Potato Late Blight in Developing Countries

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Abstract

Potato is the fastest growing major crop in the developing world with important economic impact on many resource-poor farming families. Many factors limit production and profitability, with hundreds of millions of dollars spent yearly on fungicides alone, but little is known about direct losses, with experts agreeing that they are variable and frequently significant. Late blight is most severe in the mountainous areas of developing countries where weather conditions are favorable for disease. Variable topography and continuous production of potato and other late blight hosts, including tomato and in the Andes pear melon, make prediction of disease initiation or severity difficult.

New and potentially more aggressive pathogen populations have been introduced into Asia and both mating types are present in a number of Asian countries. There is not yet clear evidence for the role of sexual recombination or oospores in nature in Asia; nor has it been established that new populations have made disease management more difficult. However, this can probably be inferred from what has happened in Europe and the US. New populations exist in Latin America but A1 and A2 populations are generally separated geographically, except in Mexico where sexual recombination is common. Sub-Saharan Africa still has the US-1 population.

The social context is an important factor in late blight management in developing countries. Most farmers have no formal training in biology and view disease with a pre germ-theory perspective. Building capacity among farmers for making the right decisions about disease management is most effective if it includes basic information about biology and ecology. Farmers with little education also can not be expected to understand the intricacies of pesticide risk, and late blight control with fungicides is one component of an epidemic of pesticide poisoning and other chronic health problems currently plaguing the developing world.

Epidemiological studies in the tropics demonstrate some important differences in the way late blight develops from that of the temperate zone. In the tropics, particularly in the highlands, aerial inoculum is present most of the year from a number of sources. This makes sanitation activities (removal of cull piles and volunteer plants) of little apparent value in some parts of the developing world. In spite of the generalized importance of foliage blight in the developing world, tuber blight is apparently unimportant in many areas. The reasons for this are not clear.

Host plant resistance is the primary disease management strategy, and resistance is probably used more in developing countries. Many cultivars released as resistant have “gone down” as virulence was selected in the pathogen population. In contrast, resistance in some cultivars has held for decades. A gene from the wild species *Solanum bulbocastanum* has provided resistance against a number of pathogen populations and is currently being tested on a larger scale. Fungicides are used almost everywhere that late blight is a problem and fungicide use is increasing. Optimization of fungicides may be one of the best investments for short-term impact with resource poor farmers. Newly

available fungicides based on phosphite may provide economical and safer alternatives to fungicides currently used.

Introduction

To appreciate the importance of potato late blight in developing countries one needs to understand the role of this crop in the livelihoods of the rural poor. Production and consumption of potato are declining in industrialized countries, but just the opposite is happening in most developing countries. In the 1960s about 11 percent of all potatoes were produced in developing countries, while now the figure is over 30%. China now leads the world in potato production and area planted. Potato production and consumption are growing throughout the developing world, except in Andean countries where the potato has been a subsistence crop for millennia. In the developing world, growth in potato production is occurring in areas not commonly associated with the crop. For example, potato is the fastest growing major crop in the great lakes area of Uganda, Rwanda, Burundi and DR Congo, where it has increased by about 250% since the mid 1990's. In these areas, potatoes play an important role as both cash and subsistence crop for highland farmers.

Potato production in most developing countries is characterized by low yields. The national average yield in Ecuador is 12 T/ha; in parts of Sub-Saharan Africa it is even lower. In contrast, average yields in North America and Western Europe are over 40 T/ha (FAOSTAT data, 2006). One might be tempted to think that low yields in developing countries are due to poor growing conditions (poor soils, low temperatures, water stress), but this is not always the case. Simulation studies indicate that potential production in the highland tropics approaches 100 t/ha (Haverkort 1987). Although this is a simulated yield potential, yields attained at experimental stations, as well as on high-input farms, often exceed 50 t/ha (El-Bedewy *et al.* 2001). There is an enormous gap between national averages and attainable yields, which implies a tremendous potential for improving livelihoods through more profitable and sustainable production of the potato crop.

Many factors other than disease cause yield instability in developing countries, including low soil fertility, water stress and frost. However, diseases are important and late blight is considered the most important (Bisht *et al.* 1997; Fontem & Aighewi 1993; Haverkort & Bicamumpaka 1986; Higiro & Danial 1994; Khan *et al.* 1985). Because of the high spatial and temporal variability of late blight incidence and severity, there are no good estimates of direct losses in developing countries. Potential severity, which ignores the effect of interventions such as fungicide spraying, resistance and cultural controls, was estimated applying a GIS framework using late bight forecasting models (Hijmans *et al.* 2000). Output mapped as fungicide sprays per season needed to control the disease indicates potential severity was high for Northern Europe and the North-Eastern US, but also just as high in many developing areas, including the Andes, southern Brazil and parts of Sub-Saharan Africa (Figure 1).

Although the extent of direct losses is not known, frequent reports of severe losses support the general consensus of the importance of this disease. In a down-scaled replay of Ireland in the 1840's, late blight swept into Papua New Guinea (PNG) in 2003 and razed the crop. PNG had been one of the few remaining blight-free areas, so farmers did not use fungicides. With a susceptible local cultivar and weather conditions favorable to disease, most fields were completely destroyed. Since then, farmers have begun using fungicides and production has resumed.

Even where fungicides are used, continued wet spells often lead to major epidemics, as occurred for example in 2004 in Egypt[1] and 2006 in Northern Peru and Kashmir. Even when epidemic conditions are not widespread, farmers in developing countries may get behind on spraying and loose control of the disease. In one study in Ecuador designed to look at tuber diseases, 10 of the 122 fields selected at planting had to be dropped from the study because they were completely destroyed by blight (Oyarzún *et al.* 2005). The survey was done during the rainy period but it was not a particularly bad year for late blight.

Albeit sketchy, quantitative data do exist for the use of fungicides to control late blight in developing countries. The International Potato Center (CIP) estimated fungicide use in developing countries at $750 million (Anonymous 1997). This figure is now outdated and therefore is certainly very conservative since access to and use of fungicides has increased in the last decade. Case studies in developing countries indicated that most applications on potato are for control of late blight (Crissman *et al.* 1998; Ortiz *et al.* 2001).

Biophysical context

Highly variable landscape. In highly diversified agricultural systems of the tropics, potatoes may be found anywhere between 1000 and 3800 meters above see level, but typically they are found above 2000 m. Production in mountains leads to high spatial diversity for many factors, but one of the most important is temperature. In areas were potatoes are commonly grown in the Northern Andes (2800-3400 m) daily average temperatures are fairly constant during the year but range from between 9 and 12°C depending on altitude (Figure 2). Temperature is a strong driving factor for late blight so the temperature gradient linked to altitude quickly translates in the minds of farmers into a gradient of late blight severity. Since temperatures are generally below the optimum for blight development in this environment (Andrade-Piedra *et al.* 2005c; Grünwald *et al.* 2000), the more one descends down the mountain, the more severe the disease. In the highland tropics late blight is not the disease of cool wet conditions (as in the temperate zone) but rather of warm wet conditions, i.e., on the lower slopes or valley bottoms. Because of the lower temperatures in the highland tropics, late blight epidemics generally progress more slowly than in the temperate zone. Evaluating disease progress using disease simulation contrasting historic temperature data from tropical and temperate environments consistently shows that disease development is faster for temperate zones (Figure 3). Both the stability of temperature throughout the year and the diversity of temperature at different altitudes have implications for disease epidemiology and management in the tropics.

Potato production in many highland tropical areas is year-round, with variations in the amount planted generally following local rainfall patterns and prevailing prices. The highland tropics are also the home of several alternative hosts for *P. infestans,* including tomato and pear melon (*S. muricatum*). These hosts overlap geographically with potato

[1] These epidemics are described in more detail in the Web page of the Global Initiative on Late Blight (GILB), http://gilb.cip.cgiar.org/index.php .

and provide additional opportunities for pathogen survival and reproduction. Wild *solanaceous* hosts may grow in humid areas and thereby support pathogen growth during drier periods (Chacón *et al.* 2006).

The Pathogen and its population dynamics. A number of reviews have been written on the biology of *Phytophthora infestans*, the pathogen causing late blight of potato and tomato. All of these, including a recent one (Forbes & Landeo 2006) have given detailed descriptions of the biology of the pathogen. This information will not be repeated here except to briefly mention that *P. infestans* is an oomycete pathogen like downy mildews and shares the important characteristics of that class of organisms, including asexual propagation via sporangia that may infect directly or give rise to infectious zoospores and sexual reproduction via oospores. Two compatibility types A1 and A2, generally referred to as mating types, must be present for sexual reproduction.

Based on reports in the literature, one can get a fairly general idea of the genetic structure of the pathogen population in most parts of the developing world, although in some cases basically all that is known is that the population is not simple. Nonetheless there are still rather large areas where the population is thought to be simple (one or a few clonal lineages), and this includes most of South America and sub-Saharan Africa. The population attacking potato in South America is made up of 3 geographically isolated clonal lineages: EC-1 in the central and northern Andes, BR-1 in Brazil and the eastern southern cone and US-1 in Chile (Brommonschenkel 1988; Deahl *et al.* 2003; Forbes *et al.* 1997; Fry & Goodwin 1995; Oyarzun *et al.* 1998; Perez *et al.* 2001; Reis *et al.* 2003; Rivera *et al.* 2002). Similarly the population attacking potato in sub-Saharan Africa appears to be even more simple, being composed of just one clonal lineage, US-1 (McLeod *et al.* 2001; Vega-Sanchez *et al.* 2000).

In Asia the situation is more complex. Recent or relatively recent surveys have demonstrated the presence of both A1 and A2 genotypes in several countries, including China, India, Indonesia, Japan, Korea, Nepal, Pakistan and Thailand. (Ahmad *et al.* 2002; Ghimire *et al.* 2003; Gotoh *et al.* 2005; Kato *et al.* 1992; Koh *et al.* 1994; Nishimura *et al.* 1999; Singh & Shekhawat 1999). Other studies have found only A1 mating types in certain countries, such as Bangladesh, Sri Lanka, Philippines, Taiwan and Vietnam (Hossain *et al.* 2002; Nishimura *et al.* 1999; Somanchandra 2000), although one wonders if A2 populations have not spread from neighboring countries since these studies were done. Apparently only A1 mating types are found in Vietnam, although little more is known of the population (A. Hermensen, personal communication). There is as yet no clear evidence for the role of sexual recombination or oospores in nature in Asia; nor has it been established that new populations have made disease management more difficult. However, this can probably be inferred by what has happened in Europe and the US.

In contrast to all other developing countries, in the central highlands of Mexico the population of *P. infestans* is clearly sexual and genotypic diversity is high (Flier *et al.* 2003; Grunwald & Flier 2005; Grünwald *et al.* 2001).

If one looks beyond potato to other hosts of *P. infestans*, such as tomato, then the situation is different. In many parts of the developing world it is assumed that the US-1 lineage was dominant, if not exclusive, on potato and tomato and has since been replaced by introduced clonal lineages or sexual populations (Goodwin *et al.* 1994). It would appear, however, that the US-1 lineage was not replaced on tomato in most areas. US-1 is still the primary population on tomato in the central Andes (Oyarzun *et al.* 1998), Brazil (Reis *et al.* 2005) and at least parts of Asia (Ghimire *et al.* 2003). US-1 is also dominant on tomato in sub-Saharan Africa where there are two sub-lineages of US-1, one adapted to potato and the other to tomato (Vega-Sanchez *et al.* 2000).

The significance of the pathogen population structure for disease management is a subject of debate and, as noted, there is no clear evidence how this factor has affected late blight severity in developing countries. Nonetheless, there is circumstantial evidence that disease in sub-Saharan Africa is controlled with fewer sprays than in environmentally similar locations in the Andes. This type of empirical assessment is fraught with unknowns. The apparent differences in fungicide use may in part be due to differences in pathogen populations, but they could also reflect differences in the relative levels of resistance of the respective cultivars, unknown climate differences or even variation in the efficacy of fungicide products used. To make a more realistic comparison between Africa and the Andes, CIP and national partners are gathering field data with similar cultivars that will then be compared using disease simulation.

Considerable emphasis has been placed on the distribution of the A1 and A2 mating types of *P. infestans*, both in the developing countries and in the North, but the effects of sexual reproduction and oospore production are not clear and may be site specific. Apparently, oospores act as sources of initial inoculum in Scandinavia (Dahlberg *et al.* 2002), but there is little evidence of this occurring elsewhere, except perhaps in Mexico (Fernández-Pavía *et al.* 2004; Fernández-Pavía *et al.* 2002; Flier *et al.* 2001). For example, oospores may affect disease management as primary inoculum where disease is seasonal, but may have little affect where potato production is continuous and initial inoculum comes from foliar infection in neighboring or nearby fields.

The presence of isolates of both mating types does not necessarily imply a sexually reproducing population. In some countries there is only one clonal lineage (one mating type) and high host-specificity (Oyarzun *et al.* 1998) while in others countries both mating types are present, but the population also has a clonal structure and is highly host-specific (Suassuna *et al.* 2004) (Table 1). High host specificity is a “barrier” to sexual reproduction when A1 and A2 genotypes are restricted to different hosts, and post-reproductive barriers can also exist (Oliva *et al.* 2002). In the case of US-1 (A1) and BR-1 (A2) isolates from Brazil, recent data gathered from several crosses revealed extremely low viability and germination. Low oospore fertility may be another factor preventing the establishment of a recombining population (Santa Cruz & Mizubuti, unpublished data).

If genetic recombination leads to increased variability and increased potential for ecological adaptation, this may change disease dynamics. Ecological conditions affect distinct stages of the life cycle of *P. infestans*, influencing late blight development. There is a considerable amount of data on the ecological requirements of *P. infestans* generated in temperate climates but information about environmental effects on late blight development in subtropical and tropical areas is limited. Ecological adaptation occurs and it would be reasonable to assume that the different stages of the pathogen life cycle could have developed different ecological requirements in warmer regions. At present, the strongest evidence points to the origins of *P. infestans* in the tropical highlands, making more plausible its adaptation to lowland areas or hot summer seasons. This is an interesting aspect of population biology that needs to be investigated.

When quantifying the effects of temperature on basic epidemiological components in Brazil, major differences were detected between isolates of a lineage that infects potato (BR-1) and those of a lineage that are adapted to tomato (US-1) (Mizubuti *et al.* 2002). Interestingly, there were differences in weather requirements between isolates of the same lineage depending on their origin; US-1 isolates from Brazil seem to be more tolerant to higher temperatures than those of the US-1 isolates from Northeast United States (Mizubuti & Fry 1998). These differences can affect the applicability of forecast systems and simulators. For instance, in a low altitude region (650 meters above sea level - masl) where US-1 isolates predominate, no late blight epidemics developed on potatoes during the summer, nevertheless all forecast systems evaluated Batista *et al*. (2006) (BLITECAST, SIMCAST, NegFry, and Wallin) recommended fungicide sprays. Adjusting for differential ecological responses of the pathogen genotypes may be required for better late blight management in tropical and subtropical areas.

In addition to temperature, topographical features can affect survival of sporangia exposed to solar radiation. At higher altitudes, UV irradiance is higher and its effect on viability of pathogen propagules is more deleterious. The half-life of *P. infestans* sporangia at lower altitudes was estimated around 30 minutes (Mizubuti *et al.* 2000) while at highland tropics (2600 masl) the half-life was about 20 minutes (Belmar and Grünwald, unpubl.; Figure 4). Higher sporangia mortality combined with lower average temperatures in highland tropics would result in lower disease progress rates, but the lower rate of potato development extends the time for the host-pathogen interaction, which in turn leads to longer epidemics. Temperature should be considered when planning fungicide usage, because some products seem to have higher efficiency at lower temperatures (Mayton *et al.* 2001).

Virulence in the pathogen population is a characteristic that attracts significant attention in the literature, but for several reasons it appears that race-specific resistance has not been an important factor in disease management. Potato has a very low multiplication rate, and specialized seed systems are virtually nonexistent in developing countries. For these reasons, cultivar turnaround is slow. A new cultivar takes many years to increase its proportion of yearly production so deployment of resistance based on changing cultivars is impractical. Furthermore, virulence in the pathogen seems to be a highly variable characteristic. Studies have shown that virulence is selected quickly in populations (Goodwin *et al.* 1995; Sujkowski *et al.* 1996) and there would appear to be little or no cost to the pathogen for loss of avirulence. Populations with very complex virulence structures are found where the main cultivars have few or no known major R genes (Derie & Inglis 2001; Forbes *et al.* 1997; Peters *et al.* 1998; Shattock *et al.* 1977). After workers in Canada found that the pathogen population had many “unnecessary” virulence factors, they concluded that race-specific resistance would not work (Peters *et al.* 1998). This observation could be correct for most parts of the world as a large number of cultivars released with resistance have quickly succumbed to virulent populations (Forbes & Jarvis 1994), and we know of no published records of major R genes that have protected a widely planted cultivar. Overall, race specific resistance in this pathosystem is a phenomenon of striking effect in breeders’ plots, but of little consequence in farmers’ fields.

Social context

One common characteristic of most small potato producers in developing countries is that they know very little about the processes which cause plant disease. Farmers know much about biological entities they can see, such as crops and animals, less about insects - some stages of which they don’t see- and almost nothing about microorganisms (Ortiz *et al.* 2003; Trutmann *et al.* 1993). For that reason, the common answers to the question of “what causes blight” will be anything but correct: lightening, low temperature, rain, sun while it rains, stages of the moon, bad seed, or mystical explanations (Ortiz *et al.* 2003). The historical association between potato late blight and the emergence of the germ theory lives on in developing countries as agricultural science has had little impact on the knowledge of rural people.

The lack of knowledge about basic aspects of the disease itself makes it difficult to simply teach farmers how to manage fungicides or other technologies. For that reason, workers in developing countries have been using knowledge-intensive, participatory techniques to help farmers increase their understanding of how disease occurs and how it can be managed. A number of competencies have been identified for a farmer in a developing country to manage late blight efficiently: correct identification of the disease, correct identification of weather conditions conducive to the disease and basic understanding of the life cycle of *P. infestans*; adequate selection of potato varieties; adequate use of chemical control; and frequent scouting of the plot (J. Andrade-Piedra and G.A. Forbes, *unpublished data*). One study showed that Bolivian farmers could greatly improve disease control (and income) after training in the use of fungicides, without necessarily increasing the amount of fungicide used (Thiele *et al.* 1998). The role of farmer training in late blight management in developing countries was covered in another review (Nelson *et al.* 2001).

The limited knowledge that resource-poor farmers have about pesticides, together with other factors, has led to an epidemic of pesticide poisonings and other chronic health problems in the developing world. The Food and Agriculture Organization (FAO)[2] produced an International Code of Conduct on the Distribution and Use of Pesticides. Based on this code, highly toxic pesticide (Class-I, WHO system) should be banned, because necessary protective clothing is cumbersome, expensive and almost never used (Eddleston *et al.* 2002; Wesseling *et al.* 2005). The most recent version of the code promotes corporate responsibility in pesticide trade but we have not been able to find documented examples where the industry willingly removed hazardous pesticides from a market. While the majority of dangerous pesticides are not fungicides, three important late blight fungicides (mancozeb, maneb and chorothalonil) were recently included in a list of pesticides considered to be dangerous to developing country farmers (Wesseling *et al.* 2005). The increasing number of technical and development workers decrying the current pesticide crises in developing countries concurs that in addition to effective regulation, integrated pest management and natural pest control methods are required.

Epidemiological considerations

In many parts of the world, initial inoculum from focal sources contributes to epidemics. Infected tubers, cull piles next to fields, or volunteer plants are potential sources from where inoculum could spread from within or to potato fields (Zwankhuizen *et al.* 1998). Where a recombinant population is present, oospores can serve as primary inoculum (Fernández-Pavía *et al.* 2004; Lehtinen & Hannukkala 2004; Strömberg *et al.* 1999) and also as an over-wintering structure (Turkensteen *et al.* 2000). In Mexico, oospores are formed in all types of potato tissues including tubers (Fernández-Pavía *et al.* 2004), stems and foliage [Flier, 2001 #7950], in both wild and domesticated *Solanum* species. Preliminary data suggest that oospores can indeed serve as a source of primary infection under field conditions (Fig. N3).

[2] Anonymous, 2003. *International Code of Conduct on the Distribution and Use of Pesticides (Revised Version)*. Food and Agriculture Organization of the United Nations

Reduction of these sources of initial inoculum can reduce the initial amount of disease or delay disease initiation. Thus, management strategies based on sanitation (removal of cull piles, elimination of volunteer plants, etc.) and the use of healthy seed tubers can improve disease control in many developing countries. Mexico is an example of an area where sanitation can be effective in reducing initial inoculum. In central Mexico potatoes are grown solely in summer during the rainy season; the winter includes many days with frost (Grünwald *et al.* 2002; Grünwald *et al.* 2000)]. Epidemics begin as soon as the rainy season starts and potato foliage is available. In this case, the epidemic might be initiated by a combination of asexual inoculum from cull piles and sexual inoculum from oospores (Fig. N3), but in either case the inoculum is thought to come from specific sources where the pathogen has over-wintered.

In contrast to the scenario above, in many highland tropical locations seasonal epidemics do not initiate from over-wintering inoculum sources but rather disease intensity increases and decreases throughout the year with alternating wet and dry periods. High levels of infection from aerial inoculum occur as soon as rainy seasons begin, presumably coming from a number of locations where disease continues at low levels even during the dry seasons. These locations are humid refugia where micro climates maintain disease at low levels, either on cultivated or wild hosts. In many highland tropical areas, rain patterns are variable and it is easy to find areas wet enough for blight to occur at any time in the year. Because of the presence of disease throughout the year, potato plants get infected in early stages of development, often at or just after emergence, and the spatial pattern of early infections in diseased fields is frequently uniform (Garrett *et al.* 2001). It is assumed that early, non-focal infection occurs in fields because aerial inoculum originating from multiple non-point sources is deposited throughout the field. In these areas, presumably, the contribution of sanitation at the field or farm level is less important for disease management because high levels of inoculum come from other cultivated or wild solanaceous hosts in the surrounding areas.

Based on these premises and to better understand inoculum dynamics in a low altitude region (650 masl) of a tropical country, recent work was carried by Lima et al. (2005) aimed at quantifying survival of *P. infestans* in infected tomato plant parts and the availability of aerial inoculum. The pathogen survived for only up to 35 days. Sporangia in the air, monitored with Rotorod and Burkard spore traps that operated year round, could be detected almost every week. Sporangia were captured by the Burkard and Rotorod spore traps in 41 of 53 and in 42 of 46 sampled weeks, respectively (Figure 5). The greatest numbers of airborne sporangia were detected from March to July. Most airborne inoculum captured with the Burkard trap were detected between 6:00 and 18:00 h. Airborne inoculum is abundant and is likely to be much more important to late blight outbreaks than inoculum originating from crop debris.

Because of the risk of early infection, initial protection with fungicides is critical. In spite of this, early spraying is difficult. Plant emergence is notoriously irregular in developing countries for a number of reasons but primarily because seed is of variable physiological development and poor sanitary quality. Farmers generally wait for a significant portion of plants to emerge and by this time many plants have been exposed to inoculum. To combat this situation, late blight management strategies recommend a first spray of systemic compounds (Fernández-Northcote *et al.* 2000), but this has only partial effect as most systemic compounds today will constrain but not eradicate existing lesions. As another approach to solving the problem of early protection, researchers have treated seed with systemic fungicides prior to planting, but this generally does not protect plants after emergence (Kirk *et al.* 1999; Powelson & Inglis 1999). Recently, however, researchers in Argentina were able to control blight in plants until 40 days after emergence by treating seeds with a formulation of the systemic compound iprovalicarb. They attributed the control to the fact that they treated freshly cut, non-suberized, tubers and to the characteristics of the compound (Andreu & Caldiz 2005).

In spite of the importance of foliar late blight in many highland tropical areas, there is little evidence that tuber blight is important. There is a paucity of research that would either support or disprove the importance of tuber blight, but the fact that most national programs in developing countries do not work on this problem is an indication that it is perceived as not being important. There is at least one reason why tuber blight could occur in the highland tropics but go unnoticed. Potatoes are grown year-round and potato crops at any stage of development may be found in adjacent fields. Potatoes are harvested at all times of the year, so ware potatoes are not stored, but rather sold to consumers immediately after harvest. Rotted or abnormal tubers are culled during harvest. Small or latent infections caused by *P. infestans* on tubers would probably not have time to develop into a perceivable problem. Seed potatoes are stored in the highland tropics, but in small quantities for domestic use or sale to neighbors. Seed rot occurs, but farmers simply check seed stocks periodically and discard rotted seed. Hypothetically, tuber blight could be part of the tuber rot complex.

Nonetheless, what little research that has been done would indicate that tuber blight incidence is low, although the reasons are not clear. A recent study in Ecuador found that infected tubers were generally fewer than 0.1% (Oyarzún *et al.* 2005) and it appears to be a minimal problem in the Toluca Valley of Mexico (Torres & Garcia E 1992), where foliage blight is severe. Other reports on tuber blight in Mexico show ranges of 0-15% tuber infection (see Grünwald & Flier 2005 for a discussion). Given the apparent low frequency of infected tubers, there is little reason to assume that tubers play an important role in as a source of initial inoculum. And, as was noted above, many fields are planted when blight is already present and the relative role of aerial inoculum would seem much more significant.

Managing late blight in developing countries

Resistance. For a polycyclic disease such as late blight, the rate of disease progress determines the increase in severity and reducing this rate is the main goal for disease management. Of all the tactics that one might consider, the two most widely used, and arguably the most effective, are host resistance and fungicides. The contribution of host resistance to slowing disease progress can be large and for that reason resistance should be the principal approach for effective late blight management in the developing countries. Comparative analyses of late blight intensity on susceptible cultivar Alpha and resistant cultivar Norteña illustrates how effective a resistant cultivar can be. At 40 days after emergence, disease severity was 100% and 4% in Alpha and Norteña, respectively (Grünwald *et al.* 2000). The partial resistance of these and several other Mexican cultivars was found to be durable over a period of 40 years under Mexican growing conditions exposed to a sexual pathogen population (Grünwald et al. 2002).

Host resistance is probably used more in developing countries than in the industrialized countries (Forbes & Jarvis 1994), and there are numerous potato cultivars with measurable levels (some high) of resistance to late blight that are now part of production systems in different parts of the world (Table 2). Nonetheless, many susceptible cultivars are still being grown and there are cultural and economic factors that can restrict adoption of new, resistant ones (Walker *et al.* 1999). Cultivar change occurs more readily in less developed economies, so development workers are now in a window of opportunity that closes as markets become more specialized. To facilitate cultivar adoption, participatory plant breeding and selection is now being used by breeding programs in developing countries (Walker *et al.* 2003).

Fungicides. Because of the still-limited use of host resistance, fungicide use is the most widely-used measure for late blight control. Despite the fact that its use increases production costs and has negative consequences for environment and human health, the efficacy of fungicides is appealing to resource-poor farmers and fungicide use is a common practice in almost all developing countries. Nonetheless, there are numerous steps that can be taken to improve or optimize fungicide use. Here optimization is intended as the most cost-effective use of a fungicide to produce a healthy crop with the least impact to environment and human health. Optimization may result in an increase in fungicide use, but it is more likely to lead to a reduction. Ways in which fungicide use may be optimized include some decisions made prior to application, including selection of an appropriate compound, dosage, and application technology (in almost all cases the latter refers to optimum use of a backpack sprayer). Once these decisions have been made, fungicide timing may be the greatest challenge facing farmers in developing countries.

Each of these general areas of optimization involves several alternatives, but most resource-poor farmers lack knowledge about the "what, when, how and how much" of fungicide spraying. For example, most do not know the difference between a contact and systemic fungicide, and many do not know the difference between a fungicide and an insecticide (Ortiz *et al.* 2001). Farmers often mix two fungicides with the same active ingredient, or make mixtures that virtually double the effective dosage. The primary source of information for most of these farmers is the pesticide dealer (Crissman *et al.* 1998; Ortiz *et al.* 2001). Fungicide timing recommendations from pesticide vendors frequently involve broad indications, such as “every 5-10 days”. These are sometimes qualified with vague criteria such as “spray every week if weather is favorable for blight, otherwise spray every 2 weeks”. Unfortunately, farmers often find out too late that weather was favorable for blight.

Decision support systems (DSS) exist that can help optimize fungicide timing. Optimization can result in a reduction of fungicide used or a greater disease control efficacy per unit of fungicide (Thiele *et al.* 1998). Unfortunately most DSS for control of potato late blight were developed in the temperate zone (USA, Europe, Australia) and are inappropriate for developing countries as they rely on computers and weather data loggers, neither of which is available to most resource-poor farmers. Nonetheless, there are some examples of computer-based DSS being used, or at least tested, in developing countries. Severity values of Blitecast were adjusted for use in Morocco (Sedegui *et al.* 1999) and a potato late blight forecast system, JHULSACAST, was developed for Western Uttar Pradesh, India (Singh *et al.* 2000). The fungicide forecast system SimCast, developed for temperate upstate New York, was adapted and validated for the highlands of central Mexico (Grünwald *et al.* 2002; Grünwald *et al.* 2000). In this work, the main environmental variable responsible for making spray advisories under tropical highland conditions in the Toluca valley was precipitation. Relying exclusively on precipitation in making spray advisories would have resulted in the same number of sprays as were actually forecast in the full model. Thus, the authors concluded that the possibility exists of developing a spray advisory system for resource-poor farmers relying solely on use of inexpensive rain gauges.

The International Potato Center and some researchers in Bolivia (Fernández-Northcote *et al.* 1998/1999; Parker & Navia 1991) have been working on the development of DSS in Latin America, but these tools have primarily been designed for local conditions. They have not been validated under widely varying growing conditions, nor have they been tested with a range of cultivars differing in resistance or time until physiological maturity. For these reasons, the vast majority of potato farmers in developing countries do not have clear guidelines for fungicide timing in the control of potato late blight and most farmers opt for calendar spraying (Ortiz *et al.* 2001). Adapting DSS to potential changes in climate may pose additional challenges (Garrett *et al.* 2006).

Host diversity. Another tactic that can reduce the rate of disease increase is the use of mixtures of plant genotypes, either mixtures of different potato genotypes, or different crops (e.g., potato and faba bean). Experiments have been done in both the temperate zone (Europe and the US) and in highland tropics (Ecuador and Peru). A recent field study in Peru, Ecuador and the US showed that the magnitude of the benefit of host diversity for reduced disease is correlated with the likely level of outside inoculum (Figure 6) and the difference in resistance between the components of the mixture (Garrett *et al.* 2001, Garrett *et al.* in review). The relative effect of host diversity will be more noticeable if the susceptible cultivar is mixed with a highly resistant cultivar. The suppressive effect of host diversity may also depend on the overall level of disease severity (Pilet *et al.* 2006). Further research on host diversity is needed to determine whether it is a potential tool for disease management in the highland tropics and how it may most effectively be combined with other management techniques.

Avoidance. One way many developing country farmers have learned to reduce initial inoculum is to avoid the disease (Thurston 1990) by choosing locations or times to plant in which they avoid heavy late blight pressure. These times and places have low levels of initial inoculum and the weather conditions are often not conducive to infection. Generally, there is a trade-off when farmers avoid late blight in this manner as yield potential is sacrificed to drought or threatened by frost. For example, in some highland parts of Ethiopia and Ecuador, farmers plant in the dry season when sources of inoculum are scarce and late blight is easy to manage, however, potato yields are very low because of insufficient soil moisture.

There are examples of how farmers have used planting date to avoid early infection and thereby reduce the duration of the epidemic. In the northwestern plains of India, late blight epidemics usually start after the second week of November. A series of field experiments were carried out to determine the effect of planting date — by changing planting date, plants can escape disease (the host is susceptible and the pathogen is present, but environmental conditions are not optimal). On average, planting in the last 10 days of September resulted in less severe late blight epidemics (Arora *et al.* 1999; Sekhon & Sokhi 1999). Similarly, potato planted early in the highlands of Mexico before the onset of the rainy season escaped late blight.

Avoidance has been an important tactic of traditional agriculture. One clear phenomenon associated with the advent of chemical fungicides, and to a lesser extent host resistance, has been the movement of potato production into areas or times of the year when blight is more severe to take advantage of increased yield potential. The introduction of resistant cultivars into Sub-Saharan Africa resulted in the planting of potatoes in wet, as well as dry seasons. This, in turn, led to year-round potato production and year-round inoculum production, which exacerbated the disease problem (Turkensteen 1988).

Silver bullets. Since the discovery of the R-genes with large effects from *Solanum demissum*, researchers have dreamed of finding a single solution to blight. More recently, the quest for simple solutions has been in the realm of biotechnology, so that the late blight silver bullets could become value added to existing cultivars that are entrenched in particular markets. To date, we are unaware of any single-pronged solutions that have given sustained protection, neither resistance genes (from potato or other sources) nor highly specific and effective fungicides (such as the phenylamides). The most recent candidate silver bullet is the resistance conferred by R-genes from *Solanum bulbocastanum*, which has held up against all the isolates against which it was tested (Song *et al.* 2003; TaeHo *et al.* 2005). These genes, nonetheless, are very similar in structure to other R-genes and their durability in farmers' fields has not yet been demonstrated.

Conclusions

Three points are of primary concern when evaluating the current scenario on late blight management in the developing countries. First, fungicides are widely used but there is great variability in usage patterns, even within a small geographic area. Second, cultivar resistance should be more commonly utilized. Third, farmer education is crucial for better management of late blight.

On a short-term basis, optimization of fungicides should be considered as the most likely successful management practice. Growers in the developing countries are used to managing the disease almost solely based on fungicide applications, but in many situations irrational use of chemicals results in serious economic, health and environmental problems. Epidemiological research should be fostered in the developing countries to optimize fungicide usage without compromising profit. Health concerns should also take precedence, although this is more of an issue for insecticides, it can also impact fungicide usage. The upsurge in research on the use of generic phosphite-based fungicides may lead to economically viable fungicide strategies that pose little risk to human health.

The use of resistant cultivars can benefit all types of growers – from subsistence farmers to large businesses normally associated with the chip industry. Nevertheless, one would expect that what all growers, regardless of type, would like to have is a resistant cultivar with excellent commercial features. Certainly, this constitutes a challenging issue that breeders have to face if expanded usage of resistance is to be achieved.

Finally, efficient late blight management in a near future can only be achieved with effective farmers' education as a foundation. The lack of knowledge about plant diseases and limited education levels of farmers in developing countries impose major constraints on the understanding of plant disease management. Technology transfer and implementation are not easily accomplished. Thus, educational programs aiming at better late blight management in the developing countries should be a priority for funding agencies and research institutions.

Table 1. Distribution of A1 and A2 mating types and *Phytophthora infestans* population structure in some developing countries

Region	**Country**	**Population**	
Africa			
	Ethiopia, Kenya, Uganda	A1, clonal, host specific	(Schiessendoppler & Molnar 2002)
	Morroco	A1+ A2	(El-Korany 1994; Sedegui *et al.* 2000)
	South Africa	A1, clonal	(McLeod *et al.* 2001)
Asia			
	China, India, Indonesia, Japan, Korea, Nepal, Pakistan and Thailand.	A1 + A2	(Ahmad *et al.* 2002; Ghimire *et al.* 2003; Gotoh *et al.* 2005; Kato *et al.* 1992; Koh *et al.* 1994; Nishimura *et al.* 1999; Singh & Shekhawat 1999).
	Bangladesh, Sri Lanka, Philippines and Taiwan	A1	(Hossain *et al.* 2002; Nishimura *et al.* 1999; Somanchandra 2000)
	Russia	clonal (Siberia) recombinant (near Moscow)	(Elansky *et al.* 2001)
Latin America			
	Argentina, Brazil, Paraguay,Uruguay	A1+A2, clonal, host specific	(Brommonschenkel 1988; Deahl *et al.* 2003; Reis *et al.* 2003)
	Bolivia	A2, clonal, host specific	(Goodwin *et al.* 1994)
	Chile, Ecuador, Peru**,**	A1 clonal, host specific	(Forbes *et al.* 1997; Perez *et al.* 2001; Rivera *et al.* 2002)
	Colombia, Costa Rica, Honduras, Panama, Venezuela	A1 clonal	(Gualtero Cuellar & Garcia Dominguez 1998; Paez *et al.* 2002; Rodriguez 2001)
	Mexico	A1 & A2, sexual	(Grünwald & Flier 2005; Grünwald *et al.* 2001) (Flier *et al.* 2003)

Table 2. Late blight resistant varieties released in developing countries

Region	Country	CIP number	Local name
South and Central America			
	México	NA	Norteña
		575049	Moserrat
		720054	Tollocan
		720044	Sangema (Rosita)
	Bolivia	385240.2	Chaposa
	Colombia		Monserrate
		382119.20	Unnamed
	Costa Rica	386040.9	Birris
		386056.7	Floresta
	Ecuador	NA	Santa Catalina
		384638.1	INIAP-Sta. Rita
		388790.24	INIAP-Fripapa
		382119.20 B	INIAP-Rosita
		388749.3	INIAP-Margarita
	Guatemala	382170.101	ICTA Xalapan
	Panamá	381381.13	IDIAP 92
		381390.30	IDIAFRIT
		382171.10	PRECODEPA
	Perú	384866.5	Amarilis-INIA
		377744.1	Kori-INIA
		380496.6	Chagllina-INIA
		376180.6	Atahualpa
		384688.2	Chota-Roja UNHEVAL
		377740.2	INIA-Chota
	Venezuela	380013.2	Andina
Sub-Saharan Africa	Burundi	381381.9	Rukinzo
		381381.26	Ingabire
		382147.18	Jubile
	Cameroon	381381.13	Cipira
		381406.6	Tubira
	Ethiopía	378501.16	Sissay
	Kenya	381381.13	Tigoni
		381381.20	Asante
	Rwanda	381381.3	Nderera
		381395.1	Ngunda
		382120.14	Kigega
		383140.6	Mugogo
		386003.2	Mizero

	387233.24	Gikungu
Uganda	381379.9	Kisoro
	381381.20	Victoria
Zaire	378699.2	Kinigi
	380583.8	Baseko
	380606.6	Enfula
	386022.22	Nurula

Figure 1. Map depicting global zonation of potato production zones based on predicted number of protectant fungicide sprays needed to control late blight. Predictions based on Blitecast, a late blight forecasting model, run within a geographic information system.

Figure 2. Relationship between average daily temperature and altitude in the highlands of Ecuador.

Figure 3. Comparison of simulated disease increase curves using simulated temperature data from three places in the tropical zone located at 2600, 3000, and 3400 m above sea level., and one place in the temperate zone located at 319 m above sea level. The simulated temperatures for the tropical places were obtained with the equation *temperature = 25.3358 - 0.0047 x altitude*, and for the temperate place from Andrade-Piedra et al. (Andrade-Piedra *et al.* 2005b). Simulated disease increase curves were obtained using the LB2004 version of LATEBLIGHT (Andrade-Piedra *et al.* 2005a; Andrade-Piedra *et al.* 2005c). All simulated epidemics started with 1000 sporangia per square m of ground at one day after emergence and the parameters for the host-pathogen interaction were those of the potato cv. 'Amarilis' and the EC-1 clonal lineage of *Phytophthora infestans* (Andrade-Piedra *et al.* 2005c). The mean daily period with relative humidity above 90% was 18 h in all cases.

Figure 4. Survival of sporangium of *Phytophthora infestans* exposed to direct sunlight at Freeville, NY ( ) and Metepec, Mexico ( ).

Figure 5. Number of sporangia of *Phytophthora infestans* captured in Burkard (A) and Rotorod (B) samplers installed in Viçosa, Minas Gerais, Brazil (650 meters above sea level), a tomato growing region. Data are cumulative weekly number of sporangia.

Figure 6. Relationship between relative mixture response (RMR) and increasing levels of outside inoculum, where outside inoculum levels were predicted to be higher for longer time periods of potato production and greater regional potato acreage. The RMR is defined here as the ratio of disease severity in a mixture over the weighted mean severity for the cultivars composing the mixture when grown in single genotype stands. When the RMR equals one, there is no effect on disease of mixing the cultivars, when the RMR is less than one there is a benefit, and when the RMR is greater than one there is a detriment (from Garrett and Mundt 2000, Garrett *et al.* 2001, and Garrett et al. in review).

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