AFRICA	1

TOTAL: 252 samples

and most consistent characters are stylet length in 2nd stage juveniles and fenestral length and number of ridges between the anal pore of vulval fenestra in cyst terminal areas. Using these characters for species identification,161 populations of P.C.N. were identified. For preliminary species identification the color of the developing female is characterized.

A cannonical variate analysis of 2nd stage juveniles and cyst terminal areas showed that populations coming from the same geographical area were very similar but sometimes they differed greatly (i.e. samples collected in southern areas of Peru and in Bolivia).

Studies using protein gel electrophoresis, scanning electron microscopy and controlled mating of selected British and Peruvian populations of G. rostochiensis showed no differences between them. The Peruvian "white" G. pallida (Otuzco) was slightly different from a "white" British G. pallida (Cadishead) when bands of protein pattern were compared. Intraspecific mating between populations from different origins were successful. Differences between species but not within were found by the use of scanning electron microscopy. With populations already identified, a map on distribution of species in Latin America shows a distinct distribution since the two species occupy different zones in the Andes. The demarcation line between the two species is near 15.6°S. With few exceptions populations north of this line are mainly G. pallida. Those from areas around Lake Titicaca and further south are predominantly G. rostochiensis with few G. pallida or mixtures of both species. Furthermore, when some populations were tested on potato plants containing H_1, H_2 and H_3 resistance genes, the presence of G. rostochiensis pathotypes which overcome the H_1 gene was confirmed in populations from Peru and Bolivia. Populations of G. pallida reproduced freely on these plants, showing a great variability.

Another area to which time and effort has been dedicated is the classification and determination of pathotypes in the Andean region by the use of differential plants. This is of twofold importance. First, the Andean region is considered the area where the P.C.N. evolved and therefore, one expects to find in these regions a wider spectrum of pathotypes than those found in the potato growing areas of Europe and other countries. The second reason why classification is crucial is that it provides a basis for selecting a group of representative populations to use in screening for resistance, and also dictates the areas where these resistant genes will be useful in controlling the nematode. As result of these points and due to the variability found with the Andean populations of P.C.N. a new scheme for pathotype identification has been erected. Moreover, the distribution frequency of pathotypes has been established with Andean

populations and from these results (Table 2) it is clear that P_4A and P_5A are the predominant pathotypes. It is also evident from these studies that useful differential plants for Andean populations are not yet available.

In order to understand the above mentioned distribution of P.C.N. species and their variability a series of studies with some selected populations were carried out under different environmental conditions to investigate the effect of temperature, daylength, host and soil on their rates of development.

Results showed no fundamental differences between British and Peruvian populations of the same species. However, Peruvian G. pallida seems to develop successfully at a wider range of temperature than the "white" British G. pallida. In general, G. pallida showed better adaptation to low temperature than those of G. rostochiensis.

Daylength had an indirect effect through the host on the rate of invasion and development of both species. However, the long term effect of daylength on the speciation and distribution of potato plants must have exerted a selection pressure on P.C.N. species.

In Britain an unusual effect was found which might have favored G. rostochiensis and helps explain its early predominant distribution: When British commercial varieties were tested with British populations of G. rostochiensis and G. pallida, the cultivar Record showed lower hatching and multiplication rate of the G. pallida population than with the other potato varieties.

Results of studies carried out under natural conditions showed that reproduction of G. rostochiensis was significantly higher in warmer sites than in the colder ones. All populations reproduced better at southern localities (16-17°S) than in central and northern localities (7-12°S).

Competition between species was also studied by inoculating eggs at Otuzco population (P_5A) and Arequipá (R_1A) in one pot. The reproduction of P_5A was lower under the conditions of southern localities than the R_1A populations.

Results on the effect of six soil types on nematode reproduction of seven populations showed that in general the soil from Arequipa (17°S) was the best one, and two of three populations of G. rostochiensis reproduced better in this soil than in that one from Cañete (12°S on the Coast). Two of three populations of G. pallida reproduced better in the soil from Cajamarca (7°S) than in the other soils tested.

Table 2

FREQUENCY OF PATHOTYPE DISTRIBUTION IN LATIN COUNTRIES ACCORDING TO THEIR REACTION ON DIFFERENT CLONES

PATHOTYPE IDENTIFICATION	RESISTANT SOURCE	FREQUENCY NUMBER	%
P_1 B (*)	S. multidissectum	1	1.9
P_2 A (*)	S. kurtzianum	6	11.5
P_3 A (*)	S. vernei GLKS	1	1.9
P_4 A ($P_2$2)	S. vernei $(VT^n)^2$ 62.33.3	13	25.0
P_5 A ($P_2$3)	None	20	38.5
R_1 A ($R_0$1)	S.tub.ssp.andigena	1	1.9
R_1 B ($R_0$4)	S.tub.ssp.andigena	1	1.9
R_2 A ($R_0$2)	S.kurtzianum	3	5.8
R_3 A ($R_0$3)	S.vernei GLKS	6	11.5
	TOTAL:	52	100.0

* No equivalence in European classification.

The last line of research covered under this general section of populations studies has been the host-parasite relationship in an effort to understand the host range of P.C.N. species in solanaceae and non solanaceae plants. To accomplish this objective, several collecting trips have been made in 1976, 1977 and 1978 in Colombia, Ecuador, Peru and Bolivia. Soil samples have been taken from wild and cultivated potatoes, Solanum spp., other crops and common weeds in potato fields. During the collecting trips made to the southern highlands of Peru (Department of Puno) and Bolivia, near the shores of Lake Titicaca, a field infection of Oxalis tuberosa, Tropaelum tuberosum, Ullucus tuberosum and some Malvaceous weeds by cyst-nematodes having white female color was observed. Only Chenopodium guinoa was observed to be infected by a yellow colored female Globodera spp. The interesting point is that these nematodes also seem to attack potatoes. Further research with these nematodes is underway to see if they belong to the same species of P.C.N. or they may either be newly evolved and geographically restricted races or, contrary to the present belief, the P.C.N. are not restricted only to Solanaceaous plants. In light of these studies a theory on the evolution and dissemination of potato cyst-nematodes has also been proposed.

II Screening and Breeding for Resistance at CIP

This project differed from any other breeding program from the very beginning in three ways.

A. It did not start with any resistant source, but the ever increasing germ plasm collection (4,000 in 1972 and 12,000 in 1978) was to serve as base material to be evaluated for possible sources of resistance.

B. The nematode races found locally were not classified and presented already in 1972 a greater variability than the ones known in Europe. In fact, the first resistance breaking pathotype was reported in 1956 when 60 resistant lines brought to Peru by Toxeopus were as resistant to race R_1A (A) has been tested many times here but this race is practically non-existent in Andean countries. Thus a study on nematode populations had also to be initiated. (See first section of this report).

C. The breeding lines emerging from such a program were to be useful throughout the entire 3rd world countries wherever cyst-nematode problems exist, and this required an advanced knowledge of regional nematode problems. Thus a program started mainly as a screening program. At first cultivated and wild species were screened but after the Planning Conference (1974)

and in view of the difficulties encountered in utilizing wild sources and the fortunate portion of having such a large selection of cultivated accessions, it was decided to concentrate at CIP only on cultivated species and leave the wild species to other programs, some with which CIP had contracts (i.e., S.V.P., Holland; Max Plank, Germany; Cornell, U.S.A.) to be received as a more advanced material.

To find resistance to a wide range of nematode populations the minimum number of nematode populations agreed upon was four. Thus 12 tubers per clone were requested from the germ plasm collection. They were inoculated with four different nematode populations (3 tubers per population) which were selected on the basis of their geographical distance, Otuzco - Huancayo - Cuzco and Puno. These populations have the name of the area in which they were collected and Table 3 shows their species and reaction to differential clones.

Results of the general screening program can be seen in Table 4.

In every trial the number of plants rating resistance have to be retested to insure that they are not escapes. In the beginning tests performed at La Molina gave a relatively high proportion of escapes, plants which grow poorly also tended to be rated wrongly. If a plant has a low root ball count for the second time, the total number of cysts are assessed. However, as can be seen from Tables 5, 6 and 7 the standards for selection were initially very low. An up-to-date list of resistance selections has been obtained by putting the combined data into a computer. This includes clones which have undergone several tests including one on inheritance for resistance as well as clones that have not been tested for a second time. Some because they were tested recently, others because they have in the meantime been eliminated from the collection or they had no extra tubers (most common reason) because we lost interest in clones with resistance to Cuzco, as this population is so variable and tests unreliable. One has to add to all this that the germ plasm collection is currently undergoing a reduction process by elimination of duplicates. This will be an important aid in further screening and breeding as a lot of space and time has been spent screening the same susceptible ones or conversely intercrossing the same resistant ones.

To illustrate this further 4 groups of synonyms in the collection are shown. Group 133 - three of our first selections below to the very same group and an additional 3 were picked up in later years. Nevertheless, our first work on the genetics of resistance was done with 3 different clones which are now reported to be the same. Group 131 - illustrates a second kind of problem, i.e. 9 clones grouped as synonyms which do not behave similarly to the different tests populations puts a question mark on the grouping or on the resistance test which compiles data from several years. Furthermore, they can never be rechecked now, as number 3 indicates that

Table 3

NEMATODE POPULATIONS USED IN SCREENING TESTS

Diff. Plants	P5A (OT)	P4A (HYO)	P4A (CUZ)	R4A (PUN)
S. tub.	+	+	+	+
S. and. H_1	+	+	+	+
S. mult. H_2	+	+	+	+
S. and. x S. mult. H_1 H_2	+	+	+	+
S. kurt. KTT/60.21.19	+	+	+	+
S. vern. GLKS. 581642/4	+	+	+	+
S. vern. (VT^n) ^{2}62.33.3	+	-	-	-

+ = susceptible

- = resistant

Although populations from Huancayo and Cuzco react similarly to tester plants and thus belong to P4A their behaviour as testing populations is quite different as Cuzco cysts have less viability, seem to have less reproductive capacity, seem to be composed of several types. Resistance to Cuzco is more often found especially when tested with European clones derived from wild species.

Table 4

LIST OF MATERIAL SCREENED FOR RESISTANCE TO THE POTATO CYST-NEMATODES, GLOBODERA SPP.

CLONES FROM	N°	RESISTANT REACTION TO OTUZCO	HUANCAYO	CUZCO	PUNO
Germ Plasm	2065	66	98	120	189
Bitter	90	10	23	20	10
Frost Resistant	207	7	8	-	-
High Yielding	37	0	0	-	-
RNN Selections	29	5	2	4	7
Ayacucho	19	0	3	-	-
Mexico*	50	3	4	3	1
Cornell	4916	296	790	-	456
Germany*	9	0	5	1	3
Holland	11	2	7	4	3
Webb	30	0	3	0	0
TOTAL :	7463	389	943	152	669

* Need to be retested due to poor root growth.

Table 5

RELATIVE RESISTANCE OF GERM PLASM CLONES

Clone	Cysts Av. of 5 Pots	% Cyst Reduction Relative to Renacimiento
P_4A (HUANCAYO)		
700280	742	72.2
700371	674	74.7
701958	607	77.3
RENACIMIENTO	2,667	0
P_4A (CUZCO)		
700516	322	77
701478	383	73
20014	488	65
20018	153	89
RENACIMIENTO	1,399	0
R_4A (PUNO)		
700382	190	90.8
700578	287	87
RENACIMIENTO	2,612	0

Table 6

RELATIVE RESISTANCE OF GERM PLASM CLONES

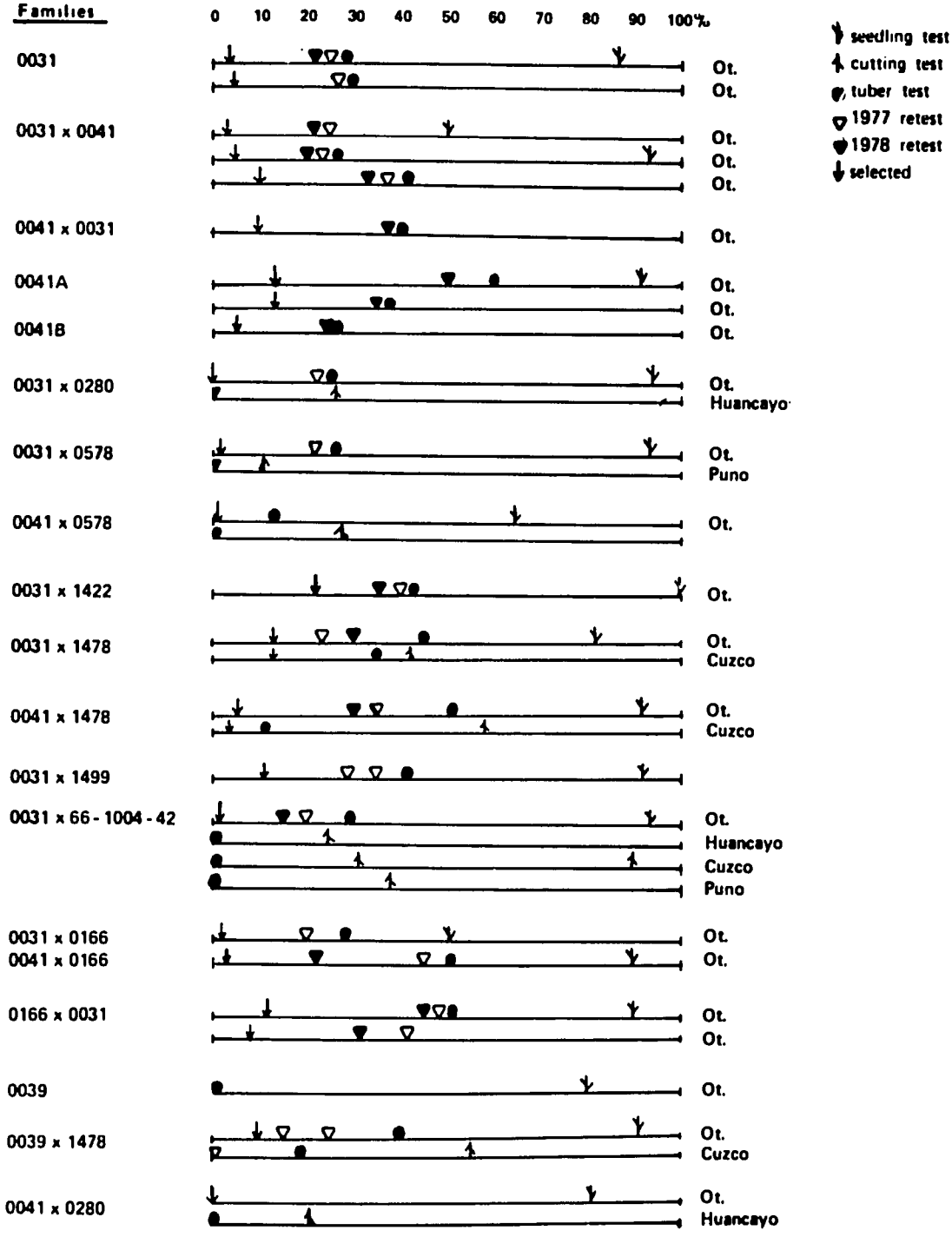
Clone	Cysts Av. of 5 Pots	& Cyst Reduction Relative to Renacimiento
P_5A (OTUZCO)		
700031	238	95.4
700041 A	215	95.9
700041 B	261	95.0
700166	222	95.8
701421	180	96.0
701422	101	97.9
701452	217	95.9
701478	387	92.6
701498	180	96.6
701499	259	95
701513	205	96.1
701535	148	97.0
701821	168	97.8
702770	195	96.3
RENACIMIENTO	5,255	

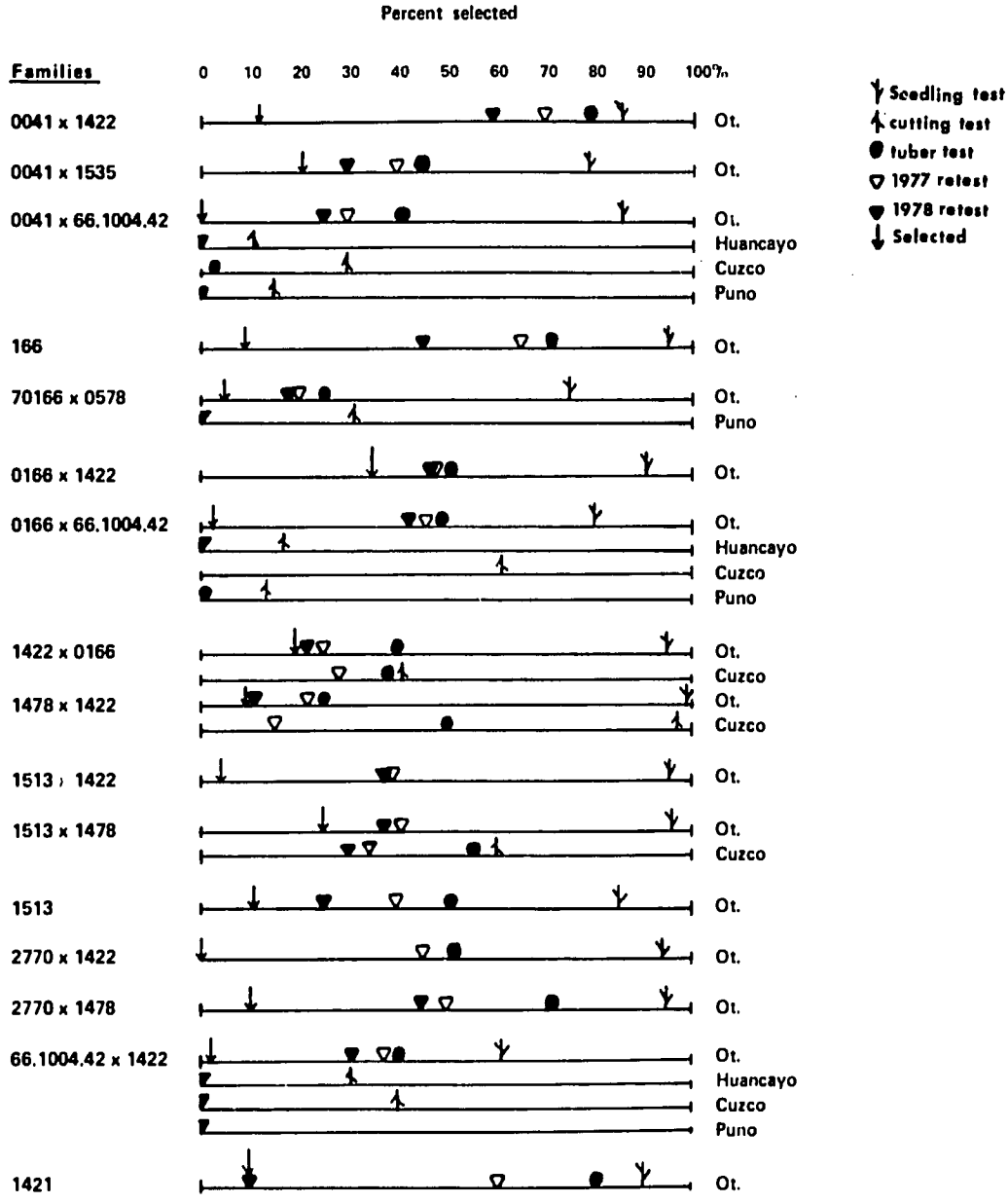
Table 7 The influence of bitter potatoes on the number of nematodes in sterilized soil as compared to the S. andigena variety, Renacimiento. The clones tested were S. juzepczukii, except for 3 S. curtilobum.

Clones No. Nematode Sample	Name	Number of cysts	Cysts as % of check
Huancayo			
700299		417	16
700301		630	75
700902	Azul camotillo	160	6
701014	Huataqui	105	8
701323	Cabeza amarilla	318	14
702116	Yuracc Mallku (cur)	100	4
702204	China Mallku (cur)	286	11
702334	Ukuki (cur)	195	7
702443	Parina	386	15
702444	Ruckii	693	27
702822	Ucucuri blanca	417	18
Check	Renacimiento	2,500	
Otuzco			
702443	Parina	1,185	32
702445	Piñaza	1,059	29
Check	Renacimiento	3,611	
Puno			
700229		100	4
700301		318	12
700301		337	13
700381		160	6
700902	Azul camotillo	919	34
Check	Renacimiento	2,500	
Cuzco			
700301		538	22
700944	Santiaguina	486	20
700962	Ccaippe	352	14
701014	Huataqui	621	25
701410	Shiri redonda	597	24
702334	Ukuki	893	36
702443	Parina	382	15
702444	Ruckii	511	21
Check	Renacimiento	2,400	

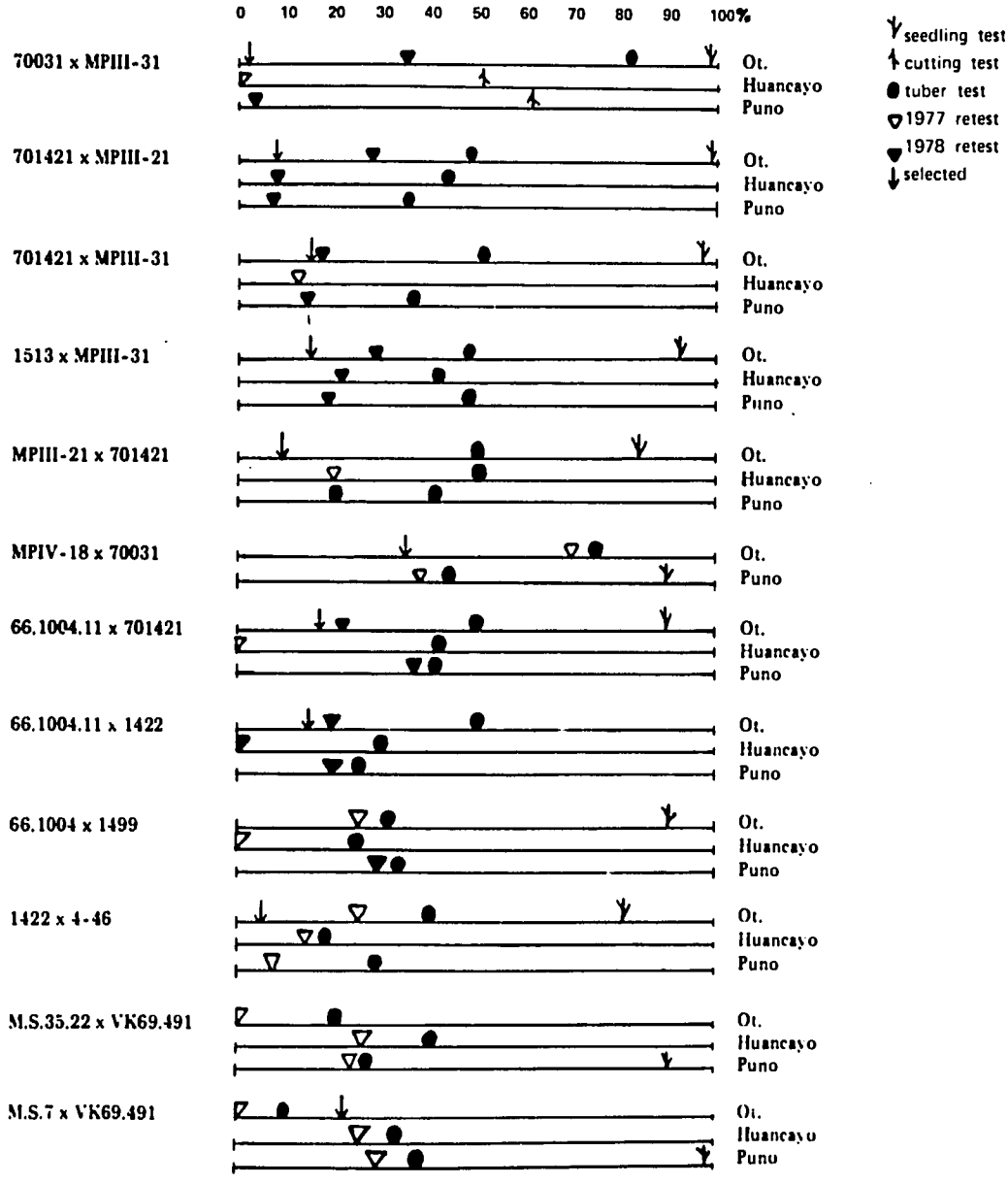
AMONG ANDIGENA CLONES

Percent selected

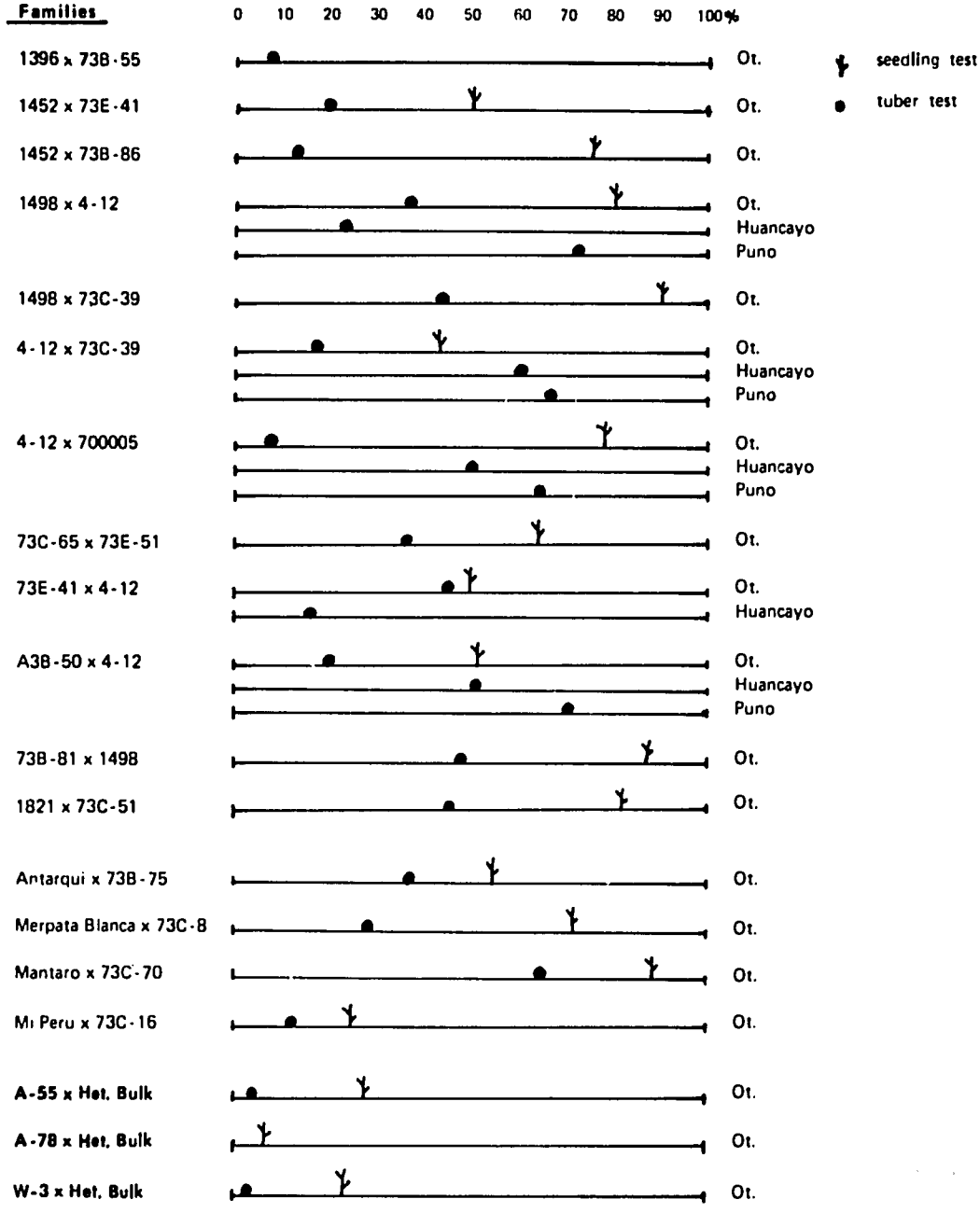



Percent selected
Families
0 10 20 30 40 50 60 70 80 90 100%
0041 x 1422
Ot.
0041 x 1535
Ot.
0041 x 66.1004.42
Ot.
Huancayo
Cuzco
Puno
166
Ot.
70166 x 0578
Ot.
Puno
0166 x 1422
Ot.
0166 x 66.1004.42
Ot.
Huancayo
Cuzco
Puno
1422 x 0166
Ot.
Cuzco
1478 x 1422
Ot.
Cuzco
1513 x 1422
Ot.
1513 x 1478
Ot.
Cuzco
1513
Ot.
2770 x 1422
Ot.
2770 x 1478
Ot.
66.1004.42 x 1422
Ot.
Huancayo
Cuzco
Puno
1421
Ot.
Seedling test
cutting test
tuber test
1977 retest
1978 retest
Selected

Hybrids between Tuberosum x selected Andigena



BACK CROSSES AMONG ANDIGENA – (1977-78)



it has been eliminated. Group 92 - shows that some diploids from S. ajanhuiri have shown fairly consistent reactions of resistance. Thus, next year with this additional information on groups we will be able to sort out groups or clones individually in the collection which really possess resistance at an acceptable level to be utilized as plants (Tables 8, 9 and 10).

In general resistant genes are present in low frequencies except in the bitter potatoes triploid S. juzepczukii and pentaploid S. curtilobum but these were not considered good sources of resistance as they are very difficult to cross (Tables 11 and 12).

The resistance found was not of a very high degree but were selected as certain clones consistently gave lower root ball, as well as total cyst count readings. Furthermore, even though the resistance was partial, it was still race specific.

The resistances found were mostly the population from Otuzco (P_5 A) which rates in the tests with European differentials as the most aggressive one.

Figures 1, 2 and 3 are an attempt to summarize not only the behavior of the ones utilized when intercrossing and selection was done, but also the method utilized to screen the progeny. Tables 13 is an overall view of the state of populations created.

Genetics of Resistance

The first study on the resistance of clone 70031, 70041 and 70166 gave a 50% resistance based on a seedling test and a repetition test. (Landeo, Dow & Scurrah, 1975). Actually, when the cut of line for resistance was lowered to no more than 10 cysts on root ball - (previous cut of line was 15 - as the parents had shown 10-15) the number dropped to about 30% and with further selection to no more than 6 cysts the number has dropped to 10-15%. Since our cut of line has varied and become more rigorous it has been impossible to fit a genetic model to these clones. Furthermore, these may be one and the same clone, further throwing us off the mark.

Nevertheless, we obtain 20% of resistance. When selfing one can postulate 3 genes, and when the three are together we get a higher level of resistance, while 2 or 1 gene will give many more cysts and will fall beyond our cut of line. Perhaps clone 1421 and 1422

TABLE 8

EVALUATIONS FOR RESISTANCE TO GLOBODERA
PALLIDA ROSTOCHIENSIS

ID NO	HYO	OTZ	CUS	PUN	SPP	SYN	STATUS
700031	1	2	1	1	AD	133	1
700041	1	2	1	1	AD	133	3
700166	1	2	1	1	AD	133	3
701499	1	2	1	1	AD	133	3
701513	1	2	1	1	AD	133	3
701908	1	2	1	0	AD	133	3

1 active 2 lost 3 eliminated

TABLE 9

EVALUATIONS FOR RESISTANCE TO GLOBODERA
PALLIDA ROSTOCHIENSIS

ID NO	HYO	OTZ	CUS	PUN	SPP	SYN	STATUS
700117	2	1	2	1	AD	131	3
700155	1	1	2	1	AD	131	3
700249	2	1	1	1	AD	131	3
700261	1	1	1	2	AD	131	3
700490	1	1	2	1	AD	131	3
700491	1	1	1	2	AD	131	3
700493	1	1	1	2	AD	131	3
700495	2	1	1	1	AD	131	3
700509	1	2	1	1	AD	131	3

1 active 2 lost 3 eliminated

TABLE 10

EVALUATIONS FOR RESISTANCE TO GLOBODERA
PALLIDA ROSTOCHIENSIS

ID NO	HYO	OTZ	CUS	PUN	SPP	SYN	STATUS
702320	1	1	2	1	AJ	92	3
702323	2	1	2	2	AJ	92	3
702325	2	1	1	2	AJ	92	3
702326	2	1	2	2	AJ	92	3
702562	2	2	2	2	AJ	92	1

1 active 2 lost 3 eliminated

TABLE 11

EVALUATIONS FOR RESISTANCE TO GLOBODERA

P A L L I D A R O S T O C H I E N S I S

ID NO	HYO	OTZ	CUS	PUN	SPP	SYN	STATUS
700299	2	2	2	1	JU	416	1
700301	2	1	2	1	JU	0	1
700895	0	1	2	1	JU	0	1
700902	2	1	2	1	JU	0	1
700944	1	1	2	1	JU	29	1
700962	1	1	2	1	JU	416	1
700964	1	1	2	1	JU	29	3
701014	2	1	2	1	JU	0	1
701022	2	1	1	1	JU	0	1
701283	2	1	1	1	JU	29	1
701323	2	2	2	1	JU	416	1
701353	0	2	2	2	JU	0	1
701410	1	1	2	1	JU	415	1
701783	2	1	1	2	JU	0	1
702008	1	1	2	1	JU	29	1
702053	2	2	2	2	JU	0	1
702305	2	1	2	1	JU	424	1
702443	2	2	2	1	JU	0	1
702444	1	1	2	1	JU	0	1
702445	1	2	2	1	JU	0	1
702448	1	2	2	1	JU	0	3
702491	2	0	0	0	JU	0	1
702581	1	2	1	1	JU	0	1
702620	2	1	2	1	JU	29	1
702626	1	2	2	1	JU	424	1
702630	1	1	2	1	JU	416	1
702631	1	1	2	1	JU	416	1
702635	1	1	2	1	JU	416	1
702699	1	1	2	1	JU	416	1

1 active 2 lost 3 eliminated

TABLE 12

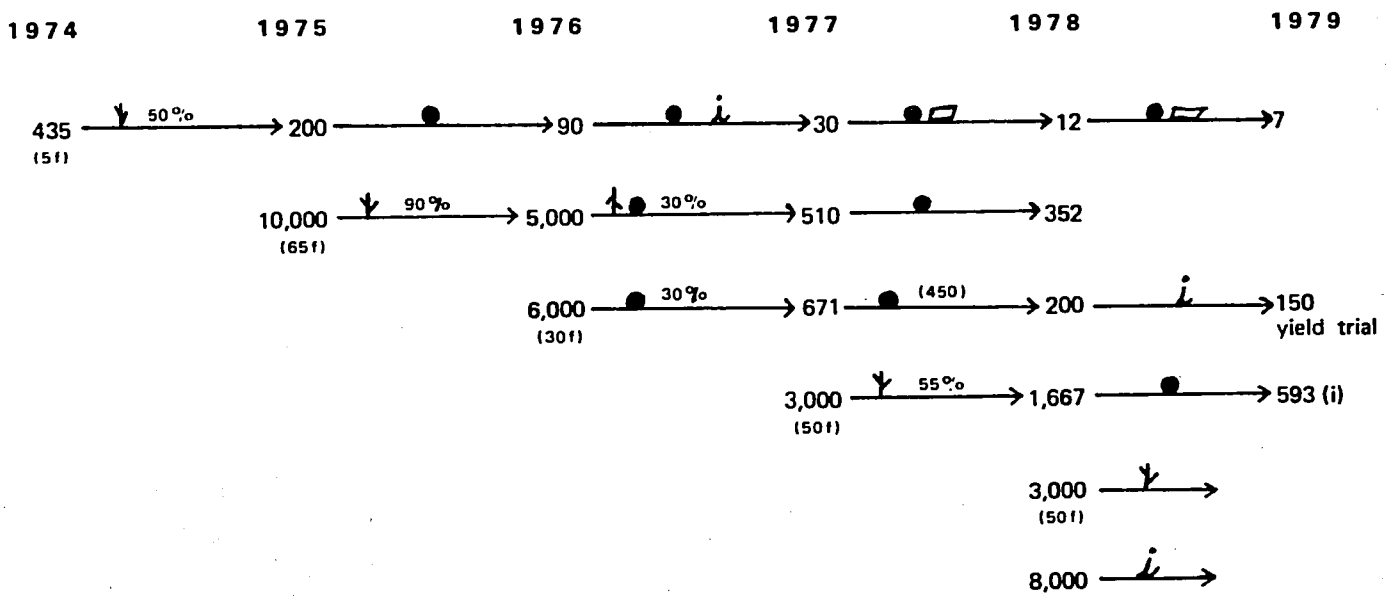
EVALUATIONS FOR RESISTANCE TO GLOBODERA

P A L L I D A R O S T O C H I E N S I S

ID NO	HYO	OTZ	CUS	PUN	SPP	SYN	STATUS
700264	1	1	2	1	CU	296	3
700265	0	2	2	1	CU	296	3
700266	1	1	2	0	CU	296	3
700267	1	2	1	1	CU	296	1
700272	2	0	2	0	CU	296	3
700274	1	1	2	1	CU	296	1
700281	1	1	1	2	CU	296	1
700289	2	1	1	1	CU	296	3
700291	2	1	1	1	CU	296	1
700296	1	1	1	2	CU	296	3
700297	2	1	1	2	CU	296	1
700586	2	1	1	1	CU	296	1
700626	2	1	1	1	CU	296	1
701040	2	1	1	1	CU	0	1
702115	2	2	2	2	CU	296	3
702116	1	1	2	1	CU	0	1
702211	2	1	2	1	CU	0	1
702334	0	2	0	1	CU	0	1
702355	1	1	2	1	CU	0	1
702357	1	1	1	2	CU	0	1
702455	0	0	2	1	CU	296	1
702713	2	0	1	2	CU	0	3
702723	1	1	2	1	CU	0	3
702939	1	1	0	2	CU	0	1

1 active 2 lost 3 eliminated

Table 13 — Summary of breeding and selection



Seedling test
Tuber test
% Percent resistant selections
Field trial
Increase in field

have these three genes present as they gave higher frequency of progeny resistant, or they may possess different genes altogether.

In 1977 two more and possibly 3 more clones were discovered in the germ plasm collection. These differed in two very important ways for the clones previously selected:

1. They were resistant to P_4A and in addition were not very good hosts to P_5A although were rated as susceptible, and;

2. Their resistance was of much higher level (0 cysts on root ball and 14 new cysts on soil in first test). These clones are expected to contribute significantly in obtaining resistance to pathotype P_4A. These clones are susceptible to G. rostochiensis and may also serve as a differential clone which operates in reverse of most differential clones.

Crosses have been made but progeny has not yet been studied to see how the resistance is composed or inherited.

In conclusion we feel that from the last 3 years of working with CIP's germ plasm, we have created a small population of S. andigena with a higher level of resistance than the ones originally found in the parents, in addition have added a few valuable new sources but it still represents a narrow base, which however, can easily be broadened with other andigena as well as other resistant breeding clones.

Other Sources of Resistance

Clones sent from other breeding programs were also utilized, albeit in a slow way as some of these were received in botanical seeds or flower with difficulty. The clones obtained from the Max Plank Institute contributed modestly to resistance to Huancayo and Cuzco populations. More recent arrivals seem to have a higher degree of resistance. Clones from Cornell University rated susceptible - until a year ago when intercrosses among wild species have been sent, but a crossing program with these clones has not been initiated and they represent very primitive material. Clones from Holland have been absent, with the exception of their tester clone also utilized often as a parent VT^{n2} 62.333 which rated resistant to 25% of Andean population but has never yet flowered under the conditions utilized for crossing. In 1978, nine breeding clones from Huijsman's program at the S.V.P. have rated highly resistant to P_4A and mostly susceptible to P_5A. In an attempt to better utilize these, in intercrosses with the andigena selections to P_5A, a greenhouse in Huancayo is currently being fitted with lights and they will be grafted on tomatoes.

Thus we feel that from the breeding point of view we have arrived at a "take off" point with several identified sources of resistance at hand already in cultivated forms and a not yet tapped sources of resistance in wild species which can be utilized easier by utilizing haploid S. andigena or unreduced gamets wherever possible.

III. Management

This term is identified as a pest management system that in the context of the associated environment and the population dynamics of the pest species, utilizes all suitable techniques and methods in a compatible manner as possible and maintains the pest populations at levels below those causing economic damage. Thus, pest management means a system approach that encompasses not only the immediate objective of preventing pest losses but also consideration of long-term objectives with regard to economics; society and the environment.

Some of the tactics useful in pest management and which can be integrated into a practical viable strategy are: plant resistance, cultural controls, biological control, pesticides and others. In this line of research and during the past five years a few studies have been carried out to follow the recommendations given by the previous Planning Conference.

As the interrelationships between nematode populations and plant metabolic processes are not well known, the water relations, nutrient uptake and photosynthesis have been investigated in susceptible and resistant plants to understand better the factors limiting known growth and eventually yield of P.C.N. infested plants. Results showed that resistant varieties grown in infested soil used water more efficiently than susceptible ones due to greater stomatal resistance and leaf water potential. Photosynthesis was decreased by nematodes, in both types of plants and uptake of N and K were also affected.

When British commercial potato viarieties were tested for tolerance on two sites (infested and uninfested with G. rostochiensis), the degree of tolerance to nematode attack was related to the amount of calcium accumulated in the dry matter of plants growing on the uninfested site and this relationship may have been due to the efficiency with which different cultivars used water (i.e. Pentland Crown).

In Peru, field tests of native and commercial varieties as well as advanced material from other programs have been conducted to determine their degree of tolerance with the following criteria:

a. Potato clones or cultivars which yield more than a standard variety (100%) without applying nematicides (NN).

b. Potato clones or varieties which increase in yield due to nematicide application is not more than 30% (N-NN).

Results of these tests showed that the varieties Ticahuasi and Huaytapallana possess a certain degree of tolerance when compared with the most common commercial varieties. (Table 14).

When selected clones from other programs were tested with the same purpose, twelve clones yielded more than 21 TM/Ha, showing that these clones could be grown in infested fields without danger of large yield losses. However, use of such material should be limited to areas where the nematode is widespread because large nematode multiplication occurs on these material or in situations where a strategy of integrated management is planned.

The effects of different factors (i.e. N-P-K fertilizer levels, and crop rotation) on the yield of potato plants and on the multiplication rate of P.C.N. have also been studied. Results in Table 15, show that in spite of a uniform nematode infestation, there has been a better yield response to P application than to N and K treatments.

The study with crop rotation is in progress and it is still too early to present clear results or even conclusions. However, in another experiment the effect on P.C.N. populations of some plants used in the Andes as vermifugs has been investigated. Results showed a reduction of nematode reproduction (G. rostochiensis)in plants such as Tagetes minuta, lupinus albus and mentha viridis. The highest reproduction of P.C.N. was obtained in potato plants associated with plants of Cucurbita maxima and Chenopodium quinoa.

When interaction of G. pallida and several fungi on potatoes were studied, the number of new formed cyst on plants inoculated simultaneously was depressed. It appears that fungi used in this experiment infect roots in the presence of G. pallida, a factor which retard nematode development. The fungi tested were: Phoma exigua (two varieties), P. andinum and Colletrotrichum coccodes. No cyst infection by the fungi was noted in cysts examined.

Regarding the aspects of natural enemies of P.C.N. it has been found that larvae emergence from cysts kept in agar plates inoculated with Ulocladium botrytis and Drechslera halodes was suppressed. A species of Tricholadium sp. also inhibited the larvae hatching but to a lesser degree. All the fungi tested were isolated from naturally infected eggs of Globodera pallida. When Drechslera halodes and cysts of G. pallida were inoculated on potato plants growing in pots the final number of cysts was significantly lower (80%) than in the control.

Since bitter potato varieties were found to possess varying degrees of resistance to several nematode populations it is advisable to utilize these varieties in rotation schemes wherever a possible market exists for this crop.

TABLE 14

SELECTED CLONES FOR TOLERANCE TO THE POTATO CYST-NEMATODES

GLOBODERA SPP.

Material Tested	Yield		
	NN	N	N-NN ≤ 30%
High yielding			
66-563-13	34,500	-	-
374063-2	26,100	-	-
374106-4	25,500	-	-
374102-1	23,490	-	-
375553-25	23,400	-	-
Frost resistant			
375570-53	28,200	-	-
375597-4	25,500	-	-
375581-1	24,000	-	-
375570-30	23,490	-	-
Commercial varieties			
Ticahuasi	9,180	12,870	28.7
Renovación	9,510	17,370	45.3
Mariva	8,850	13,440	34.2
Antarqui	8,640	13,410	35.6
Renacimiento	6,390	15,120	57.7

TABLE 15

EFFECT OF N-P-K- FERTILIZER LEVELS ON THE YIELD OF A POTATO CROP GROWN IN A PCN INFESTED FIELD

TREATMENTS (N-P-K)	YIELD (Kg/Ha)
S* - 2S - S	29,680
S - S - 2S	26,050
2S - 2S - 2S	26,580
2S - 2S - S	24,680
0 - 2S - 0	17,480
0 - 0 - 2S	9,080
2S - 0 - 0	8,390
0 - 0 - 0	8,910

* S = Standard rates/Ha N = 160 Kg P = 200 Kg K = 200 Kg

R E F E R E N C E S

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A REVIEW OF THE RESEARCH PROGRAM ON THE DEVELOPMENT OF RESISTANCE TO THE ROOT-KNOT NEMATODES *Meloidogyne* spp.

P. Jatala and H. Mendoza

Prior to discussing the research progress on the root-knot nematodes, it is of interest to briefly review the history on the progress of obtaining resistance to the potato cyst-nematodes *Globodera* species.

Initial testing for resistance to the potato cyst nematode was begun about 1947 and it was not until 5 years later that a resistant individual was identified. It took an additional 10 to 12 years before a resistant cultivar possessing a single dominant gene was released. It is equally interesting to note that the effort in such research was not only by one institute but the concern of different institutes in four countries including the Great Britain, Germany, Holland and the United States. Occurrence of the new races of the potato cyst-nematode further complicated the matter. Nematologists and plant breeders are still attempting to solve the problem which is taking over 3 decades.

Prior to 1974 a limited amount of work was done on the development of varieties resistant to *Meloidogyne* species. This was probably due to the fact that potatoes were predominantly grown in the cooler climates of the world and where *Meloidogyne* species are not considered as a world wide economic problem on potatoes. Since one of the CIP's efforts was to extend the range of potato culture into warmer climates such as the lowland tropics and the attempts were successful, a program was initiated at that time in order to search for and utilize the resistance to these nematodes in these adapted potatoes. Relatively speaking, this program is still in the infancy stages as compared to that of the cyst nematode research.

Following the recommendations of the First Planning Conference on Nematode Control Strategy, held in 1974, major emphasis in searching for resistance to root-knot nematodes was placed on screening cultivated potatoes of the CIP germ plasm collection. Screening was conducted primarily in a uniformly *Meloidogyne incognita acrita* infested field. An average of four to six tubers of each clone were planted in two

different locations in the field. When conducting the experiments under screenhouse conditions, tubers were planted in 500 cc clay pots containing approximately one gram comminuted M. incognita acrita infected tomato roots. In addition to the clones of CIP germ plasm collection, over a thousand clones of diploid Solanum material from the North Carolina selections as well as 750 clones from other programs with certain desired attributes were also tested for resistance to the root-knot nematode (Table 1). Prior to their maturity, plants were removed from the soil and their roots were examined for nematode infection. A root-knot index of 0-4 was used for rating the relative susceptibility of plants to the root-knot nematodes. The criteria used for rating of resistance or susceptibility is as follows:

0 = Immune = no root galling or nematode reproduction,

1 = Resistant = trace of root galling and/or nematode production,

2 = Moderately susceptible - moderate root galling and/or nematode reproduction,

3 = Susceptible = severe root galling and/or a high nematode reproduction,

4 = Very susceptible = very severe root galling and/or a very high nematode reproduction.

Tubers were examined for surface deformation due to nematode infection. Those with no apparent surface symptoms were stored for two months prior to re-evaluation. If there was still no apparent surface deformation after this period, tubers were sliced and examined for the presence of the nematodes inside. Data indicated a rather low percent of the plants of the germ plasm collection, diploids or of other selections exhibiting any degree of resistance. Similarly, the levels of resistance to the nematodes were low (Table 1). It was suggested that intercrossing these material as well as outcrossing them to selected genotypes should be considered in order to fully utilize the genetic resources. Data obtained from the tuber examination when compared to those of the root infection, revealed no correlation of infection in these two plant parts. Roots of some clones were severely infected by the nematodes but their tubers were not and vice-versa. This indicated that resistance of roots and tubers to the root-knot nematodes may be independent of one another. Different types of resistance of potatoes to the root-knot nematodes is presented in Table 2. Apparently there are two types of tuber resistance. The most common type of tuber resistance is the absence of surface galling or deformation. However, the developing and egg laying females may be present inside of tubers. Deep-seated infection has no effect on symptomless expression of infected tubers but would cause more internal symptoms than external galling. The least common tuber resistance was the type where there were no external or internal symptoms.

TABLE 1

CULTIVATED POTATO MATERIAL TESTED FOR RESISTANCE TO
MELOIDOGYNE INCOGNITA ACRITA

Material Tested	No. of Clones	% Resistance	Levels of Resistance
Germ plasm	5865	1.8	Low
Diploid	1020	2.7	Low
Other selections	750	1.9	Low

TABLE 2

TYPES OF ROOT-KNOT NEMATODE RESISTANCE IN POTATOES

1.-	Root Resistance	
2.-	Tuber Resistance	No External Symptoms No Internal Symptoms
3.-	Root and Tuber Resistance	

Since at the early stages of screening it was found that the frequency and level of resistance in the cultivated potatoes of the CIP germ plasm was rather low, parallel studies in screening wild tuber bearing Solanum species were conducted.

A total of 65 tuber bearing Solanum species represented by 482 accessions and 8060 genotype were tested for resistance to the root-knot nematodes. Reaction of these material to M. incognita acrita is given in Table 3.

Roots of 3.5% of genotypes showed a galling rate of 1 or less (Table 3). Although this percentage is rather low, it is significantly higher than that of the result of the germ plasm material. Also the level of resistance was significantly higher. Plants with high levels of resistance or immunity were retested. Solanum chacoense PI 197760 (CIP No. 760917) and S. sparsipilum PI 230502 (CIP No. 70147) selections had the highest immune genotypes from these two accessions were selected for further use in breeding programs. Data indicated that S. sparsipilum CIP No. 760147.7 was the most resistant genotype and showed immune reaction to the root-knot nematodes in several tests. This genotype as well as those of S. chacoense were also tested for resistance to Pseudomonas solanacearum, Globodera pallida (3 races), G. rosthochiensis (1 race) and Nacobbus aberrans. They were found to be highly resistant to these organisms. It appears (as in other hosts) that the resistance to Meloidogyne and Pseudomonas is probably governed by the same set of gene or genes. Therefore, once a plant is resistant to Meloidogyne it is most probably resistant to Pseudomonas. This is not true however, in the reverse situation since all the Pseudomonas resistant plants that we tested were highly susceptible to Meloidogyne. Certain progress has been made in combining Meloidogyne resistance with others such as Pseudomonas and Phytophthora in Phureja material. Result of interaction studies involving Meloidogyne and Pseudomonas will be discussed under the report of the progress of interaction research.

Since several resistant and immune material were identified in S. sparsipilum, S. chacoense, S. phureja and several tetraploid andigena group, a combination of inter and intra specific crosses of these material were made and progenies were tested for resistance to the root-knot nematodes (Table 4).

A total of 6482 genotypes of 105 families developed in the above mentioned crosses were each inoculated with 4000 M. incognita acrita eggs and seedlings were allowed to grow in a screenhouse in La Molina. Two months later the roots were removed from soil and evaluated for nematode infection as described earlier. Results of this study will be presented in detail in a separate paper discussing breeding for resistance to the root-knot nematodes. However, it is interesting to mention that the crosses involving S. sparsipilum as female parents resulted in the highest segregating immune progenies. Results suggest that there is a material effect on the inheritance of immunity to M. incognita acrita. Similarly, it appears that susceptibility is partially dominant to resistance or

TABLE 3

THE REACTION OF SOME TUBER BEARING *SOLANUM* SPECIES

TESTED FOR RESISTANCE TO *MELOIDOGYNE INCOGNITA ACRITA*

	No. Tested	% Resistance	Levels of Resistance
Species	65	40.8	Low to very high
Accessions	482	18.6	Low to very high
Genotypes	8060	3.5	Low to very high

TABLE 4

COMBINATION OF THE INTER AND INTRA SPECIFIC CROSSES OF DIPLOID AND TETRAPLOID *SOLANUM* SPECIES USED FOR RESISTANCE TO *MELOIDOGYNE INCOGNITA ACRITA*

Female Parents	Male Parents				Total Families	Total Genotypes
	S. spartipilum	*S. chacoense*	*S. phureja*	Tetraploids		
S. sparsipilum	3	5	8	-	17	846
S. chacoense	3	1	-	-	4	264
S. phureja	20	1	14	-	35	3566
Tetraploids	-	-	-	49	49	1806
TOTAL	26	8	22	49	105	6482

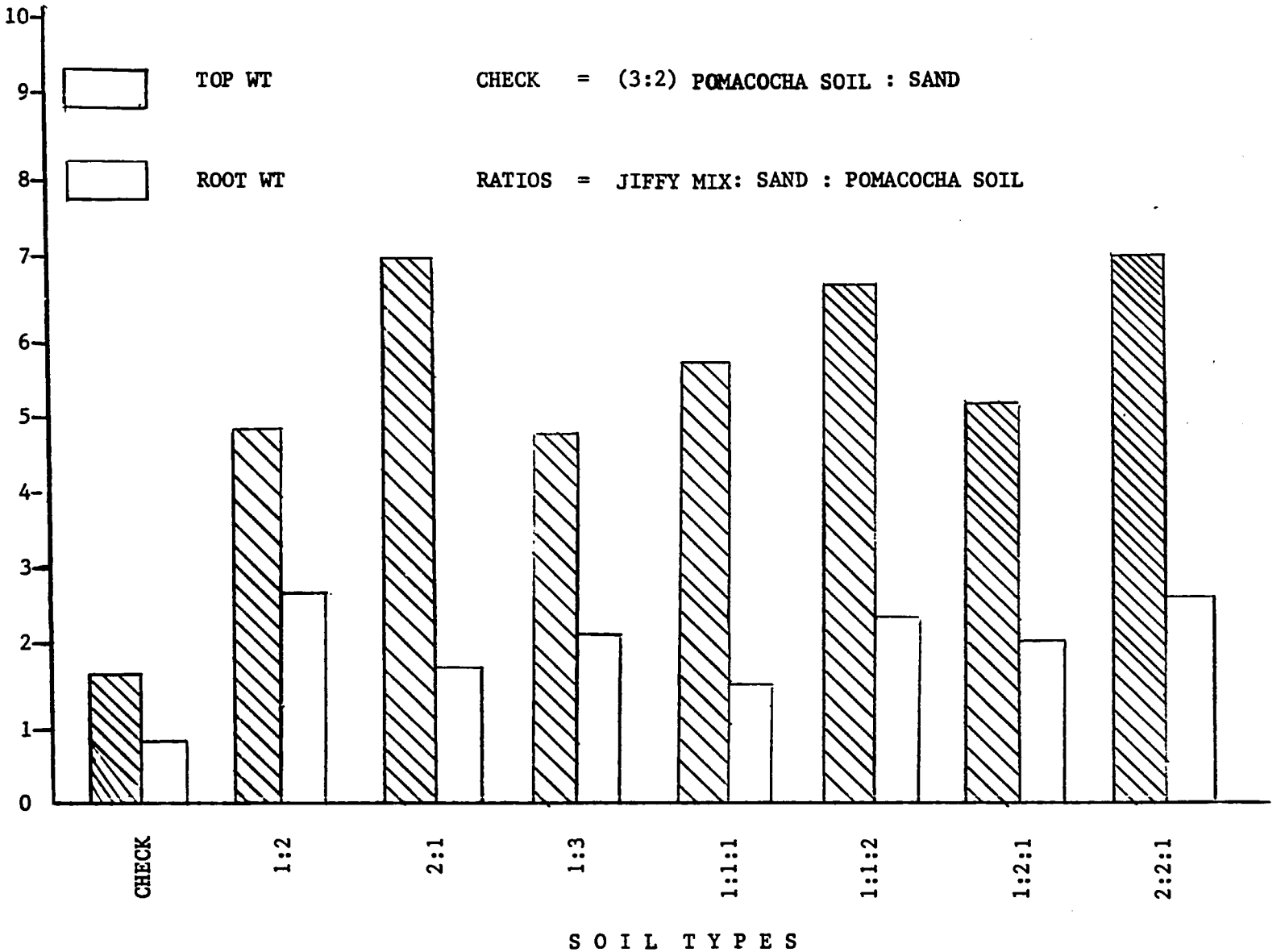
immunity. All the immune genotype of this test were saved, replanted and over 400 crosses of intra-diploid and diploid-tetraploid combinations were made. This includes intra and inter specific combinations of crosses. It is interesting to note that the parents used in these crosses have many desired attributes such as adaptability to lowland tropics, Pseudomonas, Phytophthora and virus resistance in addition to immunity to the root-knot nematodes. It is apparent that obtaining resistance or immunity to Meloidogyne species has been achieved at a much more rapid pace than that of the potato cyst nematode.

Several andigena clones selected in the Cornell University program as resistant or immune to five species of the root-knot nematodes of the United States populations were tested for their reaction to the Peruvian root-knot nematode population of M. incognita acrita. All these plants showed very susceptible reactions to the Peruvian root-knot nematode population. This confirmed the possibility of occurrence of races in this group of nematodes. Further study of the race distribution warrants attention and crosses with resistance to various races is essential in incorporating resistance to these nematodes. It is interesting to note however, that Peruvian population of M. incognita is probably a more virulent race and attacks a larger number of plants than other races. Therefore, it may be a better population to screen against in order to have a wider stability in resistance.

Finally, in addition to screening and searching for resistance to these nematodes, various methodologies were tested in order to increase the efficiency of the program.

Due to limited availability of space and the need for testing a large number of families and genotypes developed in the breeding program, a methodology for a rapid and efficient seedling screening had to be developed. Use of the small 4 oz plastic cups were considered and tested. However, majority of the seedlings did not develop and died. To determine the effect of soil type on the growth of the seedlings in these cups, a variety of soil mixtures were used in an experiment. Young seedlings were transplanted in plastic cups containing various soil mixtures. A 3:2 Pomacocha soil: sand mixture (which were normally used in Nematology Program) was used as check soil type. Two weeks after transplanting, seedlings were inoculated with 5000 Meloidogyne eggs. Two months later plants were removed from soil, roots were examined for nematode infection and plant height, fresh top and root weights were recorded, there were no differences in the intensity of nematode infection among treatments. However, there were significant differences of plant height, fresh top and root weight among treatments. Plants grown in various soil mixtures had significantly higher top and root weights than the check soil. The soil mixture of 2:2:1 Jiffy mix: sand: Pomacocha soil was the best medium for seedling test Fig. 1. This soil mixture is now being widely utilized in the nematology program. This method provides an efficient and rapid seedling screening procedure for a large number of pathotypes against both root-knot and cyst nematodes.

GROWTH OF POTATO SEEDLINGS IN DIFFERENT SOILS TYPES



REVIEW OF THE FALSE ROOT-KNOT NEMATODE (NACOBBUS SPP.)

RESEARCH PROGRESS

P. Jatala

The false root-knot nematode is considered as one of the most important nematode pests of potatoes in certain Andean regions of Peru and Bolivia. Although the occurrence of this nematode in these areas was well known, there was a limited amount of information on its geographic distribution in other South American countries as well as a number of species attacking potatoes, its host range and its biology on potatoes. The aim of this research was to investigate the importance of this nematode as a pathogen of potatoes in addition to determining its geographic distribution, host range and biology.

Potato growing areas of Bolivia, northern Argentina (partly), southern Peru, Ecuador and southern Colombia (partly) were surveyed for the presence of Nacobbus spp. In addition to this survey, a comprehensive study on the geographic distribution of this nematode in the southern Peru, Department of Puno, where this nematode is considered the most important pest of potatoes was conducted with the cooperation of the scientists from the Estación Experimental de Puno.

It was found that practically all the potato growing areas of Bolivia and most of the fields in the southern highlands of Peru were heavily infested with this nematode. In Peru, Nacobbus spp. is also distributed in certain areas of central and northern highlands. Only a certain potato growing area of northern Argentina was examined and was found to be infested with this nematode. Recent reports indicate a rather wide distribution of this nematode in the North Central part of Argentina. In Ecuador, Nacobbus spp. were found in two different location on tomatoes and potatoes. No Nacobbus spp. was found in the fields visited in Colombia. Presence of this nematode has also been recorded in Mexico. World distribution of this nematode includes: Argentina, Bolivia, Chile, Ecuador, England, Holland, India, Mexico, Peru, Russia and the United States.

In South America Nacobbus spp. are found primarily in the highlands where the temperature during the growing season ranges from 14 - 17° C. In Ecuador, however, this nematode was found in an area where the average temperature ranges from 22-24° C. It was also found that this nematode

infected potato roots and reproduced rapidly during the summer months in the greenhouse experiments in La Molina. Similarly, it was found that the parasitic activities of this nematode increases in higher temperatures. This was confirmed in an experiment when at high temperatures (22 - 26° C) the resistance of potato to Nacobbus spp. was broken. In addition, it was found that this nematode has a rather wide host range and attacks the plant species in most families except those of the Gramineae.

Data indicate that Nacobbus species have a rather wide temperature adaptability in addition to having a wide host range and can become a problem in warmer climates.

A comprehensive taxonomic study of the Nacobbus species attacking potatoes was conducted in cooperation with Dr. A. M. Golden, USDA Nematologist, Beltsville, Maryland. A total of 26 populations collected from Argentina, Bolivia, Ecuador and Peru were examined morphologically for taxonomic identification. Although there were differences in morphometrics among the nematodes of these various populations, the variations were within the broad limits of several populations described by Sher for N. aberran in his revision of the genes in 1970. He retained only two species in N. dorsallis and N. aberrans, and synonimized N. batatiformis, N. serendipiticus and N. serendipiticus bolivianus under N. aberrans. However, we view N. aberrans as a species complex involving two or more forms rather than a single homogeneous species. We base this view on morphometrics of populations examined, on the original description of N. aberrans and its three "synonyms", and on the fact that in host tests by the original authors of N. batatiformis this species did not develop on any of six potato varieties tested. An extensive morphological study involving specimens from more collections and parallel host range tests are needed to clarify classification in this group. Until this is completed, all known Nacobbus species found in South America up to the present time are considered to be the N. aberrans complex.

Since the symptomatology of Nacobbus infection is primarily the galls produced on roots and there is no apparent tuber infection, the following experiment was conducted to determine if tubers are also infected.

l ato tubers collected from a field heavily infested with N. aberrans were carefully washed, planted in 3,600 cm^3 clay pots containing methyl bromide-fumigated soil, and grown in a screenhouse. Two months after emergence pot contents were soaked in water to remove soil. Roots were checked for nematode damage; infected parts were stained in acid fuchsin-lactophenol and cleared in lactophenol. Microscopic examination revealed nematodes in various stages of development in all infected roots. Similarly, others collected from the same field were sectioned (2 mm. thick), stained, and examined. Many tuber sections contained nematodes in the

3rd, 4th and 5th stages of development. Most sections containing nematodes were from the outer layer of the tubers, the tuber skin and the flesh immediately below the skin. These findings indicate that (a) tubers are infected by the nematode and (b) the importance of infected tubers as a source of dissemination of N. aberrans. The presence of nematodes on or near the surface of tubers may facilitate control by hot water or chemical dip treatment.

As a part of studying the biology of the nematode, possibility of the survival of N. aberrans under desiccation was investigated. Soil samples collected from a heavily infested field were air-dried on a laboratory bench and maintained in that condition for one year.. Relative humidity of the soil during the period varied from 7 - 9 percent. Periodically, young tomato seedlings were transplanted in 4 oz. plastic cups containing this air dried soil. After two months roots were washed and rated for nematode infection. Parallel soil analysis in extracting egg masses and vermiform nematodes from the air dried soil was conducted at transplanting. Data indicate that N. aberrans can withstand desiccation for at least 8 months (Table 1). Egg masses extracted from the desiccated soil up to 8 months contained eggs. Similarly, a few immature adult female which were quiescent stage were also recovered. This would indicate that both eggs and immature adult females are the two stages which withstand desiccation and are the means of survival of this species in adverse conditions. It is concluded that the infected tubers and the adherent dried soil on tubers are the two basic means of dissemination of this nematode. Similarly, it is safe to conclude that a hard prevailing wind may also serve as a factor in dissemination of this nematode which may be present in the dried soil.

Since both Meloidogyne species and N. aberrans often occur together, it was difficult to obtain pure culture of the latter. However, air drying the infested soil 2 to 4 weeks prior to planting a susceptible host, would provide an efficient method for obtaining a pure culture of N. aberrans.

The findings reported above have contributed to the understanding of the biology and importance of this nematode on potatoes. However, information on the life cycle of this nematode on potatoes is rather limited and warrants attention. Similarly, obtaining resistance would be of great importance in controlling this nematode which is among the top three important nematode parasites of potatoes.

Table 1

SURVIVAL OF NACOBBUS ABERRANS UNDER

DESICCATED CONDITIONS

Source of inoculum	Root galling index[1]			
	1 month	3 months	5 months	8 months
Moist infested soil	2.5	2.3	2.8	2.4
Infested dried soil (RH7-9%)	2.2	2.0	2.3	2.0
Control	0	0	0	0

1. 0 = no root galling to 4 = very severe root galling.

PROGRESS ON CYST NEMATODE RESEARCH IN THE NETHERLANDS

A. F. van der Wal

Introduction

Breeding for resistance to the potato cyst nematode has been practiced by the Foundation for Agricultural Plant Breeding (S.V.P.) in Wageningen for over 25 years. In this period, a close cooperation between the Foundation, the Plant Protection Service, and over a hundred private plant breeders was developed. This cooperation resulted in 26 cultivars with potato cyst nematode resistance in the Dutch List of Varieties 1978. Twenty-two of them possess resistance to pathotype Ro1; cultivars (Elkana, Mara, and Veenster) have combined resistance to the pathotypes Ro1, Ro2, and Ro3 and one (Pansta) has resistance to the pathotypes Ro1, Ro2, Ro3, and Pa2. In 1972, Huijsman and Lamberts reported the existence of 16 resistant cultivars in the Dutch List. Then only cultivars with resistance to *G. rostochiensis* were introduced. Some of these cultivars have a very high yielding capacity, e.g. 'Astarte'. In a relatively short period, combined resistance to *G. rostochiensis* and *G. pallida* was incorporated into new cultivars. It has been proven, once again, that the efforts of governmental institutions, such as the Foundation for Agricultural Plant Breeding and the Plant Protection Service, combined with those of private plant breeders, can be very effective in producing new resistant cultivars.

Sources of Resistance

CPC-1673 is the most common in Dutch cultivars as an Andigenum source of resistance to pathotype Ro1. Resistance to pathotype Ro1 has been obtained from *S. vernei* clones as well, e.g. SVP VT^2 (60-7-1). Resistance to the pathotypes Ro2 and Ro3 and pathotype Pa2 (*G. pallida*) was also found in other species than *S. vernei*. Huijsman and Lamberts (1972) have listed the species which were screened for resistance by SVP. At present, only cultivars with resistance from *S. andigenum* and *S. vernei* are on the list of varieties.

Combined resistance to all pathotypes known in the Netherlands up to pathotype Pa3* was found in S. vernei.

Much attention has been paid to the screening of S. andigenum and S. vernei and much less work has been done in the Netherlands on the other species. It is not justificable to conclude that only resistance from S. andigenum or S. vernei are useful but, on the other hand, resistance from other sources has not been incorporated yet into the Dutch cultivars.

The wild species S. sparsipilum and S. gourlayi are screened for resistance on a large scale. Many breeding lines have, apart from S. vernei genes, genes from S. leptophyes, S. oplocense and S. spegazzinii.

Inheritance of Resistance to the Cyst Nematode

The Dutch work on the inheritance of resistance to the potato cyst nematode has been published before (cf. Huijsman, 1955; Huijsman and Lamberts, 1972; Huijsman, 1974). These genetic studies have been performed on the inheritance of the major gene resistance to pathotype Ro1 from S. andigenum, and from S. vernei, and on the inheritance of resistance to pathotype Pa2, a system, in which the effects of major genes are veiled by the effect of a polygenic system. The inheritance of resistance of parental clones is determined in order to inform private plant breeders.

Screening Procedure

The procedure consists basically of two different parts:

1. large capacity screening by means of the root ball test;

2. small capacity (ca 10,000 annually) screening using the flotation test.

The former has the advantage of being labour extensive, and therefore, suitable for discarding the clearly nonresistant clones. The latter is used as a final test for those clones that show resistance. The 80% reduction criterion is here used to separate resistance from nonresistant clones. The flotation test is used in the same way by both the SVP

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* Recently, resistance to pathotype E (Pa3) was also found in S. andigenum clones from Dr. M. de Scurrah.

and the Plant Protection Service in order to maintain the link between the resistance standard used by SVP in the material they supply to private breeders and the standard used by the Plant Protection Service, when progenies of these issued clones come back after back-crossing in order to be tested for eelworm resistance; this being part of the acceptance procedure in the list of varieties.

Variation in results of tests between seasons is due to a large extent to fluctuations in the water potential and/or temperature outside the optimum range for nematode infection and reproduction. These optimal conditions of soil water potential and temperature are well known, but a simple system to maintain such conditions in glasshouses has not yet been devised.

In the last two years some progress has been made in this respect, and we have now entered the stage of careful introducing the new routine. The standardization of soil, fertilizer, and inoculum (egg suspensions instead of cysts) will also reduce variance. The maximum multiplication found under optimal conditions in a 200 gram pot was about 70 times, whereas multiplications of 30 to 50 times are normal on susceptible hosts.

Another advantage of watering the plants automatically is that quarantine can be maintained more easily. Apart from virus infections via aphids carried with the air input, the most common source of contamination is the transport of aphids by the people who have to take care of the plants, and others who enter the glasshouse.

Reductions of variation between replicates is especially useful when the search for lower degree resistance (non multiplication) is introduced. Furthermore, the number of cysts produced on the root system is not always a good measure in quantitative experiments, where the multiplication factor has to be determined accurately. At the initiative of Dr. Huijsman, an electronic egg and larvae counter was developed at the Technical and Physical Engineering Service. The performance of the prototype is promising. Calibrations have shown a linear relation between the counts of the instrument and the classical microscopic counts. The prototype is now being further developed to make it easier to handle. For these experiments, the inoculum consists of cysts in a nylon net bag in order to recover only the newly formed cysts for the flotation test and electronic egg countings.

Two glasshouses have been constructed this year, one on the grounds of the Foundation and one at the Plant Protection Service. The glasshouse on the grounds of the Foundation is designed to maintain aphid-free conditions during the growth of the plants. This glasshouse is specially used to grow botanical seed for tubers, and to grow wild and primitive

species. Short day conditions can be achieved in one of the four compartments of the glasshouse, and all four compartments are equipped with additional light facilities.

A new glasshouse on the grounds of the Plant Protection Service is used to screen for eelworm resistance, in addition to already existing facilities.

Trends in Research

Present research is directed towards finding further resistance to pathotype Pa3. Some genetic work is in progress to analyze the inheritance of the resistance to pathotypes Pa2 (D) and Pa3 (E), mainly to inform plant breeders what they can expect from back-crosses with the resistant clones.

Furthermore, the genetic diversity of the population of pathotype Pa3 in The Netherlands is given much attention. The multiplication on various testers of a series of isolates of pathotype E is being determined. A representative sample of pathotype Pa3 is used to test the value of newly detected resistance sources in a certain region. Only after this check has been completed, is the resistance source issued to the private plant breeders.

Research on tolerance appears on the list of the Foundation's projects.

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BREEDING FOR RESISTANCE TO ROOT-KNOT NEMATODES IN POTATOES

B.B. Brodie

The root-knot resistance program began in 1973 when selected clones from the Cornell University collection of Solanum tuberosum subsp. andigena were evaluated for resistance to root-knot nematodes. That year we evaluated approximately 1500 clones of Solanum tuberosum subsp. andigena against populations of Meloidogyne incognita acrita, M. incognita, M. arenaria, M. javanica, and M. hapla. From these evaluations, we selected 15 clones that exhibited some degree of resistance (rating of 5 or less) to this mixed root-knot species population. These 15 clones were evaluated against each Meloidogyne sp. separately and 5 clones were selected that had resistance to 2 or more species.

These 5 clones were bulk crossed, i. e., each clone was pollinated with bulk pollen from all the other clones. These crosses were made in an attempt to increase the level of resistance as well as to obtain resistance to several species in a single clone. Progeny from these bulk crosses were tested against each of 5 root-knot species. These crosses produced two families with a high level (rating 3 or less) of resistance to the 5 species of Meloidogyne. Resistance to M. incognita acrita had the highest frequency with up to 100% of the progeny in one family resistant to this species. Resistance to M. incognita was found in all families with up to 42% of the progeny in one family resistant to this species. Only 3 of the families contained progeny with resistance to M. arenaria, M. javanica, and M. hapla.

Resistant seedlings from this test were retested against extremely high inoculum densities of the 5 Meloidogyne species. Resistance was confirmed in 80% of the seedlings initially graded resistant to M.incognita acrita, in 78% to M. hapla, and in 50% to M. incognita, in 45% to M. javanica, and in 0% to M. arenaria.

Twenty eight clones from these crosses were selected for evaluation against each root-knot species separately. From these evaluation, 7 clones were selected as having good resistance against two or more species. One clone was resistant to 3 species, M. incognita, M. arenaria, and M. javanica. No clone was resistant to all species.

These 7 clones were bulk crossed in an attempt to increase the level of resistance as well as to obtian resistance to all root-knot species in a single clone. Progeny of these crosses are now being evaluated against each Meloidogyne sp. separately.

In 1977, S. sparsipilum, S. chacoence, and S. phureja were introduced into the root-knot resistance program. Seeds of intercrosses of these species were obtained from CIP. The progeny of these crosses were known to contain resistance to M. incognita acrita (Peru population). They are now being evaluated against M. incognita, M. arenaria, M. javanica, and M. hapla.

BREEDING FOR RESISTANCE TO GLOBODERA ROSTOCHIENSIS

In the Cornell Potato Breeding Program we routinely evaluate for resistance to Globodera rostochiensis. This is now done in pot tests using naturally-infested field soil. Ratings for resistance are done on root ball examinations. Root balls with 0-5 cysts are rated resistant, and thos with more than 5 cysts are rated susceptible.

Several thousand clones from the program on utilization of andigena potatoes have been tested. To date, we have 42 clones from the 3rd cycle of selection with resistance to G. rostochiensis Race A. The clones were derived from several accessions. The clones, accession, and origin are given in the following table.

Clones Resistant to *Globodera rostochiensis* from the Cornell Andigena Program

Clone	Accession	Origin
M 593	PI 161737	Mexico
M 614	PI 214430	Peru
M 650	PI 233982	Bolivia
M 654	PI 233987	"
M 663	PI 233998	"
M 730	PI 243430	Colombia
M 736	PI 243436	"
M 750	PI 243453	"
M 757	PI 245321	"
M 770	PI 246516	Peru
M 800	PI 258886	Bolivia
M 824	PI 280890	Argentina
M 832	PI 280903	"
M 834	PI 280907	"
M 835	PI 280908	"
M 837	PI 280910	"
M 840	PI 280915	"
M 842	PI 280923	"
M 857	PI 280944	"
M 901	PI 281004	Bolivia
M 933	PI 281041	Peru
M 998	PI 281139	"
M 1032	PI 292097	"
M 1044	WRF 1293	"
M 1064	WRF 1540	Bolivia
M 1097	WRF 1770	"
M 1140	CCC 308	Colombia
M 1141	CCC 309	"
M 1177	CCC 1561	Peru
M 1348	CEP 360	Ecuador
M 1371	G11285	Peru
M 1372	G1169 X	"
M 1414	G 18887	"
M 1564	CPC 2956	"
M 1576	CPC 3020	"
M 1678	CPC 5227	"
M 1802	G 18189	"
M 1838	G 1992 X	"
M 1918	627	"
M 1924	673	"
M 1939	1099	"
M 1961	BAL 71226	Argentina

BREEDING FOR RESISTANCE TO POTATO CYST NEMATODE AT CIP

M. de Scurrah and A. van der Wal

Introduction and Objectives

The potato cyst nematode is now a recognized problem in 47 countries. In these countries or parts of them potatoes have been cultivated for many years and play an important role in agriculture and nutrition. Third world countries that fall into this list are mainly the Andean countries, some elevated parts of Central America, Greece and Tunisia in the Middle East and in India the Nilgiris region (Mai 1977). Resistant varieties are one of the more efficient tools available to European farmers in keeping population density levels of the potato cyst nematode below the damaging levels (Huijsman 1960, Cole 1962, Jones 1970). In the third world countries long rotations and nematicides are the only means of control; the latter has been long standing traditional cultural practice in the Andean countries but strict rotation patterns have been collapsing under the pressure for more food production and nematode populations tend to rise. This phenomenom is particularly evident where land holdings are small. There is a negative correlation between nematode infestation and size of land owned by family or community. From information of crop ecology (i.e. what crops are grown in an area) and the land-tenure system, one can predict which will be the troubled areas for high nematode density and consequently heavy yield losses. The "mini-fundio" or very small farm, is the norm in practically all of the Bolivian highland (1/3 ha is the average family holding), the Titicaca region of Peru, many highland communities in southern, central and northern Peru and the region of south Colombia fall into this category.

In the agro-economic survey of the Mantaro Valley done by CIP, they found that the average size of farm was 0.6 ha, that 40% of cultivated land was potatoes and more so in the higher areas, that they had a certain rotation pattern, with a fallow period. The first and second year after fallow potatoes are planted with an average yield of 6.61 tn/ha the first year and 2.93 tn/ha the second year on the left side of the river and 4.10 tn/ha the first year and 2.28 tn/ha on the right side. The input of fertilizer is high and practically the same for both years.

Another constraint - other than smallness, which tends to shorten potato rotation is high altitude, above 3,400, potatoes become the most economically important crop and often as is the case of bitter potatoes are the only crop which climbs up to 4,000 m. Some areas near volcanoes in Ecuador are problem pockets, and again a large portion of Peru and Bolivia where smallness and high altitude are often combined. A third kind of area where losses due to nematodes is reported is a favorable potato growing area which caters to the market of a nearby big city, making potatoes an economically attractive crop, shortening rotations often leading to monoculture and reporting tremendous nematode problems. These areas usually only survive on yearly nematicide treatment, but the farmers tend to be economically more solvent than the first two types. Cerro Punta in Panama, Merida in Venezuela, and Huasa-Huasi in Central Peru, are examples of this. Thus, most of the heavy losses are suffered by the small farmers of the Andes, and probably these observations hold true to other third world countries. Thus nematode pest management becomes of prime importance if one thinks of raising the productivity of the temperate regions of the third world with particular emphasis on small farms.

It is evident, that if one wants to provide farmers with resistant varieties to manage nematode populations one has to address oneself to the variability of the nematode to insure that a particular resistance will actually stand up in a given area and thus a breeding program of this broad scope needs to have several build in components:

A. A screening program for new sources of resistance has to be actively maintained to indentify new and diverse sources of resistance. This can be pooled from CIP's screening program as well as other screening programs around the world.

B. A strategic breeding program aimed at combining different genes for resistance from different sources as well as upgrading the material already at hand. This would also involve gene transfer from wild (mostly diploid) to cultivated species as well as to utilize the resistances found in cultivated species.

C. A feedback screening against many different pathotypes of clones selected from "B" to see the extent of their effectiveness, and

D. A "normal" breeding program in which clones from B and selected by C are utilized as parents in conjunction with high yielding tolerance, good adaptation, resistance to wart virus phytophthora and quality. It is proposed also that CIP's project of botanical seed be kept in mind here to check out possible combinations that segregate a high proportion of resistors to several nematode populations as well as a more or less uniform yield.

Definition of Resistance and Methods to Measure it

There is no disagreement in the literature on what is meant by resistance to potato cyst nematode e. g. the ability of a plant to impede reproduction of the nematode - (it is not correlated with yield and some resistant varieties suffer damage and yield loss from the invading larvae and subsequent necrotic reaction to stop syncitial or transfer cell induction); but there is disagreement on how to measure it and furthermore, as many host genotypes are found which considerably reduce nematode reproduction but not 100% there is further disagreement on what degree of nematode reproduction are acceptable levels of resistance.

The first workers who screened for resistance developed the root-ball test (Ellenby 1952, Mai & Peterson 1952) and defined resistant any plant that showed below 5 developing females while any one above 5 cysts were considered susceptible; this line was reached pragmatically as they observed that there was a large gap, either there were 2-4 cysts or more than 80 - and their pots fell into two categories easily distinguishable. Later this method fell into disrepute (Howard 1975, Huijsman 1975 and Kort et. al. 1972) as being variable, overestimated resistance and not providing a measure of reproduction. Thus they maintain total cyst counts must be obtained. Furthermore, they maintain that this is important when breeding with G. pallida, as gene action is very unpredictable.

Huijsman and Kort also maintain that for a plant to be rated resistant it has to show a minimum of 80% kill based on eggs inoculated, and eggs obtained at the end of the plant's vegetative period. This definition was based on their previous experience of gene H_1 on pathotype P_1A (Rol) which is a single dominant gene with high penetration - meaning that there is practically no reproduction - and this is incorporated into Dutch law. Thus the resistant clones in the Netherlands have the highest degree of resistance. In Scotland and England resistance is rated as a comparison with a susceptible check and thus it is a relative resistance, the degree depending on the check variety and the breeder.

There is,however, a very strong correlation between the root ball reading 6-8 weeks after inoculation and the total cyst count at the end of vegetative period, and it can be used effectively to discard obvious susceptibility while plants showing a very low number of cysts can be kept for a total count or retested. Forrest (1978) has investigated the relationship of root ball reading to total cyst count, and states that if watering and temperature are carefully controlled the root ball method is reliable and can be repeated year after year. He reports a positive correlation (.81) and also his ranking for resistance on 13 clones based on the root ball method was repeated in total cyst counts. Kort who is a strong believer in total cyst count recognizes the usefulness of early selection and to speed up the screening of resistance for breeders uti-

lizes the root ball method as a preliminary screening. On the basis of his results he states that if less than 6 cysts are found in three pots (he adds them up) there is a 95% probability that these clones selected would also rate resistant (based on 80% kill) if total egg counts were taken. Such a high degree of resistance is hard to achieve for pathotypes of G. pallida and in particular if the starting material is S. andigena which has shown partial resistance (minor genes) and was selected on a relative basis. Thus, we think that if we achieve no reproduction or resistance defined as Pf = Pi (i.e. final population = to initial population) it would be very satisfying as this would be more or less equivalent to a non-host crop.

Although total reproduction as well as correlations of root-ball to total cyst count are influenced by soil type and other environmental factors, initially less than 5 cysts per root ball in three repetitions seems to be a good measure. Soil of plants selected can later be washed for a more accurate assessment. An additional advantage of a non-complete resistance may be the slowing down of selection resistance breaking pathotypes.

Sources of Resistance

Table 1 attempts to summarize the literature on Solanaceous species found with resistance to P.C.N.

a) Cultivated Species	Reported Resistance	Literature Citation
S. tuberosum spp.	R_1A (Ro_1) P_5A (Pa3)	Ellenby 1952 Howard & Cole 1970 Scurrah 1973, 1974, 1977
S. jusepczukii Argentina, Bolivia and Peru	R_1A P_4A, P_5A	Howard 1966, Stelter & Rothaker 1961, Cole & Howard 1966 Scurrah 1974-1975 Christiansen & Scurrah 1977
S. curtilobum Argentina, Bolivia and Peru	P_4A P_5A	Scurrah 1974, Scurrah & Christiansen 1977

b) Wild Species

S. acaule Argentina, Bolivia Peru	P_2A P_4A, R_2A P_4A, P_5A	Dunnet 1959 Schmiedieche 1977 Huijsman 1978
S. sucrense	R_1A	Mai & Peterson 1952; Dunnet 1959, Deshmuk 1970, Huijsman 1957
S. oplocense Argentina & Bolivia	R_1A, R_2A, P_5A P_4A	Ross 1969 Huijsman 1978
S. kurtzianum Argentina	R_1A, R_2A, P_4A	Huijsman 1959, 1960; Steltert & Rothaker 1965
S. megistacrolobum Argentina, Bolivia Peru	R_1A, PA_4	Cole & Howard 1962, 1966, Hjerting & Lindhart 1974
S. multidissectum Peru	P_1A	Dunnet 1958 and 1960
S. neohawkessi Peru	P_1A	Dunnet 1958
S. raphanifolium Peru	P_1A	Dunnet 1969
S. sanctae rosae Argentina	R_2A, P_1A, R_1A	Dunnet 1959, Hjerting & Lindhart 1974
S. gourlayi Argentina	R_1A, PA_2, P_4A, P_5A	Ross 1976, Huijsman 1978, Hjerting & Lindhart 1974

Wild Species (Cont'd)

S. spegazzinni	R_1A, P_5A	Ross 1954, Huijsman & Ross 1960, Huijsman 1978, Hjerting & Lindhart 1971
S. vernei Argentina (Bolivia?)	R_1A, R_2A, R_3A, P_4A, P_5A	Mai & Peterson 1952 Ellenby 1952 Ross & Huijsman 1954 Dunnet 1958, Hjerting 1974
S. sparsipilum Bolivia, Peru	P_3A, P_4A, P_5A	Scurrah 1973, Huijsman 1978
S. canasense Peru	P_4A	Huijsman 1978
S. venturii	R_1A	Hjerting & Lindhart 1974
Argentina		Rothaker 1966

It is of interest to note that all these species stem from southern Peru, Bolivia and northern Argentina. This includes the resistant S. andigena clones which seem to be products of introgression from wild species (S. oplocense). There is some evidence (Hoopes 1977) that the mechanism for resistance in some of the species are different and therefore, may have a multiple origin thus providing a basis of broadening the base of resistance. Furthermore, every genetic study of the inheritance of resistance, and every report on breeding states the existance of minor genes especially in S. andigena which will influence not only the segregation patterns but also the levels of resistance, thus the utilization of a wide spectrum of sources of resistance is advisable and the creation of a population with high frequency of genes for resistance from different provenances in the aim of this strategic program. We feel that the collection of wild species held at CIP should

be screened here, as previous experience shows that the steps involved in reporting new sources of resistance and receiving this material back at CIP is very long, unproductive and, furthermore, resistance selected may not be against pathotypes required.

There are new breeding tools available, such as a haploid S. tuberosum and the utilization of unreduced gamets which should facilitate the gene transfer from wild diploid to cultivated species and short-cut doubling with colchicine and lengthy backcrossing programs.

Potato Cyst Species Pathotypes and Resistance

The information presented on the screening program and distribution of species and pathotypes has shown that the pathotypes most widely distributed in the Andean area are P_4A (Pa 2) and P_5A (Pa 3). Thus breeding should at first be directed against these two groups. Since P_5A represents a large group which is widely distributed and characterized by being aggressive to all differential plants, it can be predicted that it is not a uniform group and that differences will show in populations as soon as a resistor to a population used in a breeding program is tested against different provenances of P_5A. In fact, this has occurred recently in Great Britain with P_4A when 2 different populations of P_4A (Pa 2) were tested against clones D47/11 and D49/1. One population (New leak) overcame the resistance of these clones while the other DF did not. Immediately, Alan Stone proposed to include these clones in the pathotypes scheme and subdivide P_4A (Howard Fulter & Stone 1977).

Huijsman suggests that a way to avoid such a proliferation of differential plants and pathotype nomenclature as well as futile work in breeding is to test a resistor clone with about 100 nematode populations of that pathotype from the area a particular breeding program services. If the clone stands up to at least 90 of them, it is released as a breeding clone, otherwise it is discarded (personal communication) and would make sense when working in areas where little is known about the race or pathotype composition of nematode populations and should be part of the feedback system i[illegible] breeding program - or to use CIP terminology: The International [illegible]. This will further help to see how variable the populations are [illegible] whether in some areas resistance breeding is a realistic goal.

Although most wild species in which resistance has been identified possess resistance to various races this has not been found in cultivated species. The same experience holds true for breeding programs utilizing wild species i.e. that after a number of backcrosses, sometimes only two, one can reduce resistance to several races to only one, keeping only the resistance for which a clone is being selected against (Mayer de Scurrah & Plaisted 1973). On the other hand, resistance to several pathotypes

has been created in a breeding program utilizing different sources of resistance. Thus for example, Dutch breeding clones have resistance to races R_1A, R_2A, R_3A of G. rostochiensis (ABC) and P_4A of G. pallida (D) combined. It thus seems that resistance is based on gene for gene action between the polygenes of the host and those of the pathogen: that a partial resistance is conferred by minor genes and are thus as race specific as the major genes which confer complete resistance. Minor genes are found more frequently and in a natural ecosystem stabilize the host pathogen relationship, while major genes are seldom and confere a great advantage to plants but the host pathogen equilibrium is precarious and can break down easily.

With these points in mind, the breeding program which really has horizontal resistance in mind has to tread on a careful balance between efficiency of the program and maintenance of polygenes by selecting with several populations (every population included in the breeding program increases the work by 100%).

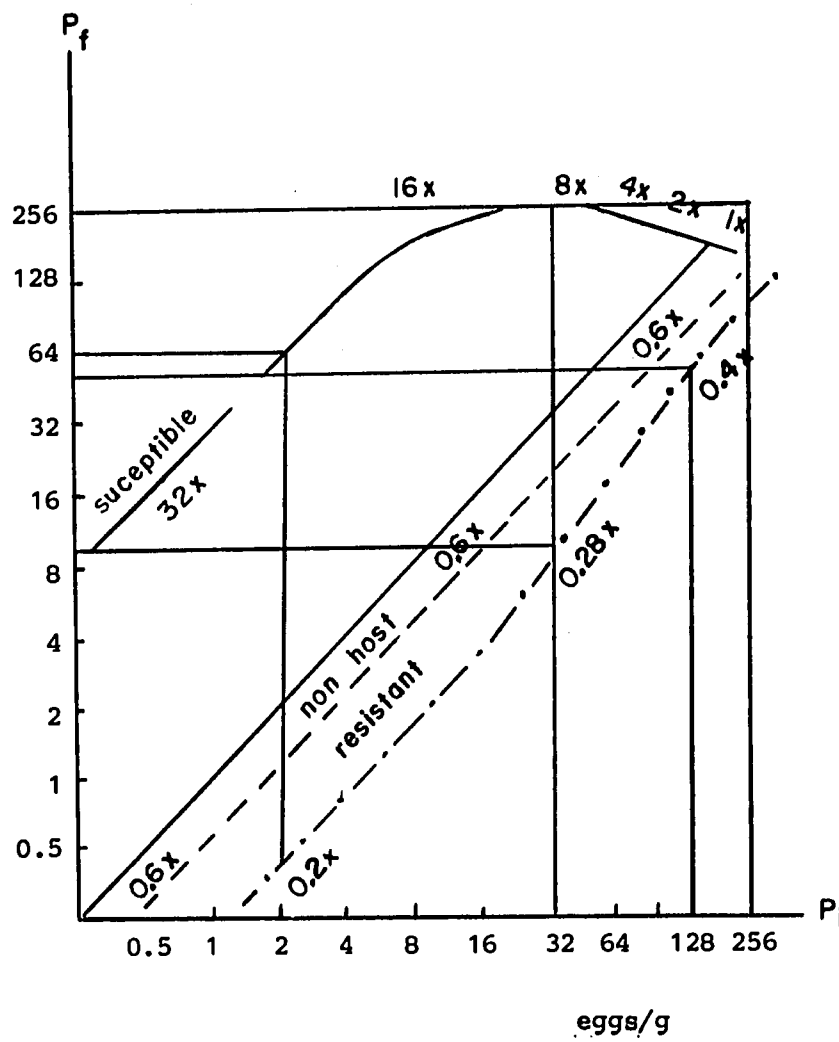
Thus a proposal for future work at CIP is to combine in crossing all possible sources of resistance available, screening the progeny will be carried out with the two pathotypes of G. pallida that are most widely distributed (i.e. P_4A and P_5A) and later in a second part test these reduced number against a number of other populations for maintenance of additional genes that have been carried across, and use these selections for further breeding.

Behavior of Resistant Clones in Infested Fields

This is the last phase of the breeding program as the ultimate goal of resistant varieties is to reduce levels of cyst nematode in the field. However, it is a very laborious endeavor to test this. Pre and post planting populations have to be assessed. This work gets compounded if several varieties or lines are being tried. Often abiotic factors such as drought and flood interfere and statistical errors arise when nematode populations are at high densities.

Figure 1 is drawn up by Seinhorst & Den Ouden which illustrates the effectiveness of resistant varieties at low densities and the difficulties in measuring this effectiveness at high densiteis. This kind of data is very important, to show what can be expected. An area where a data is lacking is the consequence of utilizing partial resistance in fields in comparison with susceptible, and non host crops in order to draw up effective rotations schemes. It is hoped that in the future this data will come out of CIP as well as out of other institutions.

RELATION BETWEEN INITIAL DENSITIES (Pi) AND FINAL DENSITIES (Pf) WHEN SUSCEPTIBLE, RESISTANT AND NON HOST ARE PLANTED



Seinhorst and Den Ouden - (Mimeo report)

If nematode behavior be assessed, it will have to be done by workers with experience and facilities in nematology - it is proposed that initially CIP be in charge of field trials for population level assessment and in other places only yield be assessed in the field and resistance be based on greenhouse experiments.

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IDENTIFICATION OF RESISTANCE AND TOLERANCE TO POTATO CYST NEMATODES AND THEIR PRACTICAL IMPLICATIONS

R. Tarté

The use of resistant and tolerant cultivars to potato cyst-nematodes is one of the most effective and least expensive control measures of these pests. Their efficient use, however, is dictated by our understanding of biological, genetical and ecological considerations involved in their relationships with the nematode populations that should be controlled in the locations where this control method is to be performed.

In this paper, a discussion is conducted on what I believe are the important aspects to consider when searching for and using resistant and tolerant genetic material for the control of potato cyst nematodes. No attempt has been made to make an extensive literature review on the subject. However, to emphasize important concepts and findings, some literature has been revised and examples are used, at times, in which nematode species other than potato cyst nematodes are considered.

In the following discussion I hope to present some information, sometimes confining consideration to aspects which are often overlooked or not necessarily of special interest to research workers in this field, but which I believe are valuable.

Search for Resistance and Tolerance

The extensive variability in potato cyst nematodes and their distribution among different ecological habitats which affect, in different ways, the relationship between potato plants and nematodes, immediately suggests three important considerations when searching for resistant or tolerant varieties. First, a proper identification of resistance and tolerance in genetic material evaluated is needed; second, a correct identification of the nematode races or variants to which such material is either resistant or tolerant must be done, and, third, the influences (external or internal) which affect the reaction of the material to the nematode should be adequately studied.

To identify resistance and tolerance we must measure the sensitivity of the host as well as the changes in population densities of the nematode parasitizing it. Since these aspects may be affected by many different factors, as a consequence of the interactions between nematodes, plants and environment, it is important to study them properly.

Identification of Resistance and Tolerant Genetic Material. Although the environment may modify it, the efficiency of resistance of a plant is determined by its genotype. The main feature of resistance is its effect on the reproduction of the nematode. Based on this criterion, a large variation among potato cultivars and wild relatives, has been found, ranging from very high resistance, governed by major genes, to intermediate degrees of resistance, governed by polygenic systems (Huijsman 1974). With potato cyst nematodes, however, even the highly resistant cloens have a certain degree of susceptibility. Apparently, they all respond to some extent to the stimulus to form a synchytium in which a nematode can feed and develop (Hoopes et al. 1978) even if the nematode is unable to complete its life cycle.

Testing for resistance is, therefore, based on the multiplication aspect of the nematode. Such testing is relatively simple when resistance is governed by one dominant gene, as generally occurs in Solanum andigena hybrids, or by a small number of dominant genes, but not so simple when minor genes are involved as in Solanum vernei hybrids. When S. vernei was introduced into the breeding program in the Netherlands, a testing method entirely different from the test for pathotype A resistance had to be developed (Kort 1974), because root ball counts as a percentage of the number of cysts produced in a susceptible variety were not as revealing as when total number of cysts produced were counted (Howard and Fuller 1975). Even in S. andigena clones, some evidence of minor genes has been found at the International Potato Center (CIP 1977) as well as in the United Kingdom, where Parrott and Trudgill (1970) observed some variability in the resistance of andigena hybrids suggested that this resistance probably depends on additional genes, rather than on differences in the H_1 gene. On the other hand, experience in the Netherlands with a polygenic inheritance mechanism as found in the tuberosum - vernei hybrids, suggests that here too, major genes are present since cysts were found readily multiplying in the roots of clones with such a resistance (Huijsman 1974). Such resistance mechanism makes it difficult to conclude that the tuberosum - vernei hybrids are a solution to the problem of pathotypes, as has been argued. Unfortunately, the resistance reaction of clones in which major genes are involved is easily overcome by small changes in the nematode population.

The existence of different degrees of resistance suggests that great care must be exerted in the identification of resistant material because external influences affecting its behavior as well as the nematode's

may modify the kind of plant reaction in such a way that resistance could be masked or could appear as if it normally occurs. If resistance is to be measured by the reproduction of the nematode, any factor which affects such reproduction needs to be considered also.

A similar consideration has to be taken when looking for tolerant material. Here the reaction of the plant in terms of damage caused by a nematode readily reproducing on it can be affected also by external influences, probably more so than the multiplication aspect of a nematode in a plant evaluated for resistance. Yield measures of nematode infected plants as compared to non-infected controls give an indication of their tolerant capacity towards nematode attacks. This capacity, however, seems to depend on the nematode population density in relation to a tolerant level. This level was determined in the Netherlands by Seinhorst and den Ouden (1971) as 6 eggs per gram of soil for the tolerant variety "Multa" as compared to 1.5 eggs per gram of soil for the non-tolerant variety "Libertas", when grown at a low nitrogen fertilizer level. The potato variety "Alpha" has been found to be tolerant to high infestations of a Heterodera rostochiensis population from Panama (Tarté and Rodríguez 1977 a). The belief that tolerance is pathotype independent has led to this kind of research at the International Potato Center (CIP 1974), where tolerance has been found in several clones from Peru and in several native cultivars from Colombia.

Identification of resistance and tolerance can be improperly recognized unless we understand the influences which affect the interactions between nematodes and the plants they parasitize.

Effect of internal and external influences. The physiological condition of the plant is a factor quite often overlooked. It may have a direct influence on the reaction of the plant to the nematode as well as on the rate of population build-up of the nematode parasitizing it. This has been demonstrated by Dolliver (1961) with Pratylenchus penetrans, who found that treatments that reduced dry weight of "Wando" pea plants moderately, such as less favorable light and temperature, excision of plant parts and limitation of the nutrient supply,increased populations of P. penetrans. On the other hand, treatments that reduced dry weight considerably, as well as removing flowers and pods, reduced nematode numbers. Undoubtedly, environment plays a major role in the physiological condition of a plant. With the same nematode species, Tarté and Mai (1974) found that a crenate-tailed variant of P.penetrans was more pathogenic to peas than a smooth tailed variant of the same population when pea plants were grown at a light intensity of 3,900 lux, but not when grown at a higher light intensity.

Environment plays a major role in the physiological condition of the potato plant, where changes in the chemical composition of the tubers

and on the subsequent growth and development of the potato crop, as affected by climate, have been found. Moreno (1974) found biochemical variations in potato tubers as affected by photoperiod; the content of free amino-acids was higher in tubers grown in short days (10 hrs.) than in those grown in long days (14 hrs.). Long-day grown tubers were small and lost dormancy rather quickly. He also found biochemical differences in potato tubers harvested in different local climates in Peru, and when they were planted in one locality, differences in the sprouting behaviour and growth occurred, giving rise to plants with different growth habits. He states that the chemical composition of the seed-tuber seems to give a definite potential for the development of its sprouts and the plant derived from it. This confirmed what Went (1959) expressed about potato tubers having different potentialities to produce tubers in plants of the following generation, according to the previous environmental conditions in which mother plants were developed.

That the physiological condition of the plant is a factor to consider when evaluating the reaction of a potato plant to a potato cyst nematode was stressed by Tarté and Rodríguez (1977a). They found in a pot experiment that the potato variety "Alpha" did not behave as tolerant, 82 days after planting, as frequently observed in Panama, when all the sprouts, except one, were removed soon after emergence, as compared to normal plants in which all the sprouts were allowed to grow. According to Dutch workers (van der Zaag, 1973), physiological age of the potato seed tuber as well as climatic influences determine the number of sprouts of seed-tubers and the duration of the rest period; and the number of sprouts has an influence on growth and development of the potato crop. The removal of sprouts in some of the tubers of this experiment merely attempted to simulate partially two different physiological conditions. This was done because "Alpha", the main potato variety grown in Panama, is planted twice a year; a large December planting, with seed-tubers imported from the Netherlands, and a smaller June planting, with seed-tubers harvested in Panama the previous season. Obviously, the physiological condition of seed-tubers originating in both localities is different, and this may explain why sometimes a low yield is obtained in the presence of heavy infestations of the nematode while most times yield does not seeem to be affected.

It is possible that when several sprouts are present, plants may compensate for the destruction of roots by the formation of adventitious roots produced through a hormonal regulatory effect. while when only one sprout is present the destructive effect is greater than the compensatory effect. In the relationship between plant damage and nematode populations it has been suggested (Wallace 1973) that both effects act simultaneously; if the inhibitory processes predominate, growth or yield is reduced; if the compensatory effects predominate there is no growth reduction and an increase in growth may occur if an excess of

growth regulatory substances is produced. This kind of influences needs to be studied more, however. In Tarté and Rodríguez's experiment (1977a), it is possible that if data were taken at harvest time or later than 82 days after planting, a compensatory effect in the one-sprout plants may have appeared, in accordance with some findings of Seinhorst and den Ouden (1971). These workers found that an inhibitory effect of the nematode dissappeared in two potato varieties when growth data was taken at a later date. This kind of evidence may constitute a difficulty when trying to develop a technique to determine tolerance by a pot method as has been recommended (CIP 1974).

There is evidence that growth regulators are probably involved in the reaction of the plant that gives resistance. Giebel and Wilski (1970) found an increase of IAA in susceptible potato plants to Heterodera rostochiensis and a decrease in resistant plants. An experiment by Dropkin et al (1969) showed that the application of kinetin to tomato plants decreased their resistance to Meloidogyne incognita and concluded that the extent of reversal from resistance to susceptibility is dependent on cytokinin concentration. It would be of interest to observe the effect of giberellic acid applications on the reaction of potato plants to cyst nematode attack. Giberellic acid is applied in some cases to promote sprouting of seed-tubers.

In addition to the effect on the physiological condition of the plant, the environment may affect some aspects of nematode behavior like dormancy, hatching, reproductive capacity, longevity and survival. Potato cyst-nematodes have a pronounced dormant period (Shepherd, 1962) in which hatching does not commence until favorable conditions are attained. Hatching may cease also in response to other stimuli. Among the factors influencing dormancy or cessation of hatching, temperature is the one more often related to Magi (in Clarke and Perry, 1977), for instance, observed a diapause commencing in July in cysts of H. rostochiensis from the previous year. This is somewhat similar to what occurs with Heterodera avenae (Kerry and Jenkinson, 1976), in which hatching commences as the temperature rises after winter and ceases in May before soil temperatures reach 20° C. This type of dormancy appears to be sychronized with the host life cycle and is often a feature of the parasitic mode of life. According to Parrott and Berry (1976). Heterodera pallida hatches less freely than H. rostochiensis at higher temperatures and is possibly adapted to lower temperatures. They suggested this would make H. pallida more persistent in soils and it may be important in relation to competition between these two species when long crop rotations are employed. Ellenby and Smith (1975) found a difference in response to low temperature between different populations of H. rostochiensis and suggested that adaptation of one population to lower temperatures than others is possibly related to the early planting and harvesting of potatoes in the area. Studies at the International Potato

Center (CIP, 1977) revealed that the Peruvian population of H. pallida is less sensitive to temperature extremes than the "white" British H. pallida.

Although temperature seems to play a major role, Dropkin (1976) has suggested that the cessation of hatching stimulus may derive from some metabolites of soil biota rather than from the physical factors of the environment. There are substances inhibiting hatching of H. rostochiensis, like diffusates of mustard roots and certain solanaceous plants (Shepherd, 1962). Magi (in Clarke and Perry, 1977) reported that root diffusates from Archangelica litoralis, Heracleus sibiricum, Anthriscus silvestris, Pimpinella saxifraga, and P. major inhibited the hatching of H. rostochiensis by 36-56%. McParland (in Clarke and Perry, 1977) found that exudates of Rhizoctonia solani also inhibited hatching of H.rostochiensis. Freshly heat-sterilized soil sometimes inhibits hatch of H. rostochiensis (Shepherd, 1962). Interestingly, hatching of H. avenae was found to be inhibited by solutions of calcium nitrate (Clarke and Perry, 1977), and it is indicated that soil infestations of this nematode can be limited by the applications of suitable amounts of the fertilizer. We must be aware of what fertilizers or other substances do to hatching of H. pallida and H. rostochiensis.

A curious situation of inhibition of hatching in H. rostochiensis occurs in Costa Rica (1). In this Central American country viable cysts are found in a soil from the Cartago area, but they are unable to reproduce in all susceptible varieties tested so far; however, when cysts were sent to the Netherlands for identification, they reproduced well and a host differential test revealed them to belong to pathotype A of H. rostochiensis (Ramírez and Bianchini, 1973).

Soil types have a marked influence on reproduction of H. rostochiensis and H. pallida. In studies conducted at the International Potato Center (CIP, 1977) it was found that reproduction of both species on soil from Arequipa was ten times that on soils from Tarma and Cajamarca. It was not evident from detailed soil analysis which factors contributed to such variation in reproduction in soils tested.

Quite often it is difficult to distinguish whether the effect of the environment is on the plant, or on the nematode, or both. A plant's response resulting from a direct effect of the environment on the nematode or on the host seems rather unusual. If we understand by environment all those factors that influence an organism's chance to survive or reproduce (Wallace, 1973), we can see how any given reaction involving two or more organisms at any particular environment, is the product of

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(1) A. Ramírez, personnal communication.

their interactions with that environment. Photoperiod for instance, plays a role in plant growth and consequently on nematode reproduction. Ellenby(in Wallace, 1973) stated that increasing day-length appears to be associated with increased number of cysts of H. rostochiensis on potato plants. It is likely, however, that such photoperiod favors increased plant growth and this in turn favors higher nematode reproduction (Wallace, 1963). The rate of invasion and development of both species of potato cyst nematodes is affected also through the host by day-length (CIP, 1977).

The tolerance level or the degree of resistance of potato plants may be influenced by soil fertility and humidity. For example, best soils gave highest percentage of tolerant plants in Peru as compared with poorer soils (Brodie and Mai, 1974). A similar consideration was indicated by Trudgill et al. (1975), who suggested that small populations of the nematode may cause economic yield looses when soils are deficient in plant nutrients. Evans et al. (1977) found that infested plants with high soil levels of nitrogen and phosphorus grew almost as well as those treated with aldicarb, while a much bigger growth response was obtained with aldicarb as compared to non-treated plants when lower initial nutrient levels were used.

Although Evans et al.(1975) found that irrigation had little effect on the water relations of nematode infested plants, except for the decreased water stress in young plants infested with many nematodes, the effect of soil moisture level probably needs to be more extensively studied. Water relations of nematode infested plants have been found to be very important in other species of plant parasitic nematodes. O'Bannon and Reynolds (1965) found that when the soil was kept at field capacity, cotton plants infected with Meloidogyne spp. grew as well as non-infected plants, but when the soil was allowed to dry to 50% of field capacity between waterings, infected plants grew more slowly than uninfected ones.

Other organisms may also play a role, quite often overlooked, in the relationship between potato plants and cyst nematodes. The existence of organisms which parasitize or prey upon Heterodera spp., has been indicated a long time ago. Van der Laan (in Shepherd, 1962) has recorded fungi, other nematodes, enchytraeids, tardigrades, Collembola, etc. Fungi found in H. rostochiensis cysts from the Netherlands and Peru include Phialophora heteroderae, Phoma tuberosa, Montospora daleae, Penicillium vermiculatum, Pseudeurotium ovalis, Anixiopsis stemioraria, Margarinomyces heteromorpha and Sclerophulariopsis sp. On the other hand, of more importance than parasites and predators on potato cyst-nematodes may be some associations between fungi and nematodes. Several experiments have shown that these associations are not just a question of competition for some resource but that they

interact at the biochemical level and as a result physiological changes occur in the host which may affect nematode populations. In a study of the association between H. rostochiensis and the causal fungus of brown root rot of tomatoes (James, 1968), it was found that the nematode did not increase the susceptibility of the roots to invasion by the fungus, but the fungus decreased the rate of hatch and invasion by the nematode and, consequently, the number of new cysts produced. On the contrary, there is plenty of evidence showing that numbers of nematodes in a plant increase when another parasite is present, like H. glycines in the presence of Fusarium (Ross, 1965), Pratylenchus penetrans in the presence of Verticillium albo-atrum (McKeen and Mountain, 1960), and P. minyus in the presence of V. dahliae (Faulkner et al, 1970). We must be aware of the fact that, quite probably in soil, the relationship between only one organism and the plant does not exist. The remark by Wallace (1973) that the incursion of a fungus into the plant system may produce a plant which is more resistant or more susceptible to the nematode, may refer to a rather common thing in nature.

Identification of nematode species, pathotypes and variants[1]. Proper identification of the nematode pathotypes and variants (biotypes) to which material tested is either resistant or tolerant is a necessity. The correct identification of the potato cyst nematodes involved means the study of their genetic variability leading not only to the identity of species and pathotypes but to the detection of variants, within and among populations, differing in aggressivity towards potato plants.

Several pathotypes of H. rostochiensis and H. pallida have been identified in Europe on the basis of the reaction of differential hosts to their attack and of some morphological characters. However, it is highly probable that many more pathotypes do exist and it should not be too difficult to discover them if proper plants containing many different genes for resistance are used. This is particularly true for the Andean region where a variability of potato cyst nematodes larger than that found in Europe have been observed. Most characteristics measured in populations from Peru, Ecuador and Colombia showed a large variability among and within populations (Canto and de Scurrah, 1975). When 34 populations of the nematode from the Andean zone were studied for female color, none

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(1) Kort et al (1977) defined pathotypes as variants of a potato cyst-nematode species which differ from others by their ability to multiply on particular potato genotypes known as differential hosts. Pathotype was proposed by Howard (1965) because biotype, the term previously used, has another connotation i.e., a group of individuals all of one genotype (Johanssen, 1909) and a pathotype although of constant phenotype, may vary in genetic constitution (Cole and Howard, 1966).

of them presented a pattern identical to those registered for the British pathotypes (Canto and de Scurrah, 1976). This large variability made it difficult to use most of the parameters considered in the European classification schemes for identification purposes. When clones with resistant genes H_1, H_2 and H_3 were tested against 44 Andean and nine European populations of potato cyst-nematodes results showed that the Andean populations were able to overcome H genes (CIP, 1977). De Scurrah (1974) indicated that among the tetraploid clones of Solanum tuberosum subsp. andigena, genes for resistance to populations from Peru are very rare.

Because only a small portion of the total nematode gene pool could have been introduced to Europe from South America, we can assume, logically, that there is less variation there than in the Andean region of South America. The results of observations and experiments led to the conclusion that populations found in the Andes do not fit into the European systems of classification of pathotypes, and this has also been observed by European workers i.e., the case of a Bolivian population which morphologically resembles British pathotype A but behaves like British pathotypes B and E. (Brodie and Mai, 1974).

A new scheme of classification was erected by Canto and de Scurrah (1977), under which British and Dutch pathotypes as well as Andean populations of the potato cyst nematode could be identified. An attempt to understand better the genetic variation of these nematodes and to provide a basis for selecting representative populations of the nematode to use in breeding and screening for resistance was the main purpose of this new scheme. Although criticized by European workers (Kort et al, 1977), who at the same time proposed an international scheme to bring together the formerly separate schemes of the United Kingdom and the Netherlands, the development of a classification system like the one proposed by Canto and de Scurrah (1977) seems more justifiable in the light of its usefulness, than the proposal of an international scheme in which only Dutch, German and British pathotypes are the main concern.

Populations which are mixtures of pathotypes are known. In such cases competition between pathotypes may occur which may change the reaction of a plant in few years. Trudgill and Parrott (1973), based on results from pot tests carried out in England with a susceptible potato variety, indicated that when pathotypes A and E occur together, A becomes dominant. It is very important that we identify these populations of mixed pathotypes, but perhaps of more importance is that we identify variants differing in aggressivity among populations. Evans and Franco (1977) indicated that determining the aggressivity of different populations towards resistant clones is of as much interest as determining the species to which they belong. Since differences in aggressivity as well as differences in morphology have been found among populations, the possibility of relating a morphological feature with a certain pathogenic behavior should

be given some concern. When examining more than 100 populations from South America and other places, Evans and Franco (1977) found considerable morphological variation among populations, with some characters showing considerable variation within populations as well.

The extensive variability occurring in potato cyst nematodes and the little knowledge of the extent of such variability makes it difficult to identify many populations properly. Hopefully, with the new classification schemes pathotype identification will be more adequate. However, emphasis should be given to identification of aggressive variants for they may make more difficult the proper identification of resistant and tolerant varieties.

Utilization of Resistance and Tolerance

Variability in nematode populations and in ecological conditions which occur in the regions of the world where potatoes and cyst nematodes coexist, undoubtedly affect the reaction of potato cultivars in different ways. Perhaps a great extent of nematode variability among populations is related to aggressivity. Some reports indicate that the behavior of several European cultivars toward potato cyst nematodes in Latin America differs from their behavior in Europe. While the Dutch variety "Alpha" normally behaves as tolerant in Panama (Tarté and Rodríguez, 1977 a, 1977 b), the same variety is very susceptible to the potato cyst-nematode in Mexico (Figueroa, 1973). In Venezuela, when 24 European resistant varieties were tested, most of them behaved as tolerant rather than resistant (Figueroa, 1973). In Panama 22 resistant Dutch cultivars were evaluated in a field heavily infested with a H. rostochiensis population (Tarté and Rodríguez, 1977 b); thirteen cultivars reduced the nematode population between 1.4 and 35.8%, whereas nine cultivars increased the population between 4.4 and 53.6%.

When differences in aggressivity occur the danger of selecting more aggressive variants is present. However, the selection of another variant has often been considered as the selection of another pathotype that replaces the one for which the variety was bred. This occurs when infections of mixed pathotypes are present, overcoming the effect of the resistant gene after 4 or 6 years (Brodie and Mai, 1974). Selection in

the United Kingdom and the Netherlands has usually resulted in the replacement of H.rostochiensis Ro1[1] by H. pallida Pa3[1] after growing up to five successive crops of a resistant cultivar bearing gene H1 (Jones, 1978).

The rapidity with which the development of new pathotypes occur depends on the distribution or density of resistance breaking genes (Huisman, 1972). In some cases this density seems to be very low or zero, like in populations from New York State that have remained pure pathotype A and have not been able to multiply on ex-andigena after several generations. In cases like this, the use of resistant varieties will probably do more to the control than the use of nematicides (Trudgill and Parrott, 1973). When the density of resistance breaking-genes is higher the necessary matings between adults occur so that good gene combinations originate new biotypes, the rapidity of their occurrence depending on the density of such genes. In some cases the density of such genes is so high that even after the first crop of resistant potatoes there is an increase of the nematode population, which makes useless the growth of resistant varieties to control the parasite (Huijsman, 1972).

The danger of selecting another race is a real one. One may argue that cropping of tolerant cultivars does not select another pathotype because tolerance is not dependent on pathotypes. This is likely to be true, however, cropping of susceptible potato cultivars, being as good hosts of the nematode as tolerant ones, did not prevent pathotype shift in the Netherlands. This was demonstrated by Kort and Jaspers (1973) who conducted an experiment in which an equal mixture of Dutch pathotype A (H. rostochiensis) and D (H. pallida) of the potato cyst nematode was bred on three potato cultivars for three successive years. A shift in pathotype ratio observed by single cyst tests on ex-andigena potatoes was found at the end of each year. They found both pathotypes and hybrids between them occurring within one and the same cysts, a situation which gives proof of hybridization and competition between species of the potato cyst nematode. They concluded that susceptible potato cultivars, used alternately with resistant cultivars will not prevent pathotype shifts. Will tolerant varieties react in the same way? The chances are that they will if competition between species or variants occur, with one of them being favored by the host, as in the former example with susceptible cultivars, or if selection pressures other than host plants are present. Due to the possibility of selecting another pathotype or aggressive variant, the continuous use of a tolerant variety should perhaps be avoided also.

The existance of some degree of interbreeding between H. rostochiensis and H. pallida is indicative that, in spite of the distinction between

(1) Race classification according to new European scheme.

both species and their pathotypes, there are no clear cut differences between them. It is apparent that H. rostochiensis and H. pallida are in the process of speciation since one or more of the three characteristic properties of species (reproductive isolation, morphological distinguishability and ecological differentiation) (Mayr, 1963) are only incompletely developed. We must be aware of the fact that the existence of some degree of interbreeding could maintain in mixed populations a genetic variability capable of altering, in a short period and depending on the kind of selection pressure involved, the resistant or tolerant reaction of a given potato variety.

Due to the danger of selecting other pathotypes or more aggressive variants it is advisable to consider, in most cases, the use of resistance and tolerance only as part of integrated control programs, where in combination with other control measures will efficiently regulate nematode numbers and maintain high yields of the potato crop. In some cases, it might be possible to use resistant varieties for a very long time. When properly used, either alone or as part of an integrated control program, their efficiency in suppressing nematode populations is not equaled by other control measures such as use of nematicides. This has been experienced by Tarté and Rodríguez (1977 b) as well as by Brodie (1977) who found that the use of a nematicide maintained the original population density of H. rostochiensis whereas monoculture of a resistant cultivar reduced the population density considerably. When managing nematode populations, control methods have to be tested under local conditions and no generalizations should be attempted. This is evidenced in some research by Tarté and Rodríguez (1977 c) who, when testing an integrated approach to the control of H. rostochiensis in Panama, found that the use of some resistant varieties alone, without a pre-plant application of a nematicide, gave a better control of the nematode than using them with a pr -plant nematicide application, and yields were about equal in both cases. In the United Kingdom, on the other hand, fumigation increased yield of the resistant variety "Maris Piper" in the presence of a high nematode infestation (Trudgill et al, 1975). Integrated control methods, therefore, should be developed accordingly for each particular location or area. The aim in all cases, however, is to suppress nematode populations.

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INTERNATIONAL TRIALS

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The potato cyst nematodes (Globodera rostochiensis and G. pallida) are the most feared and cause one of the most important diseases of potato. Although populations of these nematodes do not increase as rapidly as fungal and bacterial pathogenes of potatoes, once well established in a potato growing area they are impossible to eradicate. It is costly and difficult to keep soil populations below damaging levels and to prevent rapid spread. These nematodes occur in most temperate potato producing areas of the world. One of the main reasons that these nematodes cause an important potato disease is that at present there is no practical method to control them. Yield losses vary according to the nematode populations densities and complete economic crop failure can result when densities are high. Plant resistance and/or tolerance offers considerable promise for practical control of potato cyst nematodes in Peru, in other Andean countries, and in many other potato growing areas of the world where these nematodes occur. Furthermore, the wide variability of pathotypes (races) determined by their ability to reproduce on plants with resistance genes has already been emphasized in the previous presentations. Thus, the presence of many pathotypes and because these nematodes seem to have been associated with potatoes and wild Solanum hosts for many centuries in Peru and other countries of the Andes, there has been a greater chance for plant resistance or tolerance to evolve or develop here than in any other potato growing region, makes this region and Peru in ideal location for testing potato clones for resistance to these nematodes.

Progress made utilizing CIP germ plasm as well as genetic material from research contracts and other programs has also been underlined.

In the early phase of research in the Nematology Department, efforts were concentrated towards identification of PCN populations to be used as the most representative and on the screening of our widely diverse germ plasm to obtain new sources of resistance. As a result of these studies, resistant clones have been identified and are being used in a breeding program. At this stage of research work, it has become necessary to test this material over a wide variety of ecological conditions and with more populations of PCN representing also different areas by mean of international trials. These international trials are and will be conducted by national programs with the knowledge of CIP's regional

representatives. This cooperation involves helping National Programs by providing them with selected material and assistance in the planning and execution of trials when required. In this way, we hope to gain a better understanding of the behavior of PCN in each area where these trials are conducted and to develop resistant lines or varieties for incorporation into cooperative breeding programs.

Objectives

1. Provide resistant sources: To be utilized in breeding.

2. Provide advanced resistant material with potential to become variety if adapted to local conditions.

3. Tolerant varieties, for areas where there is no source of resistance or too much variability (i.e. Bolivia).

Organization and Coordination of the International Trials

The trials are organized according to results already obtained from tests carried out at CIP headquarters or by requisition of National Programs through CIP's regional representatives. Once the materials are sent into the regions, the regional representatives will contact the specialist or provide leadership and advise to the National Program for the execution of the trials as well as coordinate the testing activities within their region. The staff of the regional team will make sure that all the information gathered from the tests are sent to CIP/Lima.

General Procedure

Selected clones or breeding lines which CIP may provide for International trials can be suppied as tubers or samples of botanical seed and in accordance with CIP or countries limitations and/or quarantine regulations.

I. Resistant material: This material will be tested at different locations according to its degree of development, (i.e. resistance source or breeding line).

   A. CIP headquarters.

      As a first step:

      1. Tubers from resistant clones will be tested under greenhouse conditions against PCN populations from different regions which are maintained in the collection in order to establish a preliminary range of resistance (Table 1).

2. Advanced clones will be tested under field conditions to determine their yielding ability as well.

B. CIP's regions: Under supervision of nematology trained personnel and breeders of National Programs.

1. Tubers from resistant clones will be tested under local greenhouse conditions to determine or confirm their value as resistant material against local PCN populations (Table 2).

2. Advanced clones should be tested in trials for adaptation to local conditions and yielding ability.

3. When sources of resistance have been confirmed under local conditions, joined efforts between national nematologists and breeders is recommended to develop material which would satisfy local requirements or preferences.

II. Once tolerance has been confirmed from field trials at CIP headquarters, these can be distributed to National Programs for testing under field conditions.

Finally, a PCN booklet for International Trials should be prepared in order to guide and standarize greenhouse tests, as well as methods and tolerance trials.

The following procedure is suggested initially for screening for resistance.

A. Selecting populations for test: Select the most heavily infested fields for each area where PCN is prevalent.

B. Place subsamples from field samples in 8-10 cm diameter pots.

C. Plant 4 pots with local susceptible variety and 4 with resistant line to be tested. Care must be taken to water these plants daily including weekends. To protect pots from temperatures greater than 25° C by plunging them to the rim in sand beds located in greenhouses or in the shade of buildings.

D. After 7-9 weeks check the appearance of females on root balls of susceptible variety, when many females appear turn out all pots and score.

E. Scoring of test material should be as follows:

	Susceptible check	Line to be tested	Female color	
1.	no cysts	no cysts	-	test failed
2.	many cysts	no cysts	white	line resistant to *G. pallida*
3.	many cysts	no cysts	yellow	line resistant to *G. rostochiensis*
4.	many cysts	few cysts	white or yellow	partial resistance
5.	many cysts	many cysts	white or yellow	not resistant

TABLE 1

RESISTANCE TEST WITH SOME ANDEAN POPULATIONS OF PCN ON RESISTANT *S. ANDIGENA* CLONES

COUNTRY	POPS. TESTED	RESISTANT REACTION ON: 702535	702698
BOLIVIA	10	7	2
ECUADOR	10	8	4
COLOMBIA	3	3	3
TOTAL:	23	18	9

TABLE 2

RESULTS OF TESTING THE RESISTANT CLONES 702535 AND 702698 AGAINST POPULATIONS OF PCN FROM COLOMBIA UNDER PASTO CONDITIONS (DR. J. DEES' COMMUNICATION)

CLONES	REACTION TO PCN POPULATIONS FROM: LA LAGUNA	TUQUERRES	CUMBAL
ICA-PURACE	Susceptible	Susceptible	Susceptible
702535	Resistant	Resistant	Resistant
702698	Resistant	Resistant	Resistant

BREEDING FOR RESISTANCE TO THE ROOT KNOT NEMATODE

H. A. Mendoza and P. Jatala

Root-knot nematodes (Meloidogyne spp) are widely distributed in the world but limited to specific geographic areas by soil temperature and type. These parasites are favored by warm soil temperatures of 25°C and above.

Since potatoes are mainly cultivated in mild to cooler areas of the world the root-knot nematodes are not at present a major potato pest.

The damage that these nematodes produce is not only due to a yield reduction by the damage to the root system but also the loss of quality by the damage produced to the tubers. It is considered that the yield loss may be up to 25% under severe attack. However, the loss in the return of the crop may be much higher due to the damage to the tubers.

The breeding work for resistance to the root-knot nematode has been limited and only the Indian scientists have reported the development of the clone H-294 carrying resistance to this pest. Also high levels of resistance have been reported in many wild species and in some cultivated ones. However, in the last group the level of resistance is lower.

There was no major justification in the past to establish in deep breeding programs for resistance to this nematode. However, in the last four years CIP has been conducting research to adapt the potato to be grown in the lowland tropics and some promising clones have been selected. Under these environmental conditions the root-knot nematode becomes a threat for the crop not only by its direct damage but also by its interactions with Pseudomonas solanacearum, also a common potato pathogen in the hot tropics. Therefore, the resistance to Meloidogyne has become a major component on the overall goal of adapting the potatoes to grow under warm environments where potatoes were not cultivated before.

CIP has carried out a wide search for sources of resistance both in cultivated as well as in wild Solanum species. The results have already been discussed in a previous paper presented in this conference. It has been found that the level of resistance in cultivated species is low and so it is the frequency of resistant individuals. In the wild species there are more valuable materials such as Solanum sparsipilum, Solanum chacoense, and

Solanum microdontum. On the basis of these species plus the cultivated diploids Solanum phureja and Solanum stenotomum, a breeding work for resistance to the root knot nematode was initiated and so far a third cycle of selection on this widely diverse population has been completed.

Breeding Philosophy and Methodology

We considered that to maximize the utilization of all the wealth of genetic variability stored in the genus Solanum we had to utilize a population breeding approach. We also considered that the final yield of a potato clone (X) may be expressed as the following function:

$$X = f\ (A + Y + R)$$

where A, Y and R represent the effects of groups of genes for adaptation, yield per se and disease resistance, respectively. This germ plasm improvement is aimed to situations where potatoes are being grown under severe weather and pest conditions, often where non-genetic control measures cannot be applied. In this context the A genes are mainly concerned with the adaptive reaction to temperature and day length. They are thought to be, at least for the control of tuber initiation. Regulatory units with large effects which upon receiving the environmental messages would induce developmental changes.

The Y genes or genes controlling yield per se, would be mostly related to the capacity and efficiency of the plant to use the light energy and transform it into chemical energy and to store it in the form of plant material.

The third group of genes involved in the yield function are the R genes which are responsible for resistance to pests and diseases. It is well known that genes for resistance to the main potato enemies are present in either cultivated or wild forms of Solanum.

The average farmer of the developing countries uses little or no chemical control against pests and diseases. Also, the use of certified seed is limited in some countries and does not exist in others. These facts added to a frequent greater severity of pests and diseases in the developing countries, are compelling reasons for placing a greater emphasis on selection for resistance.

With these ideas in mind we have chosen the population breeding as the fastest and more efficient methodology to increase the frequency of desirable genes as well as to enhance the rate of recombination. The output of this system should be a germ plasm better fit by its adaptation, yield and disease resistance, to the needs of the developing countries.

As we have already mentioned, one of CIP's research goals is the adaptation of the potato to the lowland tropics. In these areas we have both abiotic and biotic stressing factors. Among the abiotic factors the high temperature and humidity are the main yield constraints but eventually microelement toxicity or deficiency may also be important. On the biotic side, bacterial wilt, root-knot nematodes, viruses X and Y, and late blight are considered the most important. These do not exclude that under certain lowland environments other pests and diseases may be also important such as the nematode Rototylenchus or bacteria producing seed decay or soft rots or fungus such as Chanophora which produces a leaf blight of devastating effects in Yurimaguas, one of CIP's testing sites.

On the basis of this definition of problems a breeding strategy was established to select by a combination of greenhouse and field screening the genetic materials which had to make an input into our widely diverse breeding population. This was the original population on which a cyclic selection process has been going on in the last years.

Materials and Methods

From a *Phureja-stenotomum* diploid population a sample of 1020 clones grouped in 51 families was evaluated. Twenty tubers per family were planted in 1000 cc. pots containing fumigated soil. Ten days later, 1 gr. of chopped *Meloidogyne incognita acrita* infested potato roots were added to each pot and the plants were allowed to grow. Forty days later all the root systems were carefully removed from the soil, washed and observed for nematode infection. A scale from 0 to 4 was used for rating the infestation.

The clones surviving this screening were intercrossed by bulk pollination. The offspring was evaluated by a modified method. In this opportunity as well as in all other evaluations, 40 cc. plastic pots were utilized. The substitute was formed by a fumigated mix of Jiffy mix and sand in the proportion 2:1. Seedlings were transplanted into these pots and inoculations were made 2-3 weeks later with 4000 eggs suspended in 5 cc. tap water. Reading of symptoms was made 40 days after inoculation utilizing the same 0 to 4 scale for rating infestation.

In the second evaluation 29 families with 50 seedlings each were evaluated. However, the survival of the seedlings was low due to unfavorable environmental conditions.

In the third series of evaluations survivors of the previous screening were mated to selected clones from the species. *S. sparsipilum*, *S. chacoense* and *S. microdontum*. Sixty two families with 100 seedlings each were evaluated.

Results

From the screening of 1020 diploid Phureja-Stenotomum genotypes groups in 51 families the following results were obtained (Table 1):

Table 1. The reaction of some diploid *Solanum* material to root-knot nematode

	N° Tested	N° Resistant	% Resistant
Families	51	21	41
Genotypes	1020	28	2.7

Out of these 28 genotypes which showed ratings from 0 to 1.5 only 1 had 0 ratings, 10 had rating 1 and 17 had 1.5. This was showing that immunity either did not exist or was an extremely rare event. Resistance was also at a very low frequency since only 2.7% of the population would show any indication of it. The fact that the 28 resistant individuals were distributed in 21 families was demonstrating that in this population the gene or genes for resistance were completely scattered and at a very low frequency. With the rather low number of surviving individuals, bulk crossing was made to concentrate genes for resistance to the nematode. Twenty-nine families were obtained and 50 seedlings per family were used for screening. The survival of these seedlings was poor due to unfavorable environmental conditions and among the surviving seedlings of this population the following ratings were obtained:

Table 2. Number of surviving seedlings with their respective rating for reaction to the root-knot nematode

Rating	N° of Seedlings	%
0	34	45.3
1	18	24.0
2	17	22.6
3	6	8.0
4	0	0.0
Total	75	99.9

In spite that these data was collected in a rather reduced set of individuals the results were amazing since they were demonstrating that the character was heritable and progress could be made under selection. In fact, data presented in Table 1 showed that only 1 individual out of 1020 showed rating 0 while in progeny of resistant individuals 45.3% were apparently immune.

For the continuation of the work several families were obtained including some of the resistant clones selected out of the Phureja-stenotomum progeny as well by including the species S. sparsipilum, S. chacoense, and S. microdontum. Sixty-two families were evaluated at the greenhouse and the results are presented in Table 3. This new population contained a considerable number of immune individuals which will permit the application of a strong selection for agronomical characters working on a background of immunity (grade 0) and resistance (grade 1). The data on Table 3 also shows that when at least a resistant parent is included in the crossing, the resulting progeny show a marked reduction in the percent of very susceptible individuals (grades 3 and 4), with respect to the progenies from mating susceptible parents. It should also be mentioned that in this population in addition to the resistance to root-knot nematode, also resistance to Pseudomonas solanacearum is present.

Table 3 also shows an interesting feature about the inheritance of immunity as data suggests that maternal effects may be significant. In fact, matings Res x Sus produced 27.86% of immune progenies while the reciprocal mating only produced 4.5% of immune genotypes. However, an exact measurement of these apparent reciprocal differences requires a more critical experiment designed to measure these effects.

At present efforts are directed towards transferring this variability of these diploid materials to the tetraploid level. Several 4x - 2x matings have been done and as expected a reduced number of these F_1 hybrids have shown resistance. Also they have shown a tendency to late maturity. A F_2 generation has been obtained formed by 18 families with 1300 genotypes. Also back crossing the F_1 generation to selected clones adapted to the lowland tropics, have produced 19 families with 1800 genotypes. It is expected that within these new materials there will be an increase in the frequency of immune genotypes as well as a reduction on the length of the growing cycle.

Table 3. Reaction of various diploid inter-specific crosses to *Meloidogyne incognita acrita*

Combination	N° of Fam.	% root galling index *					N° of Genotypes
		0	1	2	3	4	
Res x Res	20	51.32	10.77	35.12	2.36	0.00	1058
Res x Res	12	27.86	10.15	51.17	10.15	0.00	768
Sus x Res	21	4.50	10.00	66.35	19.05	0.07	1370
Sus x Sus	9	.12	.24	44.07	51.28	3.05	819

* 0 immune
1 resistant
2 moderately susceptible
3 susceptible
4 very susceptible

IDENTIFICATION OF RESISTANCE AND TOLERANCE TO THE ROOT-KNOT NEMATODE AND THEIR PRACTICAL IMPLICATIONS[a]

César P. Madamba[b]

The root-knot nematode Meloidogyne spp. is a major deterrent in food production. Although not as destructive to potato as the cyst nematode, it could pose a serious threat to potato growing in the warmer regions of the world. Kishore (1969) noted that among the twenty-seven species of plant parasite nematodes found associated with potato in India, only three are of major economic importance, namely: Meloidogyne incognita, M. javanica and Heterodera rostochiensis.

Chemical control against the root-knot nematode is prohibitive particularly in developing countries in the tropics where marginal farming is evident. The use of resistant varieties and cultivars is more economically feasible and practical as well as environmentally acceptable.

Recent progress in breeding for nematode resistance has been most promising and has resulted in making available for commercial use several varieties and cultivars notably in vegetable and certain field crops (Fassuliotis, 1976; Taylor and Sasser, 1978). The search for sources of resistance in other crops including potato is imperative especially on local favorites of farmers all over the world. These sources of resistance may yield interesting potentialities to the plant breeder.

Valdez (1978) reported that some 21 genera and 44 species of nematodes are attacking potato. Among them are the root-knot nematodes. These pests are not much of a problem in the other parts of the world. This explains why little work has been done to develop varieties which are resistant to these pests in countries outside of the tropics.

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[a] Paper presented at the 16th Planning Conference on Development in the Control of Nematode Pests of Potatoes. November 13-17, 1978, International Potato Center (CIP), Lima, Peru.

[b] Professor of Zoology, University of the Philippines at Los Baños and Regional Investigator for Southeast Asia, International Meloidogyne Project, Contract N° AID/ta-c-1234.

To date, sources of resistance to the root-knot nematode have been found in some clones of Solanum tuberosum and accessions of tuber-bearing wild species.

Nature of Resistance to Root-knot Nematodes

Taylor and Sasser (1978) have defined resistance to root-knot nematodes as that quality or characteristics exhibited by plants to inhibit reproduction by the nematode. The nature of resistance of plants to this nematode is not yet fully understood, but there is evidence to show that it is associated with the formation of giant cells. Thus, even if root-knot larvae enter the roots of both resistant and susceptible plants in equal numbers, the larvae may not continue to develop in the resistant plant. Because of its resistant or immune response, the plant will not allow giant cells to form. If giant cells are formed, however, these are not normal so that the larvae may still fail to develop to maturity or the female may produce few or no viable eggs.

Techniques of Screening for Resistance

Methods used to screen cultivars vary greatly among workers. Infested soils, including those naturally infested are generally used as inocula. Brodie and Plaisted (1976) have used mix inocula consisting of several root-knot nematode species. Resistance is evaluated primarily on the degree of galling.

Galling is rated on the basis of a scale varying from 0 (for no galls) to 4 (very severe galling) to 0 (no galls) to 10 (maximum galling) (Jatala and Rowe, 1976; Brodie and Plaisted, 1976).

A technique involving rooted detached leaflets of potato is used by workers at the Central Potato Research Institute in Simla, India (Nirula, 1969). The leaflets are planted in paper cups inoculated with 20 larvae. The number of galls produced after 10 days of inoculation indicates the reaction of the material under test.

Sasser (1976) had suggested a system which also assesses the degree of reproduction. Egg inoculum is used and ratings are based on the degree of galling and egg production. Galling is rated on the basis of a 0 (none) to 5 (more than 100 galls/root system) scale.

Sources of Resistance in Clones of Solanum tuberosum

About 11 commercial varieties and hybrids of potato including two lines belonging to subspecies andigena were reported to have strong resistance to common species of the root-knot nematode. Six of these have been identified from a screening test in India (Khanna and Nirula, 1964; Nirula et al., 1967 and Kishore, 1969).

Clonal crosses made by Brodie and Plaisted (1976) from among the Cornell University collection of Solanum tuberosum spp. andigena yielded two families with progenies resistant to five root-knot nematode species, namely: Meloidogyne (incognita) acrita, M. incognita, M. arenaria, M. javanica and M. hapla. Likewise, three families yielded progenies that show adequate levels of resistance to M. arenaria, M. javanica and M. hapla. All the families of the clonal crosses had progenies resistant to both M. incognita acrita and M. incognita and the frequency of progenies resistant to the nematode species was 100 and 42 per cent, respectively.

Two lines were also reported from the U.S. to have strong resistance to root-knot nematodes including M. hapla (Ross and Rowe, 1963 and Hoyman, 1974).

In the Philippines, an introduced variety and a local cultivar showed resistance to M. incognita and M. javanica, respectively (Toledo and Davide, 1969 and Lumdang and Davide, 1970). There were reports from Japan and Sri Lanka but the varieties, presumably local, were not identified (Nizhizawa, 1978 and Sivapalan, 1978).

Sources of Resistance in Related Tuber-bearing Solanum Species

The resistance to common root-knot nematode species is reported from several accessions belonging to 35 tuber-bearing related species including one unidentified Solanum species. Most of the Solanum species showed resistance to M. incognita while nine had adequate resistance to M.hapla.

In an extensive screening program in India, Nirula et.al., (1967) identified S. vernei as most resistant to M. incognita among accessions representing 38 Solanum species and high degrees of resistance in S.acaule, S. raphanifolium and S. spegazzinii. In further tests, Nirula et. al., (1969) noted high degrees of resistance to the same root-knot species in several other species of potatoes.

Jatala and Rowe (1976) observed very high levels of resistance to a similar root-knot nematode species in certain cultivars of Solanum acroscopicum, S. gourlayi, S. megistacrolobum and S. sparsiphilum maintained at the International Potato Center (CIP) in Lima, Peru. Likewise, high frequency of resistant lines in S. spegazzinii, S. capsicibaccatum, S. megistacrolobum, S. sparsipilum was observed.

Brücher (1967) tested clones of wild species collected from the Argentina Cordilleras and found that five species including an undescribed species, namely: S. bijugun, S. chacoense, S. commersonii and S. tascalense were good sources of resistance to four root-knot species.

Implications and Outlook

The development and testing of root-knot resistant cultivars may not be difficult and the selection of cultivars for use in particular fields may be relatively simple. Studies under the auspices of the International *Meloidogyne* Project show conclusive evidence that only four root-knot nematode species with a total of eight biotypes comprise the bulk of root-knot nematode populations of the world (Sasser, 1977). The rest, including some 33 species already described constitute an insignificant minority. Furthermore, the studies show no resistant breaking populations. The cultivars used in standard differential host tests show remarkably uniform reactions to biotypes from different sources. Thus, cultivars resistant to a root-knot population in one part of the world will show resistance to a population of the same species and biotype in any other part of the globe.

It should be emphasized, however, that the success of any breeding program on root-knot resistance in potatoes will depend to a large extent on the cooperation of the nematologist and the plant breeder as well as the unqualified support of international research agencies. Fassuliotis (1976) had outlined briefly the role of nematologists in such a program.

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Cultivars and hybrids of potato and related wild tuber-bearing *Solanum* species resistant to root-knot nematodes, *Meloidogyne* spp.

Cultivars/ Varieties	Meloidogyne Species[a/]					References
	inc.	acr.	jav.	hapl.	tham.	
Solanum acaule						
PI 175395	X					Nirula et al., 1967
PI 208874	X					Nirula et al., 1967
PI 210029	X					Nirula et al., 1967
PI 230562	X					Nirula et al., 1967
Black's 32046	X					Nirula et al., 1967
Solanum acroscopicum						
PI 230495	X					Nirula et al., 1967
PI 365315		X				Jatala and Rowe, 1976
Solanum ajanhuiri						
PI 233980	X					Nirula et al., 1969
Solanum bachycarpum				X(4)[b/]		Hoyman, 1974
S. bijugan						
Na 23	X		X	X	X	Brücher, 1967
Na 1352	X		X	X	X	Brücher, 1967
S. boliviensi						
PI 265860	X					Nirula et al., 1967
Black's 4797b	X					Nirula et al., 1967
S. bulbocastanum				X(/)		Hoyman, 1974
Hawke's H238-2x H239-4	X					Nirula et al., 1969
S. capsicibaccatum						
PI 205560	X	X				Nirula et al., 1967; Jatala & Rowe 1976

[a/] Meloidogyne species: inc. - *M. incognita*; aren - *M. arenaria*; jav. - *J. javanica*; hapl - *M. hapla*; and tham - *M. thamesi*.

[b/] Numbers in parenthesis refer to number of accessions.

Cultivars/ Varieties	Meloidogyne Species					References
	inc.	acr.	jav.	hapl.	tham.	
S. cardiophyllum				X(6)		Hoyman, 1974
ssp. cardiophyllum						
PI 184762.1	X					Nirula et al.,1967
ssp. chrenbergii						
PI 186548	X					Nirula et al.,1967
PI 186549	X					Nirula et al.,1967
S. chacoense	X		X	X	X	Brücher., 1967
PI 189217a	X					Nirula et al.,1967
PI 1977591	X					Nirula et al.,1967
PI 197760.7	X					Nirula et al.,1967
PI 230580	X					Nirula et al.,1967
WRF 324	X					Nirula et al.,1967
WRF 337	X					Nirula et al.,1967
WRF 888	X					Nirula et al.,1967
ERF 976	X					Nirula et al.,1967
CPIR'S 2	X					Nirula et al.,1967
CPIR'S 71	X					
S. commersonii	X		X	X	X	Brücher, 1967
S. fendleri						
PI 186560	X					Nirula et al.,1967
S. gandarellasii						
PI 233962	X					Nirula et al.,1969
S. gourlayi						
Oka 4532		X				Jatala and Rowe, 1972
S. hjertingii				X(3)		Hoyman, 1974
S. hougasii				X(3)		Hoyman, 1974
S. infundibuliforme				X(3)		Hoyman, 1974
S. kurtzianum				X(4)		Hoyman, 1974

Cultivar/ Varieties	Meloidogyne Species					References
	inc.	acr.	jav.	hapl.	tham.	
S. leptophves						
PI 210056	X					Nirula et al., 1969
S. lingnicaule						
Black's 4816	X					Nirula et al., 1969
S. marinasense				X(5)		Hoyman, 1974
S. megistacrolobum						
Oka 3931	X					Jatala and Rowe, 1976
Oka 4460	X					Jatala and Rowe, 1976
D. microdontum						
Oka 4820		X				Jatala and Rowe, 1976
PI 320312		X		X(1)		Hoyman, 1974
S. multidissectum				X(4)		Hoyman 1974
S. multiinterruptum				X(1)		Hoyman, 1974
S. ochiantum						
PI 230519	X					Nirula et al., 1967
S. papita				X(6)		Hoyman, 1974
S. raphanifolium						
PI 210049	X					Nirula et al., 1967
PI 264488	X					Nirula et al., 1967
Black's 4749b	X					Nirula et al., 1967
S. sparsipilum				X(10)		Hoyman, 1974
PI 210039	X					Nirula et al., 1967
PI 230502	X					Nirula et al., 1967
PI 310933		X				Jatala and Rowe, 1976
HHC 499		X				Jatala and Rowe, 1976

Cultivars/ Varieties	Meloidogyne Species					References
	inc.	acr.	jav.	hapl.	tham. aren.	
S. spegazzinii				X(8)		Hoyman, 1974
PI 218218	X					Nirula et al., 1967
PI 275114	X					Nirula et al., 1967
Black's 4830a	X					Nirula et al., 1967
CPIR'S 58						Nirula et al., 1967
Oka 4902	X	X				Jatala and Rowe, 1974
S. stoloniferum				X(8)		Hoyman, 1974
PI 160224	X					Nirula et al., 1967
PI 161170	X					Nirula et al., 1967
PI 195165	X					Nirula et al., 1967
PI 23477	X					Nirula et al., 1967
CPC 2282.2	X					Nirula et al., 1967
CPIR'S 41	X					Nirula et al., 1967
CPIR'S 42	X					Nirula et al., 1967
CPIR'S 43	X					Nirula et al., 1967
S. tarijense				X(%)		Hoyman, 1974
S. tascalense	X		X	X	X	Brücher, 1967
S. tuberosum						
PI 161131						Ross and Rowe, 1963
Kufri Chandramukhi	X					Nirula, 1969
Great Scot	X					Nirula, 1969
HC-294	X					Khanna and Nirula, 1964
HC-115	X					Nirula, 1969
HC-1699 (Simla-Coimatore)			X			Kishore, 1969
"Baguio"	X					Toledo and Davide, 1969
"Irish"						Lumdang and Davide, 1970
B7-147 (Penobscot XW-39-1)				X		Hoyman, 1974
spp. andigena	X	X	X	X	X	Brodie and Plaisted[a]/1976
Hawk's 2154	X					Nirula et al., 1969
PI 245926				X		Hoyman, 1974
S. vernei				X(6)		Hoyman, 1974
PI 230562	X					Nirula et al., 1967
Black's 3204b	X					Nirula et al., 1967

[a] Progenies of clonal crosses.

Cultivars/ Varieties	Meloidogyne Species				References
	inc.	acr.	jav.	hapl.	tham.	
S. spp.					
"Pintado"	X		X	X	X	Brücher, 1967
"Chalican"	X		X	X	X	Brücher, 1967

STRUCTURE, ORGANIZATION AND METHODOLOGY OF INTERNATIONAL TRIALS FOR ROOT-KNOT NEMATODE (MELOIDOGYNE SP.) RESISTANT MATERIAL

P. Jatala

I Introduction

The improtance of utilizing root-knot nematode (Meloidogyne sp.) resistant potatoes in the areas where these nematodes are of economic problem is well known and need not be emphasized any further.

The early phase of research on searching for root-knot nematode resistance was concentrated in utilization of CIP's vast germ plasm as possible source of resistance. Parallel studies in searching for resistance in the wild tuber-bearing Solanum species were initiated soon afer it was realized that frequency of obtaining resistance in CIP's germ plasm was rather limited. Immune and resistant genetic material were discovered and incorporated in other genetic sources with certain desired attributes. Since the identified immunity or resistance are only to those root-knot nematode populations from Peru, determination of the behavior of these material to other populations and species of Meloidogyne warrant attention.

II. Objectives of the International Trials

1. To determine the value of resistance or immunity of the material identified in Peru to the populations and species of the Meloidogyne occurring in other countries.

2. To select families with highest Meloidogyne immune or resistant segregating progenies under different environmental conditions to be used in the breeding program; and subsequent development of families adapted to various climates as well as being immune or resistant to as many species and populations of Meloidogyne as possible.

3. To provide national programs with genetic material with superior characteristics as compared with the local varieties in addition to having immunity or resistant to the root-knot nematodes.

III. Sources and Limitations in the Distribution of Test Materials for International Trials

Primary sources of the genetic material for international trials will be CIP/Lima.

1. The genetic material which CIP may provide for international trials will be basically botanical seeds of the selected and improved segregating populations.

2. Tuber families of the above populations which have been produced under the strict quarantine and sanitary conditions.

3. Advanced selected clones may also be provided as multimeristem cultures (in vitro).

4. All the genetic material used for international trials are to be subjected to stringent sanitary tests.

IV. Organization, Coordination and Types of International Trials

Organization and implementation of the international trials will be the same as outlined in the report of the 1977 Planning Conference on the Utilization of Genetic Resources of the Potato II. Once the materials are received in the regions the regional representatives and/or production specialists will provide leadership and advise to the National Program for the execution of the trials as well as coordinating the testing activities in their region. In certain cases when the material are sent to the countries not included in the CIP regions, the receiving scientists will coordinate with the CIP scientists the implementation of the trials.

Basically, at the early stages the trials will consist of screening for resistance and identification of the outstanding material to be used in further breeding programs. This will in turn determine the effectivity and the value of the genetic material selected in Peru. Advanced clones will be tested for yield in addition to resistance to the root-knot nematodes and the bacterial wilt *Pseudomonas solacearum*.

V. Methodology

Resistant reaction of potato accessions or seedlings to be root-knot nematodes is based on the ability of the nematode to reproduce or develop galls on the host plant. Test can be conducted in a greenhouse in 8-10 cm. pots or in the field. Field experimentation provides additional data on the resistance of the tubers when they are formed.

Potato tubers or 1- 1.5 month old seedlings are planted in a uniformly infested field or 8-10 cm clay pots. Pots containing tubers may be inoculated at planting while those planted with young seedlings should be inoculated about 2-3 weeks after transplanting of the 5 cm. long young seedlings. Inoculum may be in the form of 0.5-1.0 gm chopped Meloidogyne infected roots or 4000 eggs per pot (see instructions for obtaining inoculum). In the field, plants are allowed to grow almost to maturity while in the pots two months period after inoculation is sufficient for evaluation. After this period, roots are removed from soil, examined and the reaction to nematode is recorded as follows:

A. Root-knot nematode - root infection

1. Immune, no root galling and/or nematode reproduction.

2. Resistant, trace of root galling and/or trace of nematode reproduction.

3. Moderately susceptible, moderate root galling and/or moderate nematode reproduction.

4. Susceptible, severe root galling and/or a high nematode reproduction.

5. Very susceptible, very severe root galling and/or a very high nematode reproduction.

Plants showing a root galling of 1 or 2 should be tested again to avoid possibility of escape.

B. Root-knot nematode - tuber infection

Reaction of tubers to root-knot nematode are rated as follows:

1. Resistant, no external galling and no evidence of nematode presence inside tubers.

2. Moderately resistant, no external galling but evidence of nematode presence inside tubers.

3. Susceptible external galling and deformation of tubers.

C. Suggested Procedures for Obtaining and Applying Root-knot Nematode Inoculum

1. Inoculation with a suspension of 4000 Meloidogyne eggs per plant.

a. Materials Needed:

i. Clorox (5.25% NaOCl) or similar commercial sodium hypochlorite solutions.

ii. 200-mesh and 500-mesh three-inch Tyler sieves, standard height and stainless steel.

W. S. Tyler, Inc., Mentor, Ohio 44060. These can be ordered through Fisher Scientific Company.

iii. Pint Mason jar or similar container with large orifice and tight seal.

b. General Procedures for Obtaining a Suspension of Meloidogyne Eggs:

i. Wash soil from galled roots of a plant harvested a minimum of 45 days after inoculation. If older plants are used, make sure roots are not in an advanced stage of deterioration. Eggs from roots of an older plant will be less uniform in development than if a younger plant is used.

ii. Excise roots and wash well. The cleaner the root system, the easier it will be collected the eggs by the sieving process. If root system is large, process only half at a time.

iii. Prepare a 10 or 20% Clorox solution (v/v), (0.525% and 1.05% sodium hypochlorite, respectively). The 20% NaOCl solution frees more eggs.

iv. Place washed roots in jar, add 200ml of NaOCl solution and seal top. Vigorously shake jar manually for 4 minutes.

v. After shaking, quickly pass the NaOCl solution through the two sieves, a 200-mesh sieve nested in a 500-mesh sieve. Once original NaOCl solution has been sieved, fill jar containing the roots with water and set it aside. After the NaOCl solution has been passed through the sieves, remove the 200-mesh sieve and hold the 500-mesh sieve (containing eggs) under a slow stream of cold tap water to remove residual NaOCl. Rinse eggs from 500-mesh sieve into a 2-liter beaker.

vi. Rinse the roots at least twice with water to remove additional eggs and collect eggs by sieving as described. If you intend to collect eggs of two *Meloidogyne* species, sterilize all equipment in very hot water between collections.

vii. For determining the concentration of eggs per milliliter remove three 1-ml samples, count the eggs, and use the average to represent the number of eggs per milliliter. Representative 1-ml samples are obtained best by blowing air through the pipette into the egg suspension for a few seconds prior to removing sample. Finally, adjusting the volume of water to make 1000 or 500 eggs/ml will simplify the dispensing of eggs.

c. Applying Inocula:

i. Dispensing eggs: For general purposes eggs can be dispensed easily by using a pipette (10 ml volume). Inoculate each plant with a suspension of 4000 eggs in 10-20 ml water.

ii. Adding eggs to the soil: At least three possibilities exist: (a) eggs can be throughly mixed with soil prior to potting, (b) eggs can be added to a depression in the soil at time of transplanting or of planting seeds, or (c) in the case of plants started from seed, eggs can be added to depressions in soil near roots of 3-4 week-old seedlings. The free eggs should readily disperse in the soil, irrigate after applying inoculum.

2. Inoculation with chopped galled *Meloidogyne* infected roots.

a. Material needed:

i. Root-knot nematode infected tomato or potato roots.

b. General Procedure for obtaining inoculum:

i. Wash soil from galled tomato or potato roots infected with *Meloidogyne* for at least 45 days. Use only the galled roots that exhibit the presence of a large number of *Meloidogyne* eggs masses.

ii. Chop the roots into 1 cm. pieces and mix the inoculum well in order to obtain a somewhat homogeneous mixture.

c. Applying Inocula:

i. Apply 0.5-1.0 gm (depending on the quantity of egg masses present) chopped galled roots in the depressions made around the seedlings at inoculation time. Cover with soil and irrigate.

VI. General Comments:

In order to maintain the uniformity of the international trials for resistance to the root-knot nematodes, it is suggested that the co-operators use the inoculation procedure of using 4000 eggs as inoculum. This would provide a uniform test and the results will be near to exact.

During 1978 a number of families (Table 1) with high segregating *Meloidogyne* immune progenies were sent to Brazil,Taiwan,Philippines and Indonesia for international trials for resistance to *Meloidogyne* species. Results of the trials conducted in 1978 in these countries are not complete and, therefore, are not included here. More material will be sent during 1979 to different countries and regions for testing.

TABLE 1

BOTANICAL SEEDS OF POTATOES WITH RESISTANCE TO *MELOIDOGYNE INCOGNITA* AND *M. INCOGNITA ACRITA*

Pedigree	Quantity per Package
66P3 - TII - 2 Phubulk J	60
66P17 - JII - 1 x Phubulk T	60
66P20 - JI - 3 x Phubulk J	60
66P22 - 15 x 760147.2	60
72-P2-45 x 760147.2	60
66P3-IF.21 x 760147	30
66-P27-3 x 760147.2	30
70-P6-15 x 760147.2	30

IMPORTANCE OF PRATYLENCHUS SPP. TO POTATO CULTURE

H. J. Jensen

Pratylenchus spp., commonly known as meadow-, migratory- or root-lesion nematodes, are common inhabitants of cultivated soils throughout the world. Although some species are cosmopolitan within climatic zones, most are limited to portions of continents or specific localities. Pratylenchus brachyurus and P. coffeae are commonly found in tropical and subtropical areas; P. neglectus (P. minyus), P. pratensis and P. penetrans in temporate climatic zones. Even though all species are polyphagous, the number of host plants, often including numerous weeds, vary among species with nearly 400 plants listed for P. penetrans and less than 30 for P. coffeae. Reference to species which attack potatoes are relatively few. Seven species have been reported to attack potatoes (P. brachyurus, P. coffeae, P. crenatus, P. neglectus, P. penetrans, P. scribneri, and P. thornei). The first record of the genus attacking potatoes occurred in 1889 when a species later described as P. scribneri was found in tubers (8). P. penetrans is most often reported in temporate climatic areas and P. brachyurus is most common in tropical and semi-tropical areas.

Symptoms on Potato

While above ground symptoms of stunted patches of plants (2, 9), chlorotic vines or early dying of vines may occur on occasions during stress conditions (inadequate moisture and/or high temperature), diagnostic evidence of infection by root-lesion nematodes occurs beneath the surface. Below ground symptoms caused by all species occur on roots as conspicuous dark spots or streaks (necrotic lesions), girdling or partial destruction of secondary roots and inhibition of secondary root development. This activity usually causes a reduction in number and size of tubers. Some studies indicate that root symptoms are often involved in a disease complex with other pathogens. More important to the consumer, processor or seed producer, however, are the symptoms which occur on the tuber that directly affect the market value of the crops. Two species that occur in warm climates (P. brachyurus, and P. scribneri) also damage tubers causing small volcano-like pustules to form at the tuber surface. Such symptoms usually do not appear until four or five months after planting. After storage the pustules coalesce, shrink beneath the tuber surface and become shallow depressions (5).

Biology and Ecology

Development and life history is probably very similar for most species though host associations, moisture, temperature and other climatic and edaphic factors exert profound influence upon rate of development, population dynamics and survival. Most species closely resemble one another and are bisexual, however, P. brachyurus and P. neglectus are parthenogenetic.

Root-lesion nematodes seem to prefer the same type of environmental conditions as suited for potato culture. For example, light sandy soils seem to present an ideal environment, however, it should not be assumed that damage will not occur in heavy soils as P. penetrans is injurous to other hosts in most soils (2). Other species prefer a narrower range of conditions and are thus distributed in limited areas. Though it is very difficult to select factors which are most important in determining distribution and population levels, it would appear that moisture and temperature would rank highest among abiotic factors. Certainly biotic factors as host relationships and natural enemies are of importance but they are not often limiting factors for these polyphagous nematodes.

Interactions with Other Pathogens

There are at least 119 references to root-lesion nematodes and other pathogens including other nematodes (1). Most references relate to fungi and include: 43 with Fusarium, 37 with Verticillium, 5 with Phytophthora and 5 with Rhizoctonia. There are also 11 references with bacteria (mainly Agrobacterium and Pseudomonas) and another 18 references with other nematodes (principally Meloidogyne). Very few interaction studies have used potato as a mutual host. Obviously the limited activity indicates that researchers have experienced difficulty of using the potato host as their greenhouse or laboratory model. Verticillium and root-lesion (P. penetrans) interaction studies have often been negative because Verticillium wilt symptoms will not consistently develop in small-scale experiments.

A trend, if not a consenses of interaction studies with Pratylenchus penetrans as one partner and a fungus or a bacterium as another, is that a 'synergistic' effect of combined organisms is greater than either one alone. Also symptoms of a particular disease, caused by the bacterium or fungus partner, usually appear more rapidly. Symptoms produced by the nematode alone, however, are not altered. Another result of interactions that becomes apparent is that the population of nematodes increases (6).

Control

Extensive work on exclusion of the pest or prevention of recontamination from infected tubers with a hot-water treatment or special storage condition has been reported. Tubers infected with *P. brachyurus* treated at 50°C for 45-60 minutes eliminated all stages of the nematode (4). Care must be taken to avoid immature or mechanically damaged tubers as much of this material would not survive treatment. Storage of *P. brachyurus* infected tubers for 20 weeks in 5°C in 95% humidity is also an effective control but may not be economically feasible (4).

Other cultural practices such as manipulating moisture and tillage in various temperature situations have only been studied for a few species. *P. brachyurus* populations decrease in winter due to absence of hosts, drought and low temperature (3). Early harvesting has also been suggested as a partial remedy for *P. brachyurus* (9). Most species are polyphagous and opportunities for rotation with non-susceptible crops are limited. Good weed control is essential during the growing season and during the absence of a crop because various weeds are host plants for most species. Ecological studies of *P. penetrans* indicates population numbers correlate with diameter of the roots and such crops with small roots harbor fewer nematodes and are better rotation crops (7).

Chemical control is probably the most popular control measure for *Pratylenchus* spp. Although the practice of fumigation continues to become increasingly expensive, population suppression occurs very rapidly, usually much quicker than by other means.

Although the role of root-lesion nematodes as pests of potatoes may not be as dramatic as other nematodes, additional studies particularly in the areas host-parasite relationships and interactions with other pathogens should demonstrate that these nematodes should be considered as very important potato pests.

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OTHER NEMATODE PESTS: IMPROTANCE AND CONTROL

R. D. Winslow

Other Nematodes of Potatoes

Of the nematodes not dealt with in detail so far, the stem and tuber nematodes, Ditylenchus spp. are the most important. Other of local importance are species of Belonolaimus, Criconemoides and Longidorus. Of doubtful or minor importance are species of Tylenchorhynchus, Helicotylenchus and other spirals, Radopholus, Rotylenchulus and Xiphinema. Neotylenchus abulbosus (= Hexatylus viviparus) was associated with damage to potatoes in USSR, but this fungivor is probably just one of the many secondary organisms found in rotting tissue (Protopopov, 1971), the rot being caused by primary pathogens such as Ditylenchus or one of the many fungal or bacterial pathogens of potato.

Ditylenchus dipsaci and D. destructor, the Potato Stem and Tuber Nematodes

D. dipsaci, with its many races and wide host range, is a difficult nematode, or nematode complex, for the taxonomist (Viglierchio, 1971). D. destructor was separated from it by Thorne (1945) in USA, while Russian workers proceeded to fragment D. dipsaci, erecting several new species, including D. allii, D. fragariae, D. floxidis and D. trifolii, but these were not generally accepted outside USSR. Teploukhova (1968) confirmed D. destructor as a separate species on various morphological grounds, but Metlitski (1968) another Russian worker, thought otherwise, deciding that of the above mentioned species, only D. dipsaci was valid, D. destructor and the others being junior synonyms of it. This must have caused some confusion at the time, but in general Soviet nematologists seem to have continued to regard D. destructor as a valid species. Fragmentation of D. dipsaci continues, species in recent Russian literature including D. allii, D. galeopsidis, D. humili and D. sonchophila. Barabashova (1976) advocated erection of still more species.

Morphologically D. destructor and D. dipsaci are very similar, but they can be distinguished as follows: D. destructor has a sloping overlap of the intestine by the oesophageal glands (D. dipsaci has not), a postvulval sac extending 2/3 of the distance to the anus (in D. dipsaci it extends half way), a rounded tail tip (finely pointed in D. dipsaci) and six incisors in the lateral field (four in D. dipsaci). A phys-

iology difference is that D. destructor is said to be incapable of anabiotic drought survival, while D. dipsaci is noted for this ability. D. destructor attack on potatoes is virtually confined to the tuber, where parasitized cells collapse, causing stresses in the tissues and consequent cracking of the tuber surface (Fig. 1). The nematodes are to be found in the whitish "mealy" tissue at the interface between healthy and diseased tissue, which gradually darkens to brown or black in color as secondary organisms - fungi, bacteria, microbivorous nematodes, etc. - enter and intensify the rot (Fig. 2). In contrast to the above lesions, which are usually superficial, lesions caused by D. dipsaci may extend throughout the tuber, the affected tissues being spongy and yellowish to brown in color (Seinhorst, 1957). Also, D. dipsaci attacks the aerial parts, causing typical stunting, thickening and distortion. D. dipsaci is said to attack the middle lamellae of cell walls, rather than the cells themselves, causing the tissues to become disorganized and the plant to become puffy or bloated.

Another difference between the species is that D. destructor can live on a wide range of fungi and higher plants, whereas the host range of D. dipsaci is almost confined to higher plants. It is unlikely that its many fungal hosts play a significant role in overwintering or persistence of D. destructor, however, since weed control and removal of infested tubers are effective control measures.

D. destructor - the Potato Tuber Nematode

This is, or was, the more important of the two species. Outside the USSR it is found mainly in northern Europe, Canada and northern USA. In Canada and USA (Thorne, 1961), it had its heyday some 20-30 years ago, when it was also of some importance in Europe (Seinhorst, 1957). Faulkner and Darling (1961) studied its host-range and pathogenicity in the USA, showing that it could, as noted above, reproduce on many fungi and higher plants, and that the nematode alone could cause serious disease, but secondary organisms helped to complete the rot. Dallimore (1960) described the sequence of symptoms, and Anderson (1962) studied the nematode's feeding, reproduction and embryology. Roediger (1960), Spray (1960 a) and Goffart (1961) studied its distribution, host-range and pathogenicity in Germany. Duggan and Moore (1962) found it a localized pest in Ireland, where clovers acted as reservoir hosts. More recently it was still a local problem in Ireland (Moore 1971 a) and was troublesome in Sweden also (Andersson 1971). Currently, nearly all the publications about it are from the USSR, so we must conclude that it is a major pest there and apparently of little importance elsewhere. Why it should have ceased to be research worthy in non-Soviet countries is a mystery, but there are a number of possible reasons. According to Russian investigators, better control of weeds (reservoir hosts), visually cleaner seed, higher fertilizer rates and earlier harvesting are all

Potato attacked by potato tuber eelworm

1. external

2. internal

aspects of modern potato growing and hygiene. This incidental control, if it exists, is reminiscent of similar control of Anguina tritici in wheat in Britain; the combine harvester is so effective in separating the galls from the healthy grains that the nematode has disappeared completely. Another nematode that may be dwindling in Britain, also for unknown reasons, is Heterodera avenae on oats, even where these are grown frequently. Increased parasitism of the nematode by fungi may be responsible (Kerry, 1975). If so, what has caused this increase?

The distribution of D. destructor in the USSR has been the subject of many studies. It is widespread in most of the western and southern republics, from Estonia to Alma Atar, and in parts of Russia proper, including the Moscow area. It is regarded as a serious pest, seemingly of more importance than Globodera rostochiensis in the Baltic republics (Krall, 1970), and annual losses caused by it in western Ukraine were estimated at some 160,000 tons (Kapitonenko, 1967). It also occurs in neighbouring European countries such as Poland, where its distribution extent is unknown, with sporadic outbreaks (Malec, 1972) and in southern Sweden, where some heavily-infested fields were found (Andersson, 1971).

The Nature of the Rot

Various Russian workers have studied the sequence of events which occurs following invasion of the tuber by the nematode (German, 1977). Following the nematodes other pathogens of potato tubers may enter perhaps using the entry provided by the nematode. Succeeding these are saprophytes such as bacteria and fungi, which feed on the tissues killed by the pathogens. Microbivorous and fungivorous nematodes follow to feed on the bacteria and fungi. In turn predacious nematodes, fungi, etc, may enter to feed on the nematodes. Invasion by secondary organisms is regarded by Soviet workers as virtually an essential part of the tuber rotting process. The biochemical processes accompanying these events appear to be many and varied, involving many enzymes. The essential changes involve the breakdown of starch to simple sugars which the nematodes can use (Safyanov, 1965) and the breakdown of proteins (Myuge, 1971). These are presumably caused by enzymes secreted by the nematodes, although Bumbu (1968) stated that no extra-intestinal digestion exists in nematodes.

Chemical Disinfestation of Soil

Several chemicals have been tested on infested soil without much success. Nemagon effectively disinfested soil but was too phytotoxic for potatoes to be grown in the same year (Kapitonenko, 1967). Basudin (diazinon) gave less than 50% control (Rasinya, 1972), and chemicals were generally regarded as too expensive or ineffective (Ismailov, 1967; Guskova, 1966;

Kikas, 1969). Seed treatments were more successful, dimethoate, fostil, carbathion (metam-sodium) and nemaphos (thionazin) being effective, although the last two were somewhat phytotoxic, being more so if used in spring than in autumn (Ismailov, 1976; Chuckantseva, 1976).

Physical and Cultural Methods

Hand sorting of seed tubers, to reject any obviously infested with D. destructor, is still regarded as one of the best methods of seed treatment (Ismailov, 1976). Stem cuttings (from infested tubers) disinfested with alcohol and rooted with hormone, gave a clean crop although yields were reduced by about 1/3, compared with untreated which had 42-45% of tubers infested (Bashkardin, 1971). Another form of hygiene is the removal of infested tubers from the field. In plot experiments this was shown to eliminate infestations even where potatoes were grown continuously (Moore, 1971 a). Only when the diseased tubers were returned to the plots did the infestation persist. It is unlikely, however, that growers could or would remove all or most of the diseased tubers.

Weed destruction is recommended to help control this serious parasite in Uzbek SSR (Usmanova, 1972). Andersson (1971) found nine weed hosts in heavily infested fields in southern Sweden and considered them the infestation source, whereas red clover, Mentha arvensis, and other weeds were important reservoir hosts in Ireland (Moore, 1971). Malec (1972) found several weed hosts in Poland, while Ivanova (1973) found D. destructor on 11 out of 13 common weeds in potato fields in the Moscow region.

Crop rotation is also an effective means of control, Ivanova (1971) finding it completely effective in preventing continuous occurrence of D. destructor in the soil. Moore (1971 a) found sugar beet supported very little infestation. Efremenko and Burshtein (1975) found buckwheat, carrot and lupin good for suppressing the nematode but Malec (1972) found carrot a host in Poland. This may indicate geographical isolates differing in pathogenicity to certain plants. Smart and Darling (1963) found four such isolates in the USA. Disease escape in the form of late planting and/or early harvesting has been recommended (Kapitonenko, 1967). This seems to contrast with the situation in Ayrshire, Scotland, where the first early variety Epicure, planted early, enjoys a measure of escape from attack by Globodera rostochiensis (Grainger, 1951). The Russian recommendation, however, advocates a shorter growth period, while in Ayrshire the growth period is shifted to embrace colder spring conditions less suited to the pest.

Increasing fertilizer rates, especially nitrogenous fertilizer, has a beneficial effect. Safyanov (1966) found that ammonium sulphate and ammonium nitrate increased yield and decreased infestation level and

storage losses; although starch content of tubers was decreased by the fertilizers, total starch per ha was increased. Moore (1971 a) in Ireland found that F Y M decreased tuber symptoms. Glez (1971; 1973) found that N P K fertilizers decreased storage losses and nematode multiplication; Shepshelev and Glez (1973) found solutions of these fertilizers toxic or inhibitory in laboratory tests, ammonium compounds and potassium chloride being more active than superphosphate.

Selecting, Breeding and Testing for Resistance to D. destructor

Guskova (1966) found 29 varieties susceptible to D. destructor in Byelorussia, while in Poland Stefan (1968) tested 92 varieties, judging only three (Drossel, Pimpernel, Rode Star) combining resistance with other acceptable characters. Moore (1971 b) in Ireland found no resistance in 15 varieties (including Rode Star) and four Solanum andigenum lines. German (1972) tested 64 varieties and hybrids, finding 11 of them to be 80% or more resistant. Kostina and Zholudeva (1974) tested 111 varieties and found resistance in 7, namely Ali, Anett, Apta, Vanda, Poet, Pekula and Khorza. Kameraz and Olefir (1974) tested over 200 wild species and found resistance in several and in S. andigenum and S. tuberosum. Ivanova (1975) tested 184 Solanum species and lines, finding 87 resistant. It is evident from the above data that Soviet workers are putting considerable effort into the process of selecting and testing for resistance.

Ditylenchus dipsaci, the Stem Nematode

There are fewer publications about this nematode than about D. destructor, indicating that it is or was a much less important pest. Its distribution is restricted to cool, moist climates and its preference for heavier soils usually not ideal for potato growing, further restricts its presence on potatoes. Southey (1971) recorded it on potato in England for the first time since 1954, indicating its rarity as a potato pest there. Just recently, however, Soviet workers have shown much more interest in it, mainly in selecting and testing Solanum species, varieties and breeding lines for resistance. Seinhorst (1957) considered it a serious pest of potatoes in parts of Germany and the Netherlands, but very little concerning it has been published recently in these countries. This suggests that it is no longer a serious pest there. Kaai (1964) examined the relationship between nematode density and crop damage. Hijink (1963) thought that D. dipsaci and the fungus Phoma solanicola might be combining to form a disease complex. Riedel and Mai (1971) confirmed that pectinases associated with the nematode were dissolving cell-wall cement, thus enzymically macerating tissues. Unlike D. destructor, which can live and reproduce on a wide range of fungi (Faulkner and Darling, 1961), D. dipsaci is normally regarded as an obligate parasite of higher plants, but Viglierchio (1971) found that it multiplied on 2 out of 19 fungi tested.

Resistance of Potatoes to Stem Nematode

Shepshelev and Chernikova (1971) found no case of complete resistance in 79 varieties and over 100 hybrids, but many cases of moderate to high resistance have been found. Nikulina (1970) found resistance in several potato varieties, and Lekhnovich and Pimskaya (1976) found resistance in introduced plants. Morozova (1973) recorded resistance in 22 varieties of S. andigenum. Kameraz et al (1974) found resistance in 15 forms of S. chacoense, 7 of S. andigenum, 2 of S. catarthrum and one each of S. fendleri, S. michaacanum and S. vernei. Shepshelev and Chernikova (1975) tested 57 named varieties, finding 8 resistant. They also tested 126 forms of S. andigenum and other wild and cultivated species, finding that more highly or moderately resistant forms were obtained from S. chacoense and S. rybinii than from S. andigenum. Again, as with D. destructor Russian workers are putting a lot of effort into the search for resistance to D. dipsaci and meeting with at least partial success.

Belonolaimus longicaudatus - the Sting Nematode

This nematode was one of a complex of nematodes, or a nematodes - Verticillium complex, associated with early death of potatoes in northeast Florida (Weingartner et al. 1974; Weingartner and Shumaker, 1977). Belonolaimus was the most damaging nematode pathogen. Yields increased by 50-150% after nematicidal treatment. It was calculated that 3 individuals of Belonolaimus per ml of soil caused a yield reduction of 32.5%.

Criconemoides onoensis

Overman et al. (1971) found yields of potatoes on marl soils in Florida were inversely related to population density of this nematode. Weed control reduced nematode numbers and increased potato yields. Although other Criconemoides species were found associated with Belonolaimus (see above) and elsewhere on potatoes there is no evidence that they caused appreciable damage in such instances.

Longidorid species

Although these nematodes are better known as vectors of plant viruses they can and do cause direct damage to potatoes. Jones (1972) regarded them as sufficiently important to warrant nematicidal treatment and Brown and Sykes (1975) studied the relationship between density of Longidorus elongatus in soil and potato yields estimating losses at 3 ton per ha for each 100 Longidorus per 200 gm soil. Sprau (1960 b) found Paralongidorus maximus associated with depressed growth in patches in potato fields in Germany.

Tylenchorhynchus

Species of this genus found in potato fields include T. capitatus, T. claytoni, T. dubius and T. martini. Vara Alcala et al (1970) found that T. capitatus caused cell-wall thickening in potato roots in Spain. Miller (1970) found T. claytoni associated with Pratylenchus penetrans in a survey of 28 potato fields in Connecticut, USA, but decided numbers were too few to justify soil nematicidal treatment. Nevertheless, Miller and Kring (1970) treated such fields with fumigant and systemic nematicides, aldicarb being most effective (90% control). Aldicarb and other systemics seem to repel T. claytoni. Weingartner and Shumaker (1977) found T. claytoni associated with Belonolaimus and other nematodes in Florida, but as stated above, Belonolaimus was mainly responsible for the crop damage. Rodríguez-Kabana and Ingram (1977) T. claytoni and 3 other nematodes associated with potatoes in Alabama. As 2 of the 3 were Pratylenchus brachyurus and Meloidogyne incognita, recognized potato pathogens, there is no evidence that T. claytoni was causing damage. Overman et al (1971) found T. martini associated with Criconemoides onoensis in potato fields in Florida but as already stated the latter was regarded as the more damaging. Kyrou (1969) found T. dubius infesting a trials site at Woburn, England and showed that it could multiply on and reduce yields of potatoes in pots. He regarded it as a potentially damaging parasite of potatoes.

Helicotylenchus and other Spirals

H. dihystera was associated with Meloidogyne incognita in potato fields in Alabama (Rodríguez-Kabana and King, 1976). Sodium aside had no effect on H. dihistera but controlled Meloidogyne incognita and increased yields. This would indicate that H. dihystera was not responsible for the damage. Ramírez A and Barriga O (1969) found spirals associated with Meloidogyne and several other nematodes on potato crops in Colombia and found potato yields greatly reduced by Meloidogyne. Presumably the spirals were of negligible or doubtful importance. Other spirals found in potato fields include Hoplolaimus and Scutellonema, but there is no evidence that they are damaging.

Radopholus similis was associated with potatoes in Rhodesia, but without any evidence of adverse effects on yield or storage (Martin and Amstrong, 1975), despite earlier reports of the nematode causing small dark necrotic lesions on tubers (Martin, 1971).

Rotylenchulus reniformis. Rebois, Eldridge and Webb (1974) showed that this nematode could cause considerable reduction in potato yields in pots. Whether similar reduction occurs in the field has not been demonstrated. R. reniformis occurred together with the known potato pathogen Meloidogyne incognita on potatoes, with depressed yields, in Egypt, but the role of R. reniformis was not clear (Abdel-Rahman et al. 1974).

Xiphinema. Cotten (1974) showed that *Xiphinema index* could reproduce on potato. Species of the genus prefer woody hosts and are found in hedgerows rather than open fields in Britain. Therefore they are unlikely to cause damage to potatoes under field conditions.

D. *Destructor* Infestation on Potato in Ireland

Effect of 7 Cropping Treatments on % Tuber Infestation

From Moore, 1971

Initial	Crop Years 1-3	Crop Year 4	Final
49%	Red clover	Potato	41%
56	Mentha arvensis	"	35
46	Grass/clovers	"	12
43	White clover	"	8.5
48	Fallow	"	0.5
45	Sugar beet	"	0.4
52	Potato	"	0.0

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INTERRELATIONS OF NEMATODES AND OTHER ORGANISMS IN DISEASE COMPLEXES

Harold J. Jensen

For the past several years nematologists, plant pathologists and virologists have seriously considered the role of nematodes in associations with bacteria, fungi, other nematodes and viruses in plant disease complexes. Although, Atkinson (2) postulated in 1892 that a combination of root-knot nematodes and Fusarium on cotton produced the most severe wilt symptoms, other investigators did not show interest in this concept until several years had passed. It is now very likely within a few years that the interrelationship role of nematodes will be of greater economic importance than the straightforward role of nematodes as plant parasites.

By February of 1976 we listed 1192 interaction references (1). Such references are dominated by fungus associations followed by those involving viruses, bacteria and other nematodes. The fungus associations receiving the most attention are Meloidogyne or Pratylenchus and Fusarium and Verticillium. Meloidogyne and Aphelenchoides with Corynebacterium and Pseudomonas are most evident in bacterial associations. Virus studies seem to be more evenly divided among the various vectors and viruses. Nematode, nematodes relationships though not studied extensively are dominated by Meloidogyne and Pratylenchus. A favorite host is obviously tomato closely followed by cotton and tobacco. Except in studies involving Trichodorus and Paratrichodorus and 'corky ring spot' (TRV) virus, potato has not been a popular host plant. Thus the resources available for this discussion are limited.

For many years most researchers accepted the concept that interactions involving nematodes with other plant disease agents was "a wound and avenue of entry procedure." Later, however, other theories began to emerge such as anatomical and biochemical effects of the nematode's saliva (enzymes) upon host tissues were noted. Other interesting developments were reported by Faulkner, Bolander and Skotland (6) and Mulge (11) who demonstrated such interactions were possible even when the nematode and other disease agent did not occupy the same infection site. Bergeson et al. (4) demonstrated another interesting concept that the presence of nematodes influenced weak parasites to become virulent pathogens. Fortunately McElroy et al. (10), Pitcher (12), Powell (13) and others

have presented reviews on this subject that have been of help to organize this presentation. My discussion will follow that developed by Pitcher.

1. Nematodes as Vectors of Pathogens Capable of Self-establishment Once in Contact with Host.

Usually, according to Pitcher, the nematode transports the pathogen, frequently bacteria but occasionally fungus spores, on its external body surface to the aptical meristems of the host. This association is better known for above ground complexes but is probably as important below ground.

Example: Heterodera pallida and Pseudomonas solanacearum on potatoes.

This study indicated that a combination of both organisms resulted in a synergism that resulted in bacterial wilt symptoms sooner and more severe than caused by bacteria alone.

2. Nematodes as Vectors of Pathogens Incapable of Self-establishment Unless Introduced below the Epidermis

This is the category that Pitcher placed those soil borne virus diseases transmitted by nematodes. Since 1958 (7) when this association was reported, nematologists and virologists have published many papers in this area. Because of recent taxonomic reshuffling the number of nematode genera involved has been increased from three to five. Currently 9 species of Longidorus have been demonstrated to be vectors as has 1 in Paralongidorus, 10 in Xiphinema, 7 in Paratrichodorus and 5 in Trichodorus (10).

Example: Paratrichodorus and Trichodorus as vectors of Tobacco rattle virus (TRV) of potato.

Since 1960 (14) when Trichodorus was shown to vector (TRV) 'corky ring spot,' 'spraing' and 'stem mottle,' of potato, numerous studies of this association have been reported. Apparently the disease occurs throughout Europe, North and South America, Japan, and very likely elsewhere. Although chemical control has been effective, resistant varieties have and are being developed for many of the virus isolates.

3. Nematodes as Mechanical Wound Agents

This of course was the original concept as nematcdes were considered: (a) to move pathogens (bacteria and fungi) into tissues as they penetrate or invade the plant, (b) to produce an easy avenue of entry by leaving an open wound (endoparasites) or a micro-puncture (ectoparasites); and (c) to aid pathogens already on the surface to gain entry as the nematodes contacted the host. Such interaction probably favors bacteria or weak fungal pathogens. Unless specific studies have been made, most general interactions fall into this concept.

Examples: Heterodera rostochiensis and Verticillium dahliae. Combinations of both pathogens shortened symptom expression disease severity.

4. Nematodes as Providers of Necrotic Infection Counts

This concept considers that modifications (necrosis, hypersensitivity or destruction) of tissue adjacent to wounds or punctures by nematodes, provide a good nutrition base for pathogens. While some pathogens (particularly fungi) may benefit from this interaction others do not since wounded tissue usually changes in texture and physiology making the wound site uninhabitable. Wound periderm, increase in phenolic and/or other breakdown products and antagonstic organisms have been considered as intolerable factors.

Example: Pratylenchus penetrans and Verticillium albo-atrum. The effects of this interaction are still under investigation with mixed conclusions.

5. Nematodes as Modifiers or Substrates

For this concept it must be assumed that all nematodes must modify plant tissue to obtain nourishment. Much work needs to be done to gain an understanding of the effects of salivary secretions upon host plant tissues. For some nematodes such as Heterodera and Meloidogyne spp. the process is very complex causing cell hypertrophy others such as Pratylenchus cause necrosis and still others as Ditylenchus are involved in lysis. Pitcher notes there may be two variations; the nematode induces production of metabolities favorable for fungus development in modified tissue or the nematode may destroy certain substances antagonistic to the pathogen.

Examples: Meloidogyne and Fusarium.
Although there may not be an example for the potato host, on tobacco the food base provided by the nurse cells (giant cells or syncytia) are favorite targets for Fusarium hypae.

6. Nematodes as Breakers of Disease Resistance

Nematodes have been reported to cause plants developed to resist bacteria and fungi to become susceptible to these pathogens. Plants developed to resist nematode frequently become susceptible to nematodes as occasionally other pathogens render resistant plants susceptible to nematodes. Causes for such breakdowns are only partly understood and are usually explained in general terms as overpowering a resistance mechanism, unfavorable climatic or edaphtic conditions, different nematode races or biotypes and different isolates or pathotypes of the other pathogens.

Examples: Most studies of this concept have been concerned with tomato varieties and Meloidogyne spp.

7. Nematodes as Competitive and Stress Factors in Epidemiology of Plant Diseases

It is inevitable that nematodes and other pathogens including nematodes are attracted to apical meristems and other host tissues. In such situations various pathogens may feed independently without effect upon other pathogens if respective populations are low enough to avoid overcrowding and excessive use of available nutrients. Very likely, however, such a balance will not be maintained and demand for space and nutrients will be very competitive. Then the situation becomes very complex with such factors as antagonism, survival of the best competitor, become involved.

Examples: Probably no documentation among potato pests involving nematodes. However, nematode-nematode interactions on other hosts can be placed in this category.

By direct feeding upon the hosts and removal of metabolites, water and other substances needed for plant growth, nematodes become a stress factor in crop production. Other pathogens which depend upon a weakened plant for invasion probably find nematodes an important partner.

8. Nematodes as Deterrents of Plant Disease

Very little attention has been given to this concept. It has been established, however, that many nematodes graze upon other pathogens particularly the fungi. Such associations have been reported for Aphelenchus, Aphelenchoides and Ditylenchus. In situations where a population level would greatly favor such nematodes they could lower the population of another pathogen.

Example: Ditylenchus destructor, Fusarium sp. and mites upon potatoes (3). This interaction involved three kinds of organisms. A major conclusion from this study was that the mites and nematodes were competing for the fungus hypae which had penetrated the potato tissue.

It should be noted that various workers have cultured this nematode on 88 genera of fungi which includes several plant parasites.

9. The Influence of Other Pathogens upon Nematodes

Although many natural enemies, including bacteria and fungi, are known to be a cause of death among nematodes, this concept deals primarily with the effects of plant pathogens on nematodes. Currently the three most common effects upon nematodes are: a reduction of the population, an increase in the population, and a change in sex ratio of the population.

Example: Heterodera rostochiensis and the grey sterile fungus (GSF) Pyrenochoeta? Studies of this interaction have resulted in two conclusions. First, the fungus decreased the hatch and consequently population and injury (8) and second, the sex ratio of males to females shifted drastically in favor of males (5).

H. rostochiensis and Verticillium dahliae on potato. This interaction of British pathotype A and the fungus resulted in increased disease severity and a more rapid appearance of symptoms when the nematode population exceeded 10 egg/gm of soil (9).

Although many interactions involving nematodes and other pathogens in disease complexes have been studied, it is unfortunate that potato was rarely involved as a host plant. Such studies, however, contribute to our understanding of the complexity of interactions. One must be aware that most studies are conducted on a small scale in controlled conditions and conclusions obtained there may or may

not apply to field conditions. Also one should be aware that such studies usually present a very difficult challenge and many negative results may only lack the influence of an overlooked climatic or edaphic factor to become a reality.

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NEMATODE-TRANSMITTED VIRUSES CAUSING DISEASES OF POTATO AND THEIR VECTORS

R. A. C. Jones

Nematode-transmitted viruses which cause diseases in plants fall into two groups called nepoviruses and tobraviruses. The former have isometric particles and are transmitted by species of Xiphinema and Longidorus. The latter have straight tubular particles and are transmitted by Trichodorus and Paratrichodorus species. Only three of these viruses are recorded as infecting potato in the field. These are the tobravirus, tobacco rattle (TRV), and two nepoviruses, tomato black ring (TBRV) and tobacco ringspot (TRSV). Table 1 gives details on strains infecting potato, vector species and distribution of these viruses.

Effects of Nematode-transmitted Viruses on the Potato Crop

New infections with nematode-transmitted TRV in the soil cause a serious disease of potato tubers, called corky ring spot (in North America) or spraing (in Europe). Symptoms are arcs of brown tissue, brown lines and/or brown spots in the tuber flesh. The arcs may be visible as rings at the tuber surface. Intensity of reactions vary depending on TRV isolate and cultivar. Unlike most potato viruses TRV is usually not passed from an affected tuber to the progeny plant derived from it. However, when progeny plants do become infected, one or more of their shoots shows stem mottle; affected stems are stunted and produce distorted leaves. Such plants may produce irregular shaped tubers with internal brown spots or arcs. Loss of tuber yield in individual plants with stem mottle averages 35% (Harrison, 1968; Todd, 1967; Beemster and Rozendaal, 1972; Richardson, 1973).

TRV is recorded from many parts of Europe and North America, and also from Brazil and Japan. It seems to be of worldwide distribution and is the only one of the nematode-transmitted viruses affecting potatoes which is of considerable economic importance on a global scale.

TBRV has been found affecting potatoes in northern and central Europe but has not been reported elsewhere except occasionally in shipments of seed potatoes from Europe to other continents. In earlier literature the disease in potato plants caused by TBRV was sometimes wrongly attributed to TRSV. Infection of potatoes is normally only sporadic and the virus

is considered of only minor importance in this crop. Tuber infection is symptomless, but necrotic spots and rings may sometimes develop on leaves in the year of infection with vector-borne virus. Secondary symptoms are similar but tip leaves may be cupped and slightly deformed and plants somewhat stunted (= bouquet disease). Bright yellow leaf markings form (= Pseudo-aucuba disease) in presence of the pseudo-aucuba strain but not in presence of the bouquet strain. Loss of tuber yield in individual plants with secondary symptoms averages 20-30% (Todd, 1967; Govier, 1962).

TRSV has been reported several times from diseased potatoes in Europe, but the causal agent responsible was later shown to be TBRV (Harrison, 1958). Recently, the Andean potato calico strain of TRSV was reported, causing calico-like symptoms in potato crops in Peru where it seems to be widespread (Fribourg, 1975, 1977). It probably occurs throughout the Andean region. Conspicuous symptoms show mainly at high altitude. Its occurrence is normally sporadic and like TBRV the virus is of minor importance to potato production except perhaps in certain restricted areas.

Calico symptoms appear initially as bright yellow areas along the margins of middle and upper leaves. These areas gradually increase in size to form large patches or even sometimes to affect the whole leaf. As the disease progresses most of the foliage may eventually turn yellow. Calico is a secondary symptom produced in plants grown from infected tubers. Tuber infection is symptomless, but plants leaf-inoculated experimentally may develop local and systemic necrotic spots and/or ringspots. Although this reaction has not been observed in the field, Salazar and Harrison (1977) suggested that the virus be renamed potato black ringspot after the symptoms obtained under greenhouse conditions.

We have evidence that another virus (code named UC), isolated in Peru from potato plants with calico-like symptoms may be a third nepovirus affecting potato (Jones and Fribourg, unpublished results). Although originally found in arracacha plants growing in mixed culture with potato in Peru, the nepovirus Arracacha virus A does not seem to be a danger to this crop because it did not infect potato systemically (Jones and Kenten, 1978).

Association virus/nematode

Although no distinct strains of TRV are recognized, many isolates of the virus have been identified and these differ somewhat in symptomatology, antigenic constitution and particle length. However, these differences are not associated with much specificity of transmission as several trichodorid species can transmit the same isolate, and several isolates can be transmitted by one *Trichodorus* or *Paratrichodorus* species

(Harrison et al, 1974). In contrast, a close specificity is shown between TBRV strains and their nematode vectors. Thus the pseudo-aucuba strain of TBRV is transmitted only by L. elongatus and the bouquet strain only by L. attenuatus (c.f. Murant, 1970). X. americanum and X. coxi are both vectors of TRSV, but it is not known which Xiphinema species transmits TRSV-Ca in Peru (Table 1).

Sites of retention of viruses in their nematode vectors have been revealed by electron microscopy of ultrathin sections of virus-carrying nematodes. In L. elongatus TBRV accumulates as a single layer of particles on the inner surface of the stylet guiding sheath (Taylor and Robertson, 1969). TRSV is found only in association with the cuticular lining of the oesophageal lumen of Xiphinema americanum, and may be present as a monolayer from the anterior end of the odontophore to the posterior end of the oesophageal bulb (McGuire et al. 1970). Particles of TRV in Paratrichodorus pachydermus have been found in association with the cuticular lining of the lumen of the pharynx and oesophagus (Taylor and Robertson, 1970).

It is thought that virus particles are selectively and specifically adsorbed onto the cuticular guiding sheath or the lining of the pharynx and/or oesophagus as virus-containing plant sap passes from the plant into the nematode's intestine. Other viruses present in the plant sap but not transmitted by the nematode are not retained at these sites. Specificity of transmission therefore seems to reflect a specific association between the protein of the virus and the cuticular surface in the nematode where the particles are retained (Harrison et al, 1974). For virus to be transmitted virus particles must dissociate from the site of retention in the nematode when saliva passes from it into the plant cell during the initial phases of feeding. Inoculation presumably occurs when the virus is carried with the saliva into a plant cell that has not been damaged too severely by the nematodes feeding.

Role of Nematodes in the Ecology of Nematode-transmitted Viruses Affecting Potato

Although a considerable amount of work has been done on the ecology of TRV in relation to spraing disease, little has been done with TBRV or TRSV-Ca with respect to the potato crop. I will therefore deal mainly with TRV here.

With TRV, its occurrence at any particular site depends on the presence of trichodorids and these are mainly restricted to light or sandy soils. The virus persists at sites in three main ways: (1) Its wide host range enables it to infect many of the plant species growing in a particular locality, including many weed species which act as a reservoir of infection. (2) It also persists inside non-feeding infective trichodorids for over a year as was shown for example in experiments in which weeds

TABLE 1

NEMATODE-TRANSMITTED VIRUSES CAUSING DISEASES OF POTATO

Virus	Strain(s)	Vector(s)	Distribution	Selected References
Tobacco rattle	Various isolates	*Trichodorus* spp.& *Paratrichodorus* spp.	Worldwide	van Hoof (1968), Harrison (1970)
Tomato black ring	(a) Potato bouquet	*Longidorus attenuatus*	Europe	Harrison et al (1961), Murant (1970)
	(b) Potato pseudoaucuba	*L. elongatus*	Europe	Harrison et al (1961), Murant (1970)
Tobacco ringspot	Andean potato Calico	(*Xiphinema* sp.)	Andean region	Fribourg (1975; 1977), Stace-Smith (1970), McGuire (1964)

were rigorously controlled for more than a year, after which a potato crop on weed free plots had a higher incidence of spraing disease than a comparable crop grown in weed-infested plots. The virus had persisted in the vector nematodes and some that would normally have fed on weeds were obliged to feed on potatoes when weeds were not available (Cooper and Harrison, 1973). (3) In infected weed seeds TRV is seed transmitted in several common weeds species.

The proportion of young tubers infected with TRV in a crop at a site depends on the population density of trichodorids present, their efficiency as vectors and how active they are. Total numbers and the proportion carrying TRV depend on the previous cropping history of the land and on the degree and type of weed infestation. Numbers of trichodorids in overwintering populations seemed a key factor in determining amount of spraing disease in Scotland because the number of trichodorids in May was more closely correlated with this than the numbers at harvest in October (Cooper and Thomas, 1971).

Soil moisture also greatly influences extent of TRV infection because an adequate film of water on soil particles is needed to enable nematodes to move through the pores in soil. Thus when soil containing trichodorids carrying TRV was adjusted to a range of water contents and planted with cucumber bait seedlings, virus transmission was greatly decreased when soil moisture content dropped from 15% to 10%. Also, in Scotland a broad correlation was found between the number of weeks between April and September in which more than 30 mm of rain fell and the incidence in different years of potato spraing disease (Cooper and Harrison, 1973).

Soil temperature also influences spread. For example, in tests in which healthy tobacco bait leaves were buried in soil containing virulferous trichodorids and the soil kept at a range of temperatures, most infection was detected at 15°C but a little transmission occurrred even at 4° C (Cooper and Harrison, 1973).

Another factor affecting local TRV spread is vertical and horizontal distribution of nematodes in the soil. Potato plants with newly infected roots and tubers typically are patchily distributed in crops, but these patches do not necessarily reflect the horizontal distribution of nematodes. For example, in one field, patches with large spraing incidence occurred where the top soil was shallow. The trichodorids occurred throughout the field but depth sampling showed that they were most numerous just above a hard soil pan, and where this was nearest to the surface the nematodes were probably redistributed through the topsoil in ploughing. Where the pan was deeper most of the nematodes were not disturbed and remained well below the developing tubers (Cooper and Harrison, 1973).

TRV spread to other sites occurs in three main ways: in virus-carrying trichodorids, infected seed tubers or infected weed seed. Virus-carrying

nematodes move only small distances laterally (< 50 cm per year with trichodorids), but may be moved further by soil cultivation in windblown soil, or in soil on agricultural implements and on the feet of animals or birds. Similarly, infected weed seed is mainly dispersed in the immediate vicinity of the mother plant but some may be distributed over greater distances, e.g. in the wind, or after ingestion by birds. Infected seed tubers are often transported over very large distances, sometimes from one continent to another.

The ecology of TRSV and TBRV has been studied in relation to other crops (c.f. Harrison, 1977). In general both modes of persistance at sites and spread are similar to that of TRV but with TBRV, persistance of the virus in dormant weed seeds is of key importance because L. elongatus remains infective only for a maximum of 12 weeks in the absence of virus-infected hosts to feed on and reacquire the virus from.

Control

Because TRSV-Ca and TBRV are of only sporadic occurrence in the potato crop and both give conspicuous symptoms, roguing out of symptom-bearing plants is an effective control method during production of seed potatoes. Neither virus is a problem in potato production for consumption.

Because TRV is usually not passed from an infected tuber to the progeny plant derived from it, it is not normally a problem in seed potato production. However, spraing disease greatly affects tuber quality and can have considerable importance in potato production for table use. Two main methods of control are available, resistant cultivars and nematicides.

Tuberosum potato cultivars are available which rarely become infected with TRV in the field. Thsi resistance is to the virus only as they are not inferior to susceptible cultivars for maintaining trichodorid populations (Harrison and Cooper, 1974). Such cultivars can be used on TRV infested land and as sources of resistance genes in breeding programs.

Treatment of infested soil with the systemic nematicides aldicarb and oxamyl and the fumigant dichloropropane - dichloropropene (D-D) greatly decrease infection with TRV in potatoes. D-D acts by killing the trichodorid vectors but the systemic nematicides prevent virus transmission by altering their behaviour (Alphey, et al. 1975). Use of such treatments, however, is limited by cost.

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USE OF RESISTANCE AND TOLERANCE TO THE POTATO CYST NEMATODE

A. F. Van der Wal

Development of Pathotypes

Genes for resistance from various sources are likely to be different. A differentiation in reaction to different populations of the nematode is to be expected and, with the existence of the new differential, a new pathotype can be described and added to the list of pathotypes. This process can continue almost indefinitely as long as resistance and differentials can be found. For +/- reactions the possible number of pathotypes is 2^n, with n = the number of differentials. Sets of differentials can be sent throughout the world to identify nematode populations. In fact, with the limited number of pathotypes described so far, this is not difficult.

However, in other host-pathogen systems, where a few hundred races have been identified, classification in various regions of the world is based on a limited set of international differentials, and an additional set of differentials of regional importance. The set of regional importance becomes necessary as soon as the genetic basis of the resistance, and the follow-up by cultivars, differ significantly.

A similar development may occur in the potato cyst nematode system, but compared to, for example, the wheat-rust system, it seems unlikely that the rate of development is the same. Rust generation time is around to three weeks under field conditions during the growing season. At least ten generations (about two seasons or two years) are needed before the new races can be recognized on newly introduced lines. For the potato cyst nematode, with one generation per year, the recognition of a new pathotype would take about 10 years, if the selection of new recombinants occurs as efficiently as in wheat rust.

The cyst nematode population in the Netherlands is considered to have a relatively narrow genetic base. After the introduction of the first resistant cultivars, some parts of the population did not respond to the resistance. This was discovered almost immediately after the introduction of the new cultivars. Because of the insufficient time (expressed in number of generations) for shifting the population considerably, selection of low frequency pathotypes could not be the only explanation. Another possibility is that the other pathotypes were present in considerable quantities and not induced by resistance (Kort, person. comm.).

If this is correct, the breeder is confronted with the even more serious problem of the representativeness of the cyst population he selects for testing.

The resistance that has been used in cultivars seems to be controlled to a large extent by only a few genes with major effects (Plaisted et al. 1972; Fuller and Howard, 1974).

The resistance based on one or two genes from S. andigenum has been often used with success, whereas the resistance from S. vernei clones seems to be affected by more genes.

It seems reasonable to suppose that these very high resistance levels (80% reduction of the initial population or more) do select in the cyst nematode populations, and that this selection causes a shift in the population leading to a gradual decrease in the usefulness of certain resistance gene(s). Although we have not yet sufficient information on the rate of frequency change in the cyst nematode population indiced by various levels of resistance, a lower degree of resistance (e.g. the non-multiplication level instead of 80% killing) might reduce the selection rate in the population.

It seems worthwhile to recommend that some research, genetic as well as economic, be carried out on the effect of lower degrees of resistance on the composition of the (mixed) nematode populations. Resistance does, in general, not last forever. Sooner or later a source of resistance becomes less effective. But in the period in which the source is effective, an increase in the potato production is obtained. And because of the relatively long generation time of the nematode,even monogenic resistance can be very effective, if used properly. "Properly" means, among other things, that there is a continuous influx of new resistant genes from various sources, and that there is a possibility of changing the seed rapidly if new pathotypes become predominant in the population. It is essential to have access to the genetic variability in wild and primitive forms of the potato (Huijsman, 1972) to build up a continuous flow of new cultivars and to keep that flow going.

Screening for Resistance

The root balltest can be used for negative selection, that is, to discard the very susceptible plants, and to identify those with very high and moderate resistance (3 classes). The clones selected this way can be retested in a flotation test.

A refinement is to count the eggs instead of the cysts (Kort, et al., 1972) in order to determine the multiplication factor exactly. It can be of the use also in genetic studies.

Screening capacity is usually limiting the number of samples that are tested. The flotation test is labour intensive and a screening of 10,000 samples per annum is already a real job. The root ball test requires less labour and 100,000 samples per annum can be handled, but here glasshouse facilities are limiting. We can with small pots now handle a maximum of about 250 plants per m^2 per test cycle, and with 3 to 4 cycles per annum the capacity is between 750 to 1000 plants per m^2 glasshouse bench. In a complete research programme, attention should be paid to improving screening methods, and one of them is to reduce the area required in glasshouses.

In view of the uncertainties presented it seems worthwhile: (1) to select very high resistance (80% or more reduction), as well as the intermediate resistance (non-multiplication), in all populations that are screened for resistance (Hermsen, 1975); (2) to test the pathotype specificity of the resistance; and, in a later stage, (3) to study the inheritance of resistance, especially that of the intermediate forms. If there is a major effect of reducing the selection in pathogen populations, when the reduction level is dropped from 80% to non-multiplication, the use of resistant genes to lower the population density can be considered as an improper use of valuable genetic resources.

A combination of other measures should bring the population density down to acceptable levels. Resistance should be used to keep the density at that level.

Tolerance

The potato cyst nematode densities do not increase any more when about 200 eggs per gram of soil are present (Seinhorst, person. comm.). Crop loss due to the injurious effects of the cyst nematode reaches its maximum already at about 50 eggs per gram. Yield/density responses are measurable in the range of 5 to 50 eggs per gram. Between about 0-5 eggs per gram no crop losses can be ascribed to the cyst nematode (data from Seinhorst).

In many infested areas of intensive potato growing the maximum densities are almost constantly present, and tolerant potatoes still produce even at these maximum densities. Differences in tolerance have been found. If the production at maximum densities of the population is the only objective of breeding for tolerance, selection can be simply based on yield differences at maximum densities.

Injury of the Potato Plant, After Cyst Nematode Infection

Infection by cyst nematodes results in a slowing in the rate of the growth already in the first weeks of plant growth. If the plant is not killed, growth is resumed after this period of delay and, when the plant is still in the vegetative phase, the growth rate can become almost similar to that of uninfected plants at a point in time several weeks earlier. (Seinhorst, person. comm.).

This growth pattern indicates a temporary malfunction of the root system. Beukema (person. comm.) suggests that tolerant cultivars show regrowth of the roots for a relatively long time. Evans et al. (1977) found that infected plants have much less extensive root systems. The amounts of lateral roots were decreased much more than those of the main roots. Microscopic examination of the infected root tissue of the tolerant cultivar 'Multa' showed that, compared to intolerant varieties, very little necrosis occurred and that very rigorous growth of callus took place, so that the old and empty giant cells were pressed together (Huijsman et al., 1969). The ability to resume root growth seems to be daylength dependent and occurs mainly during the vegetable stage.

Another aspect of production is the length of the growth period of the crop. The delay in growth due to infection is several weeks. There is a loss of time, even if the growth rate, after the restoration of the root function is equal to the rate of uninfected plants several weeks earlier. When these several weeks are part of a growth period of 5 to 6 months, one can still expect a reasonable crop yield. When, however, the growth period is only two to three months, the crop loss is significant. It is likely that tolerance is rather pathotype unspecific, although there is no proof of this yet.

Tolerance and Resistance Combined

In areas where the population density of the cyst nematode is at a maximum and where no other reasonable ways of control than resistance or tolerance are possible, tolerance should have priority. The use of resistance alone to reduce the population density does not seem advisable because of the shifts in populations, unless there is a constant influx of new resistance sources. In areas where a control strategy is planned to bring the cyst density below 50 eggs per gram, partial resistance (non-multiplication) is useful, and at this level of densities tolerance is valuable as well. The combination of tolerance with partial resistance may be possible.

For areas where control strategies can be successfully performed, tolerance is not very useful now, because there are still other feasible

alternatives for reducing the crop loss from cyst nematodes. In such areas, however, some attention should be given to the lower degrees of resistance and their effects on cyst populations and, in the long run, to tolerance.

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CHEMICAL CONTROL OF POTATO NEMATODES

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The following review on the present status of chemical control of nematodes infesting potatoes is not intended to be an exhaustive one, but mainly to highlight the possibilities and limitations of this method, including some of the experiences in India.

Although widely tested and remarkably effective, the use of nematicides for control of nematodes infesting potatoes, has not been considered a practical proposition in most of the potato growing regions of world, except perhaps as part of an integrated control programme. The high cost of nematicides, the expensive equipment required for application, the need for repeat treatments every year, etc. are among the serious disadvantages.

As against the highly volatile soil fumigants (DD, Telone, Vidden D, etc) which are rather cumbersome to apply, most of the recently introduced granular formulations (organophosphates and organocarbamates) are relatively non-volatile, nonphytotoxic, enabling application at planting time, easier to handle by unskilled operators, and often systemic/slow release in action affording adequate protection to plants in the early stages of growth with consequent valuable increases in yield. They may also protect the plants against aphids, wireworms, white grubs and other soil insects. However, the relatively high dermal and oral mammalian toxicity of these compounds and the likelihood of harmful residues in the soil and tubers are distinct hazards as compared to soil fumigants. In any case, in the developing countries prospects of large scale use of either soil fumigants or granular compounds for control of nematodes of potatoes appear to be remote, except under very special circumstances.

1. Potato Cyst Nematode (*Globodera* spp.)

Among the soil fumigants, DD (Dichloropropene-dichloropropane) has consistently given the most promising results against the potato cyst nematodes (Spears, 1964). The first large scale attempt at chemical control of the nematode was in 1946, when DD was applied to 1500 acres of infested land in Long Island, N. Y., at the rate of 45 gals/acre in a single application. Later, an eradication dosage of 90 gals of DD/acre in two applications of 45 gals each, 10 days apart with soil turned in between, was applied over nearly

5100 acres between 1955 and 1967 (Spears, 1968), mainly with the idea of protecting the mainland USA from nematode infestation. Though complete eradication was not achieved, as much as 4388 acres of land known to be infested prior to treatment were released for cultivation of potato again. A similar nematicide Vidden D was used in Vancouver Island in Canada. Ditrapex or Vorlex (DD 80% + Methyl isothiocyanate 20%) applied in a split application of 10 gals each for a total of 20 gals/acre is said to equal the eradication dosage of DD or Vidden D referred to above (Spears, 1968). In the Netherlands, more than 30000 ha of potato land are reported to have been treated with dichloropropene nematicides with marked benefits, as part of the regulatory control of the potato cyst nematode in 1972 (Oostenbrink, 1974; Hijink, 1974).

Apart from these specific instances, DD has not been used to any great extent elsewhere. In a series of experiments conducted in the Nilgiris (India) since 1964, the best results were obtained in a 2 ha field experiment in 1966 in a grower's field in which DD at 500 kg/ha gave 45-93% control as against 98-100% control in plots treated at 1000 kg/ha in two split doses of 500 kg each at 15 days interval, with the soil turned in between (Seshadri, 1970). Yield increases (var. Ben Cruschen) were of the order of over 400% and 500% in the 500 kg and 1000 kg treatments respectively as compared to untreated controls, and 103% and 196.5% respectively over the previous year's yields from the respective plots. Though economical at that time in heavily infested fields and many farmers came forward to apply the chemical on their own, subsequent increase in cost of the chemical, the need for repeat treatments every year, the cumbersome method of application, the long waiting period before planting, etc. have discouraged the use of DD on any large scale.

Besides DD, other soil fumigants like EDB at the rate of 60 kg/ha (Kyrou, 1971), Telone at 270-614 kg/ha (Jones, 1973; Whitehead et al., 1973a), Ditrapex at 600 l/ha (Mancini et al., 1974), methyl bromide et 857 kg/ha (Whitehead et al., 1973b) and Vapam at 475-2000 l/ha (Spears, 1968; Fedorko and Berlinski, 1976) have also been found effective under field conditions, though none of them have been as widely used as DD in any country.

Many of the recent granular nematicides are very promising, but most of them have either not gained wide usage or are still under experimentation. Dazomet, which liberates methyl isothiocyanata is even more nematicidal than DD and often gives large yield increases (Jones, 1970; Jones, 1973; Whitehead et al., 1973a). Two equal doses of dazomet, one incorporated in top soil, the other after ploughing, controlled the nematode better than an equal amount applied in a single dose after ploughing (Whitehead et al., 1973a). Effective control of the nematode has been reported in Italy (Giunchi

and Tocconi, 1973), in Colombia (Nieto and Barriga, 1976) and Scotland (Mackintosh et al., 1977), using dazomet at 336-490 kg/ha.

Several organophosphate compounds like phorate, phenamiphos, fensulfothion, thionazin, ethropophos, CGA 12223, Dowco 275, etc., and organocarbamates like aldicarb, tirpate, examyl, and carbofuran have been tested and found effective against the potato cyst nematodes to varying degrees (Pain and Hague, 1971a, 1971b, Den Ouden, 1971; Bunt, 1972; Wilski, 1972a; Whitehead et al., 1972; Whitehead et al., 1973c, d, e, f; Homeyer, 1973; Allison et al., 1973; Hague and Boparai, 1974; Mancini et al., 1974; Moss et al., 1975; Homeyer, 1975; Whitehead et al., 1975; Moss et al., 1976; Nieto and Barriga, 1976; Den Ouden and Van de Veer, 1977; Mackintosh et al., 1977). Of these chemicals aldicarb and oxamyl are the most extensively studied, the former much more than the latter. Aldicarb at dosages varying from 2.5 to 11.2 kg a.i./ha has been found to reduce nematode infestation with consequent increases in crop yields. Larvae recovered from treated soil had very little food reserves and only very few entered the root system of plants grown in treated soil as compared to other treatments including control (Pain and Hague, 1971a).

At a dosage of 5.2 - 10.3 kg a.i./ha incorporated in top 15 cm soil, aldicarb proved even better than 384 - 1153 kg of DD/ha in controlling nematodes (Whitehead et al., 1972). Oxamyl at the same dosage ranges is equally effective in most soil types, the degree of control and increase in yield progressively corresponding to the increases in dosages. Carbofuran at 10 kg a.i./ha have 95% control with more than 50% increase in yield according to Homeyer, (1975), while Mackintosh et al., (1977) found a dosage of 5.6 kg a.i./ha highly effective.

In general it may be stated that aldicarb is gradually replacing DD (or has already replaced it in some areas) as the most effective chemical for control of Globodera spp. Large areas are reported to be under treatment by this chemical in the Netherlands in recent years (Kort, personal communication).

While the discovery of these granular systemic nematicides may be considered a major breakthrough in our attempt to control the potato cyst nematodes, the problem of nematicidal residues in the tubers is yet to receive adequate attention. Perhaps only in the case of aldicarb we have some assuring data. According to Bromilow (1973) and other workers, up to 11.2 kg a.i./ha aldicarb applied to soil at planting time resulted in less than 0.15 ppm toxic residues in potatoes at harvest. As further losses in residues occur during storage and cooking, the residue levels in potatoes grown in soil treated with recommended rates of aldicarb at planting will not exceed those considered safe by the presently accepted standards.

Experiments conducted in Nilgiris (India) since 1968 had shown that fensulfothion applied at planting time at 30 kg a.i./ha in the next two seasons almost completely prevented nematode infestation. Even a lower dose of 15 kg a.i./ha for three seasons and 7.5 kg/ha in subsequent seasons is effective in keeping the nematode under check so as t obtain reasonably good yields. Based on the above results, a large scale chemical control programme was carried out during 1971 - 75 under the auspices of an Indo-German Agricultural Development Project to treat the entire infested area of about 200 ha. The object was to bring down the infestation level in the Nilgiris to the minimum and manage the populations further by suitable crop rotations or resistant varieties. The treatment was made mandatory under a Pest Act and the cost was met from by the Project Funds except that a nominal amount was recovered from the farmers @ Rs. 250/- (= $ 30,00)/ha treated.

Among several other newer chemicals tested in the Nilgiris since 1971 (e.g. disynston, phorate, phenamiphos, Mocap, carbofuran, aldicarb, etc.), aldicarb applied at 8 - 16 kg a.i./ha has given the best results comparable to 30 kg of fensulfothion. The levels of nematode control and crop yields increased significantly and progressively for the dosages 1 to 16 kg a.i./ha. Repeat treatments were necessary every year as otherwise the white female population on the roots shot up irrespective of the dosage of the chemical applied in the preceding year, the effect of this being reflected in the crop yield as well. Further studies have helped in determining the most economic dosage of aldicarb to be 2 kg a.i./ha ensuring reasonable levels of nematode control and crop yields.

Other findings of interest are:

i) tubers harvested from infested fields could be disinfested by exposing them to formaldehyde vapour for 12 hours or by soaking them in formalin 10% for 1 hour, without loss of viability, but with some delay in sprouting;

ii) infested seed tubers could be disinfested by dipping in 9% solution of calcium hypochlorite for 30 mts without any ill effects on sprouting;

iii) soaking seed tubers in 0.4 - 1.6% solutions of carbofuran, aldicarb and aldicarb sulfone for periods varying from 3 - 60 mts showed significant effect in preventing infestation, thereby increasing crop yields, but not as good as furrow application of aldicarb 2 kg a.i./ha.

2. Root-knot Nematodes (Meloidogyne spp.)

The problem of root knot nematodes on potato is very widespread all over the world and many species are involved. DD mixture, EDB, DBCP, and methyl isothiocyanate compounds like Vapam are the chemiclas most commonly used to control Meloidogyne spp. although DBCP may be phytotoxic and DD occasionally causes taint (Winslow and Willis, 1972). Experience in India over the years shows that DD at 200 kg/ha and EDB at 90 i/ha, give consistently higher potato yields only when used under heavy infestation conditions. Even then, their use was not economical. Aldicarb 5 kg fensulfothion 10 kg and carbofuran 4-6 kg a.i./ha did not give good results in three years' (six seasons) trials. However, Radewald et al., (1975) found carbofuran, fensulfothion, Geigy 12223, aldicarb, Nellite, Mocap and phenamiphos at a dose of 2-4 kg a.i./ha effective in controlling the root-knot nematodes. Preplant application of sodium azide at 33.6 kg/ha was found to reduce soil populations by 59-94% and increased yields by 18-24% in field tests conducted at Alabama, USA (Rodriguez-Kabana et al., 1975).

Chemical seed treatment appears to offer good possibilities though work done in this regard is meagre. Seed piece treatment with phenamiphos at a concentration of 1.8 g/l controlled M. incognita along with other nematodes like Hoplolaimus galeatus, Tylenchorhynchus claytoni and Pratylenchus brachyurus according to Rogriguez Kabana and Ingram, 1976. Many other systemic nematicides like oxamyl, methomyl and diaomidafos were tried against M. hapla but only phenamiphos at 4.75 g a.i./l consistently eliminated the nematode (Bolander and Santo, 1977).

3. Potato Rot Nematode (Ditylenchus destructor)

Soil fumigation using EDB in two split applications, with the soil turned over at the second application has been reported to successfully control the potato rot caused by D. destructor in USA (Dallimore , 1955). However, use of soil nematicides for potato rot control is stated to be uneconomic (Ismailov, 1967) besides the fact that many of these chemicals are ineffective in the heavy soils preferred by the genus Ditylenchus.

Soaking potato tubers either in Fostil 0.05-0.025% solutions for 30 mts before planting (Chukantseva, 1976) or in thionazin 46 EC at a concentration of 1% for an hour (Wilski, 1972b) effectively controlled this nematode. Carbathion was also found effective for this purpose but was phytotoxic and even adversely affected germination (Ismailov, 1976).

4. Spraing or Corky Ring Spot Disease (*Trichodorus* spp.)

Corky ring spot (CRS) believed to be caused by tobacco rattle virus is an important disease of potatoes in Netherlands, U.K. and West Germany. Soil fumigation with DD @ 200 kg/ha gave good control of the CRS for two years in field trials conducted in Scotland (Cooper and Thomas, 1971). The effect of this treatment on virus was related to its nematicidal effect on *Trichodorus*. *Trichodorus* and spraing were almost completely suppressed by DD applications @ 250 l/ha and completely eliminated by split doses of 250 + 250 l/ha at a 3 weeks-interval in Netherlands (Maas, 1975). However, potato from plots receiving 250 l/ha or more had an unacceptable flavour, which disappeared in the second crop after treatment, which still showed a good control.

Unlike in Netherlands and U. K., soil fumigation as row treatment with different rates of DD (56 to 132 l/ha), EDB (7.5 to 18.7 l/ha) or 1, 3-D (56-132 l/ha) did not effectively control CRS in Florida (Weingartner *et.al.*, 1975). However, in Colorado, soil fumigation with Telone C (280 l/ha) provided a profitable, though short term control measure for the disease (Livingston *et. al.*,1976).

Methomyl at 8 kg/ha and dazomet at 150 kg/ha decreased spread of the virus in the first, but not in the second year after treatment (Cooper and Thomas, 1971). According to Brown and Sykes (1973), aldicarb at 2 kg a.i./ha, and oxamyl and Mocap each at 5 kg. a.i./ha gave excellent control of CRS on Pentland Dell potatoes while phorate and phenamiphos only reduced spraing in King Edward potatoes. Use of phorate (3.36 kg a.i./ha) was recommended, which reduced spraing incidence by over 60%. In West Germany, phenamiphos (0.5-4 a.i./m^2) was found to be effective in reducing spraing incidence by probably inactivating *Trichodorus* or making the plants repellant to nematode (Reepmeyer, 1973).

Rotavation to a depth of 10-15 cm with aldicarb, oxamyl, phenamiphos and carbofuran reduced spraing incidence more effectively than row application (French and Wilson, 1976). In U. K. application of aldicarb (3.4 kg a.i./ha) or oxamyl (5.6 and 7.8 kg a.i./ha) at the time of planting reduced spraing incidence effectively. Carbofuran 4 F and 10 G, aldicarb 10 G and Ethoprop 10 at 3.4 kg a.i./ha alone or in various combinations with 1, 3-D and foliar applications of oxamyl 2 L (3 separate applications of 1.1 kg a.i./ha) was found to be very effective according to Weingartner *et al.*(1975).

5. Early Maturity Wilt (Associated with *Pratylenchus* spp.)

Soil fumigation with 1, 3-D (250-400 kg/ha) or a mixture of 1, 3-D and chloropicrin (85% + 15%) delayed the infection of *Verticillium*

alboatrum by effectively controlling Pratylenchus penetrans (Biehn et al., 1971). According to Cetas (1976), granular nematicides like aldicarb, carbofuran, oxamyl, etc., were found useful in the control of early maturity wilt. However, aldicarb was consistently found to be superior in increasing yields in areas where wilt complex was present, whether applied as side-dressing or preplant band application.

6. Verticillium-Potato Cyst Nematode Complex

Not much effort has been made in the control of this complex mainly reported from U. K. Soil fumigation with MB @ 976 kg/ha applied under gas-tight sheets decreased verticillium wilt and nematode (Heterodera rostochiensis) numbers, and increased yields. A nematicide (aldicarb 6 kg a.i./ha) and fungicide (benomyl either applied to seed at 0.45 kg a.i./ton or as soil application at 22.4 kg a.i./ha) combination was also effective when rotavated into the soil and increased yields (Hide and Corbett,1974).

7. False Root-knot Nematodes (Nacobbus spp.)

Nothing special to review.

8. The Reniform Nematode (Rotylenchulus reniformis)

Aldicarb was more effective than methomyl, fensulfothion or phenamiphos and significantly reduced nematode populations during the critical period of plant growth, and held populations to a low level during the entire growing season (Abdel-Rahman et. al., 1974).

GENERAL

While nematicides are powerful tools to achieve immediate kill of nematode populations or suppression of their multiplication their efficiency is shortlived and their use beyond the economic means of the average farmer, especially in developing countries. The prospects of any of these chemicals getting wide acceptance would therefore depend upon a favourable cost-benefit ratio. This in its turn may depend upon not merely the cost of the chemical, but also on the market value of the produce which may vary from country to country and even between different regions within the same country and other factors.

Many of these chemicals, as with other pesticides, are suspect in the eyes of the public. Sometimes health hazards involved become known long after the chemical has been in wide use. The recent ban on DBCP is a case in question. Data available on nematicidal residues in soil as well as harvested tubers are meagre and need to be collected for different agroclimatic conditions before general recommendations are made to the farmers.

While chemicals have a positive role in control of nematodes infesting potatoes, their practical utility will probably be enhanced if used along with other methods like adequate crop rotation, use of resistant varieties together with sound management practices using the most productive cultivars, etc., as part of an integrated pest management procedure. The combined use of two or more methods of control has in fact been practised for decades, especially in tackling the potato cyst nematode. There is, however, an urgent need for more research for developing cheaper nematicides, developing methods (like seed treatment) for minimizng their use and maximizing their efficiency, and above all for developing better methods of integrating the different methods of control.

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Potato Cyst Nematode Control in the Nilgiris, India

I. Area treated and number of farmers benefited.

Year of Treatment	Area treated (ha)	Number of farmers benefited	Quantity of fensulfothion 10% used - kg.
1970-71	1220	768	328518
1971-72	1400	791	223639
1972-73	1564	790	199425
1973-74	1227	667	111246
1974-75	1874	931	(figure not available)

II. Result of root examination in treated fields

Year	Irrigated or Rainfed crop	Number of fields examined	Number of fields with		
			No. white females	1 to 10 white females per plant	More than 10 white females per plant
1970-71	Irrigated	68	40	27	1
	Rainfed	75	52	21	2
1971-72	Irrigated	35	21	8	6
	Rainfed	110	69	35	6
1972-73	Irrigated	166	33	95	38
	Rainfed	260	44	187	29

III. Yield data from treated fields

Year	Irrigated or Rainfed Crop	Number of fields sampled	Average yield during the previous year/kg.ha.	Average yield after treatment kg/ha	Percentage of increase in yield due to treatment
1970-71	Irrigated	25	13395	18685	39.5%
	Rainfed	10	9670	12845	32.8%
1971-72	Irrigated	10	21260	25040	13.1%
	Rainfed	25	14580	16830	15.4%
1972-73	Irrigated	23	14600	20085	37.6%
	Rainfed	24	16550	22450	35.6%

PEST MANAGEMENT APPROACH TO NEMATODE DISEASES OF POTATOES

B. B. Brodie

In recent terminology related to pest control, we hear a lot about pest management. Just what is pest management? Is it just an alternative means of controlling pests without chemicals? Pest management is not simply biological control by the use of a single technique. Rather, it is an integrated, comprehensive approach to the use of various control methods that take into account the role of all kinds of pests and their environment, possible interrelationships among these pests and other factors.

Thus, integrated pest management or I.P.M., as it is commonly called, is an approach that employs a combination of techniques to control a wide variety of potential pests that may threaten crops. Integrated systems involve maximum reliance on natural pest population controls along with a combination of techniques that may contribute to suppression-cultural methods, pest-specific diseases, resistant crop varieties, augmentation of parasites or predators, or chemical pesticides as needed.

In discussing I.P.M., the terms control strategy and control tactics have crept into our vocabulary. These terms are quite distinct, but yet are interrelated. A control strategy is a basic philosophy or approach to pest control. A control tactic is a specific method or supporting technique required to carry out a basic strategy. These terms are interrelated in that a strategy may employ several tactics.

There are three basic strategies in pest control:

1. Prevention or eradication -- this strategy does not accept existence of pest and aims all tactics at prevention or destruction.

2. Containment -- this strategy accepts existence of non-economic densities of the pest and aims a tactic simply at prevention of economic losses.

3. Doing nothing -- this strategy accepts any pest density that might develop, thus relying entirely on natural control.

The latter, as a general strategy for management of all pests, clearly is unacceptable. The strategy of prevention, or even eradication, is wise in some situations; the latter mainly for recent arrivals that have not yet become widely established. The strategy of integrated pest management is basically that of containment.

Now let us consider how I.P.M. might relate to potato pests in general and to nematode pests in particular. Recent accounts of disease and pest aspects of potato protection list 3 bacteria, 20 fungi, 10 insects, and 13 nematodes species as major pests to potato production. In addition, depending upon locality, several weed species constitute severe constraints to potato production.

Pest control of potatoes is complicated and difficult, as the potato is vegetatively propagated using tubers for seed. Bacteria, fungi, viruses, nematodes, and certain insects are usually carried with seed tubers. Yet, much progress has been made in individual discipline approach to reducing to losses caused by specific pests. It is of interest to note reliance on similar pest control tactics. For example, crop rotations have been used to control practically all types of major pests such as nematodes, fungi, insects, bacteria and weeds. Yet little effort has been devoted to studying interrelationships of effective rotation schemes for one type of major pest on another type of major pest.

In the past decade, pest control of potatoes has relied heavily on pesticidal chemicals. Over 2 million pounds of insecticides, 4 million pounds of fungicides, 6 million pounds of herbicides, and significant amounts of nematicides are used annually on potatoes. The economy, recent changes in pesticide regulations, and environmentalists have dictated that alternative tactics to control pests of potatoes be sought that rely more on natural phenomena and less on synthetic compounds. Also the economy dictates that we must bring known pest control tactics together in an integrated system to control total pest problems.

Although we have sufficient knowledge and techniques for an integrated approach to managing pests of potatoes, we lack coordination of effort to realize totally integrated pest management.

The key components of pest are cultural practices or agro-ecosystems, manipulation, host resistance or genetic control, biological control, legal regulations, and limited usage of pesticides. To be effective, these components must be put together in an environmentally sound practice that provides efficient pest control.

All of these components are being utilized in an effort to manage <u>Globodera rostochiensis</u> of potatoes. The objective of this effort is

to manage population densities of G. rostochiensis at levels where spread is unlikely to occur. To be acceptable to potato growers an I.P.M. system must be developed that reduces pesticide usage and allows either monoculture of potatoes or potato culture at least one in 3 years. Such a system naturally relies heavily on genetic control or plant resistance to nematodes.

Research has shown that an integrated system utilizing resistant cultivars, non-host crops, and susceptible cultivars with chemical treatment (Aldicarb) will successfully damage densities of G. rostochiensis at desired levels. However, we do not know what effects such a system has on other nematodes such root lesion (Pratylenchus sp.) and root-knot (Meloidogyne sp.) or on other pests and diseases. We need to coordinate our efforts with scientists in other disciplines and make adjustments and trade-offs within the integrated system that will provide the most efficient control of the total pest situation.

We know, for example, that aldicarb has both nematicidal and insecticidal properties. Yet, there has been no coordinated studies on methods of application, dosage levels, and timing of application for effective control of both types of pests. More recently, we have found that the fungicide benomyl has nematicidal properties and coordinated efforts with plant pathologists are needed in the utilization of this compound in potato production.

Rotations have been used to control all major types of potato pests. Yet little effort has been made to studying effects of rotation schemes that control one type of pest on the control of other types of pests. Recent discovery of the glandular trichome type resistance in potato to a broad range of insects opens up yet a new approach to insects and certain virus disease control. Certain nematode, fungal and virus resistance have been combined in potato cultivars. There is a need to include insect resistance in this package. This can be realized only through coordinated efforts of plant breeders, entomologists, plant pathologists, and nematologists.

STUDIES OF THE INTERRELATIONSHIPS OF THE PLANT PARASITIC NEMATODES AND OTHER ORGANISMS ON POTATOES

Parviz Jatala

Studies on the interaction of important nematodes of potatoes and other organisms at CIP began in 1974 when the need was indicated. Since both the root-knot nematodes Meloidogyne species and Pseudomonas solanacearum often occur together in the warm regions and the field observations had indicated an apparent interaction between these organisms, studies were initiated to determine validity and the nature of such interaction. Pseudomonas resistant cultivar BR-73-40 (Solanum phureja x S. tuberosum subsp. tuberosum) and susceptible cultivar 'Renacimiento' (S. tuberosum subsp. andigena) were inoculated with various combinations and time sequences of inoculation by M. incognita and P. solanacearum race 3. Control plants did not receive either of the two organisms. Data on wilting were collected periodically. Results indicate that infection and wilt development by P. solanacearum is enhanced in the presence of M. incognita in both Pseudomonas resistant and susceptible cultivars. Resistance of BR-73-40 to bacterial wilt was broken when the root-knot nematodes were present. Mechanism of the synergism is believed to be that of mechanical wounding as well as physiological changes in the plants caused by infection of the root-knot nematodes.

To determine if the interaction also occurs under field condition both organisms were inoculated together or separate in a field consisting of small plots. Bacterial wilt susceptible cultivar 'Mariva' and resistant cultivars BR-73-40 and BR-63-76 were planted in these plots and data on wilting were taken periodically. Data indicated similar results to those of greenhouse studies. Resistance of cultivars BR-73-40 and BR-63-76 to P. solanacearum was broken in the presence of nematodes.

In other studies reaction of the root-knot immune and resistant breeding lines to infection by P. solanacearum was studied. Data indicate that root infection by nematodes as expressed by root galling index was directly correlated with bacterial symptoms as expressed by percent plant wilted (Table 1). Reaction of S. sparsipilum and S. chacoense (M. incognita immune and resistant clones, respectively) to P. solanacearum was directly correlated with their reaction to Meloidogyne.

Since P. solanacearum is occasionally found to infect plants in the Peruvian highlands where the potato cyst nematodes are widespread, interaction

Table 1.- Interrelationships of *Meloidogyne incognita* and *Pseudomonas solanacearum*, isolate 013 (race 3) on selected *Solanum* spp.

Treatment	Percent plant wilted		
	S. sparsipilum	*S. chacoense*	tbr. x adg. ctvr. 'Mariva'
Check	0	0	0
M. incognita	0 (0)*	0 (1.2)	0 (3)
P. solanacearum	0	5	45
Both organisms	13 (0)	30 (1.2)	83 (3)

* Number in parenthesis show reaction to nematode infection as based on root galling on a scale of:

0 = no root galling and/or nematode reproduction;

4 = very severe root galling and/or a very high nematode reproduction.

of these two organisms on the Pseudomonas resistant and susceptible cultivars was studied. Data indicated similar results to those obtained from the Meloidogyne - Pseudomonas interaction studies. However, the speed of interaction was not the same. Although there exist a synergism between P. solanacearum and Globodera pallida, the after effects were manifested at a much later stage than those obtained by Meloidogyne - Pseudomonas interaction.

In another interaction study depression of cyst nematode development was observed on plants inoculated simultaneously with G. pallida and with a fungus, either Phoma exigua, P. exigua var. nonoxydabilis, P. andinum sp. nov. or Colletrotrichum coccodes. No cyst infection by the fungi was noted in the cysts examined. Apparently, fungi used in this study infected roots in the presence of G. pallida, a factor which may have retarded nematode development.

The findings reported on the interaction of Meloidogyne and Pseudomonas on potatoes indicated the need for combining the resistances to these two organisms.