International Potato Disease Resea

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The potato, a nutritious and wholesome food, is one of man's major food crops, exceeded in terms of total world production only by wheat, rice, and maize. The potato was restricted to the Andean highlands of South America until introduced into Europe by the Spanish in the 16th century and thus is a relative newcomer among major food crops. The greatest center of diversity for potatoes is near Lake Titicaca on the boundary of Peru and Bolivia. This region is believed to be the center of origin for cultivated potatoes. Representations of potatoes in pottery and chuno (freeze-dried potatoes) found in graves in Peru give a clear archeological record for potatoes going back to 400 B.C.

00191-2917/80/03025206/$03.00/0

Some understanding of the Andean potato agroecosystems that have been developing for over 2,000 yr is useful for the design of successful disease control systems for potatoes. For centuries, disease and other pests were controlled in the Andes by natural and cultural methods; only in the last few decades have pesticides become an important component.

Andean Potato Agroecosystem

The potato ecosystem is highly complex, perhaps more so in the Andes than anywhere else in the world. For example, in Peru the potato is grown from sea level on the coast to elevations of 4,300 m. There are 10 cultivated *Solanum* spp. in the Andes, where potatoes are grown on a wide variety of soils, with and without irrigation, as an extensive monoculture, and as a highly variable mixed population. Elsewhere in the world, only one subspecies of the potato, *Solanum tuberosum* spp. *tuberosum*, is grown. According to Brush (1), there are more than 2,000 named potato cultivars in Peru. In one isolated community he

Staff member of the International Potato Center consulting with Mexican potato farmers about late blight (*Phytophthora infestans*).

:h for Developing Countries

studied in northern Peru, the traditional farmers can identify some 50 cultivars. The potato collection of CIP (Centro Internacional de Papa, International Potato Center) now numbers about 12,000 accessions.

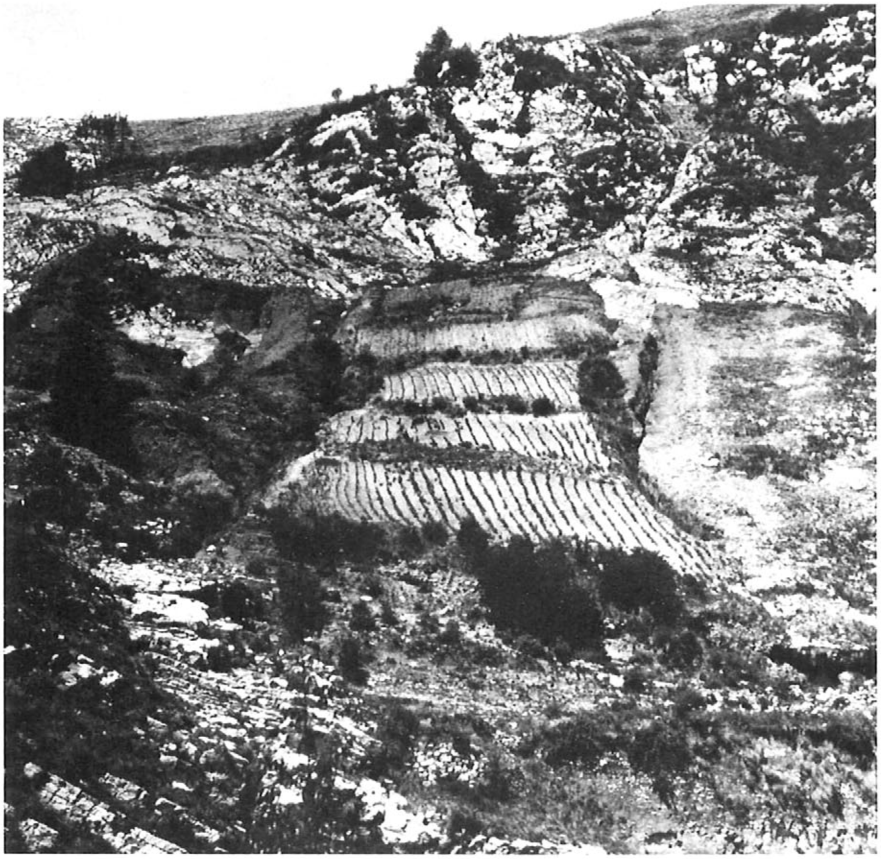
The potato in the Andes is grown under a wide variety of socioeconomic conditions ranging from immense haciendas to small farms (minifundias) of less than 1 ha. The disease control practices of the Andes were developed empirically through centuries of trial and error, natural selection, and observation. The traditional practices of disease control of the ancient Nasca, Chimu, Inca, and other Indian civilizations and the practices used today among traditional Aymara- and Quechua-speaking farmers are worth studying as a base on which to initiate improvements in systems of subsistence agriculture in developing countries around the world. For example, in Peru before the arrival of the Spanish, the Incas had a 7-yr rotation for potatoes established by law. Through centuries of trial and error, the Inca Indians had discovered that this rotation gave the best potato crops. The potato cyst nematodes (*Globodera pallida* and *G. rostochiensis*) are present in extremely high levels in most potato-growing areas of the Peruvian Andes. With the arrival of the Spanish, Inca law was destroyed and the 7-yr rotation was abandoned. Experiments in Peru have shown that populations of the potato cyst nematode are reduced with a 7-yr rotation to the extent that a crop can be produced economically (W. F. Mai, *personal communication*). Thus, what appeared to the Spanish to be a senseless custom had a sound practical basis and was an intelligent agronomic and crop protection practice.

In some areas of Peru, long rotations for the control of nematodes and fungi are still being used. Brush (1) reports that in the isolated community of Uchucmarca in northern Peru, traditional growers plant potatoes for 1 yr, then other Andean tubers, such as oca (*Oxalis tuberosum*), mashua (*Tropaeolum tuberosum*), and ulluca (*Ullucus tuberosum*), for the next 1 or 2 yr. Finally, an 8-yr or longer fallow period is used before potatoes are replanted.

Potato culture in the Andes of Colombia.

In this potato field in the Toluca Valley of Mexico, unsprayed cultivars with high levels of general resistance to *Phytophthora infestans* stand in contrast to plants of the cultivar Alpha that have been defoliated by the pathogen.

Although necessary to improve the systems of potato culture used by traditional or subsistence farmers throughout the world, changes should be made cautiously and with careful supporting research. A change made in one part of the potato agroecosystem influences other parts of the system. My experience in Colombia illustrates the



Potato culture in the Andes of Peru.

need to make changes with caution (8). In 1955, we began to increase the improved cultivar Monserrate. By 1959, a total of 700 t of Monserrate seed was available for use by farmers. Cut seed pieces were used for multiplication, although native potatoes are customarily planted as whole tubers. In 1959, the 30 ha of Monserrate planted near Bogota at 2,600 m elevation represented about 50% of the Monserrate seed available for the entire country in the subsequent season. At harvest, approximately 30% of the tubers were infected with *Pseudomonas solanacearum* (bacterial wilt). This was a severe blow to the national potato program. The infected seed from this farm was useless for seed and had to be sold for human consumption. In the same season, other Monserrate seed was produced by contract with private growers. Although no bacterial wilt was noted in these plantings, they probably were infected. Seed from these fields was sold to other private growers, and in three fields near Bogota planted with cut seed pieces from this stock, close to 100% of the plants developed bacterial wilt. A number of other fields planted with cut seed pieces suffered smaller losses from bacterial wilt.

As a result of these losses, growers became convinced that Monserrate was highly susceptible to bacterial wilt. The demand for seed declined, and the government drastically reduced its seed multiplication program. In subsequent semesters, Monserrate and other cultivars were planted as whole tubers in these same infested fields, and few plants were infected.

This experience illustrates how manipulation of the agroecosystem can change pest populations. Andean growers have used whole tubers rather than cut seed for centuries. Because the use of cut seed is common in North America and Europe, it was thought that the cut seed would be successful in Colombia. The first cut seed used rotted, due to *Fusarium* spp. This problem was rapidly solved with fungicidal seed treatment. However, the fungicide did not protect against *P. solanacearum*, and bacterial wilt became a serious problem. When growers went back to using whole seed pieces, bacterial wilt was no longer a problem. Thus, the Andean farmers' cultural practice of using whole seed was a sound disease control practice, and a slight change in the agroecosystem had temporarily disastrous results. Although changes in the traditional potato agroecosystem will not always result in disaster, their potential impact on pests must be analyzed before their widespread use is recommended.

Potato Research Programs in Developing Countries

Today, the CIP, directed by Richard L. Sawyer, is the dominant entity doing research internationally on potato diseases. CIP was founded in 1972 and is headquartered near Lima, Peru. It had older international programs as a base on which to build, such as the Rockefeller Foundation's International Potato Program that began in 1947 in Mexico and was headed by John S. Niederhauser. Another Rockefeller Foundation potato program (1952–1967) in Colombia worked in cooperation with ICA (Instituto Colombiano Agropecuario, Colombian Agricultural Institute). Under a U.S. AID program, North Carolina State University worked with the Peruvian government on potato research for 16 yr (5).

CIP's basic objectives are to increase the yielding ability and efficiency of potato production in developing countries and to increase the potato's range of adaptation to include the cold highland regions and the humid lowland tropics. Probably only 5% of the genetic variability of *Solanum* is found in the potato cultivars now in use (4). Untapped genetic resources still exist in the Andes, but these are rapidly disappearing. CIP has one of the largest collections (12,000 clones) of cultivated *Solanum* spp. in the world and is still sending teams throughout the Americas to add to their world potato collection before valuable germ plasm is lost. Future generations may find that preservation of germ plasm alone more than justifies all the support given to CIP.

CIP has not followed all the administrative and operational patterns of the older, established international centers, such as IRRI and CIMMYT. It has spent less on initial development of its headquarter facilities in Peru and has invested more of its energies and funds in research and production programs in developing countries. CIP has rapidly built up a strong outreach or regional research and training program, with staff members in seven zones in the developing countries of Africa, Asia, and the Americas.

Another CIP innovation has been to fund research projects at experimental centers in developed countries in North America and Europe that have a broad range of expertise and sophisticated equipment and facilities. CIP has contracts with 20 universities and institutions in 11 countries. This collaboration not only generates more fundamental research than CIP staff could produce with their facilities and experience but also establishes a network of cooperators around the world who form a valuable resource of experience and expertise.

The central facility for CIP is located on the coast of Peru, perhaps the driest desert in the world and where conditions are typical of arid lowland tropics. CIP also conducts research at Huancayo (elevation 3,300 m), where offices, laboratories, and greenhouses are available. Two other locations in Peru are used as major testing sites: San Ramon, in the "high jungle" area of the Amazon Basin at 800 m elevation, and Yurimaguas, in the hot, humid, tropical rain forest of the Amazon Basin at 175 m elevation.

In addition to CIP, many other programs—national, bilateral, and international—are working on potato disease research throughout the developing world. Almost every developing country that produces potatoes has some form of a national potato program. The level of expertise varies greatly, ranging from countries with only a few poorly trained technicians working sporadically on potatoes to countries such as India with sophisticated potato programs backed by a corps of highly trained scientists. Space does not permit listing all the projects or programs related to potato diseases carried out by national programs or bilateral agencies. In addition to the United States and Canada, many developed countries in Europe and Asia have bilateral programs in developing countries. The Asian Vegetable Research and Development Center (AVRDC) in Taiwan began a potato research program in 1972, when the center was started. The program was discontinued in 1979, however, with the expectation that CIP's program in Asia would expand and accomplish the objectives of AVRDC's program.

Major Potato Disease Research

Fungal diseases. Late blight (*Phytophthora infestans*) is considered the single most destructive disease of potatoes on a worldwide basis and thus receives major attention. More fungicides are used for control of *P. infestans* worldwide than for any other pathogen. Vast quantities of expensive fungicides, many imported, are applied in developing countries, mostly by hand with knapsack sprayers at a tremendous cost in time and labor.

Resistance to *P. infestans* in potatoes is recognized as specific (also called race-specific, vertical, or monogenic resistance) and general (also called race-nonspecific, horizontal, or polygenic resistance). Before the discovery of specific resistance, general resistance was the only type available, and fairly high levels were obtained. For several decades after the discovery of specific resistance in *S. demissum*, breeders incorporated one or a few *S. demissum* genes into new cultivars. *P. infestans* is highly variable and rapidly overcame such resistance, and use of specific resistance has contributed little to controlling late blight (6,7).

Much of the basic knowledge on *P. infestans* has been obtained in Latin America, especially Mexico, where discovery of its sexual stage helped explain the extraordinary variability of the fungus there. Work on *P. infestans* begun in Mexico in 1947 by the Mexican government and the Rockefeller Foundation has made important contributions to our understanding of the fungus, its variability, and the sources of resistance. Breeding material from all over the world has been tested in the Toluca Valley of Mexico, where almost all tuber-bearing *Solanum* spp. are susceptible. Many new sources of general resistance to *P. infestans* have been identified in South American germ plasm, and cultivars with high levels of general resistance have been released in Colombia and Peru.

Control of *P. infestans* has high priority for CIP, and evaluation of their germ plasm collection for sources of general resistance is a major activity. In addition to continuing the evaluation of breeding material in the Toluca Valley of Mexico, breeding lines are being evaluated in Peru, Costa Rica, and various countries of Asia and Africa. Contracts with the Swedish Seed Association, Cornell University, and the University of Wisconsin extend CIP's research on late blight.

Early blight (*Alternaria solani*) is the next most important foliar disease and causes substantial losses. Control by fungicides can be achieved in developing countries but is expensive and often inadequate or uneconomic. Little is known about resistance to *A. solani*, but CIP scientists believe that efforts to identify and utilize resistance will be necessary to control the disease in many of the drier areas of developing countries.

Although important in developing countries, little information is available on soilborne diseases, and more research is needed. Verticillium and Fusarium wilts of potatoes are widespread. *Fusarium* spp. are readily isolated, but *Verticillium* is more difficult to detect. *Rhizoctonia solani* also causes low but constant losses. Crop management techniques are most promising for control of *Rhizoctonia*.

Many other locally important soilborne pathogens may have the potential to spread and become more significant, eg, *Streptomyces scabies* (scab), *Synchytrium endobioticum* (wart), *Angiosorus solani* (potato tuber smut), *Spongospora subterranea* (powdery scab), *P. erythroseptica* (pink rot), *Sclerotium rolfsii* (basal stem rot), and *Sclerotinia sclerotiorum* (white mold). To devise control measures appropriate for small farmers in developing nations, much more information is needed on the biology, range, and importance of these pathogens.

Some fungal pathogens, such as *Puccinia pitteriana* and *Aecidium cantensis* (rusts) and *Angiosorus solani*, are at present limited to Latin America. Their potential to spread and cause serious potato losses elsewhere is unknown. CIP is screening its germ plasm collection for resistance to *A. solani*.

At CIP's lowland experiment station at Yurimaguas, Peru, where potatoes are grown outside their normal cool environment, *Choaneophora cucurbitarum*, *Macrophomina phaseolina*, and *S. rolfsii* are important pathogens. As CIP's attempts to move the potato into the hot, humid tropics are increased, other pathogens will undoubtedly also become important.

Bacterial diseases. Bacterial wilt (*P. solanacearum*) is widespread and destructive in many developing countries and is especially serious at the lower, warmer elevations in the tropics. To extend the potato's range of adaptability to the lowland tropics, *P. solanacearum* must be controlled. Races 1 and 3 of *P. solanacearum* attack potatoes in the field. Race 1 is believed to have originated in the lowland tropics and race 3 in the highland tropics, where it causes losses at altitudes over 2,700 m (8). Recently, however, both races were isolated from wilted potatoes grown on virgin jungle land at Yurimaguas. The highland origin of race 3 is therefore doubtful, and the need to breed for resistance to both races is emphasized (2).

In 1967, screening of the Colombian potato collection showed resistance in *S. phureja*. A program funded initially by the Rockefeller Foundation and later by CIP at the University of Wisconsin used *S. phureja* and other species found to be resistant at CIP in Peru to develop germ plasm for breeding programs throughout the world. Resistance to *P. infestans* and virus Y is being incorporated into the lines resistant to *P. solanacearum*, and they are being tested in Peru, Mexico, and Costa Rica. Workers at CIP have found additional sources of resistance in several *Solanum* spp., with *S. sparispilum* being the most promising (3). The cultivar Molinera, recently released with resistance to *P. solanacearum*, has been successful in infested areas of Peru.

The complex of *Erwinia* spp. causing blackleg and soft rot is being investigated by CIP in Peru. *E. caratovora* var. *caratovora*, *E. caratovora* var. *atroseptica*, and *E. chrysanthemi* are serious pathogens worldwide. Resistance to *E. chrysanthemi* has been found at CIP (3).

Nematode diseases. Various species of nematodes are major problems in potato production around the world. The most important are potato cyst nematodes (*Globodera* spp.) and root-knot nematodes (*Meloidogyne* spp.). Generally, chemical control is too expensive for potato growers in developing countries, so control through host plant resistance is emphasized, although attention is also given to cultural and biologic controls.

Root-knot nematodes are most serious in warmer potato-growing areas and must be controlled if potatoes are to be grown in lowland tropics. An interaction between *Meloidogyne* spp. and *P. solanacearum* has been reported (2). Resistance to *Meloidogyne* spp. has been found in several *Solanum* spp. in Peru and in the Cornell University contract program with CIP.

The false root-knot nematode (*Nacobbus aberrans*) has caused as severe yield

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reductions in some areas of the Andes as have *Globodera* spp. Much more work on its biology, ability to cause losses, and means of spread is needed, as it could become a serious pathogen if inadvertently distributed to other developing countries.

The origin of the potato cyst nematodes (*G. rostochiensis* and *G. pallida*) is believed to be centered in the Peruvian and Bolivian Andes. Only one race or pathotype occurs in the United States, but five are found in Europe and nine in the Andes. An intensive screening program at CIP has identified many *Solanum* spp. as resistant to one or more of these races. *Globodera* spp. are found in many developing countries throughout the world, and new outbreaks are recorded often. Stable resistance to *Globodera* spp. is essential, and the work in Peru is important to long-term control of these pathogens. Recent work at CIP on natural biologic control of nematodes has shown some fungi to be capable of destroying females and eggs of *Globodera* and *Meloidogyne* spp.

Virus and viroid diseases. Viruses are undoubtedly the most destructive group of pathogens causing yield losses in developing countries. Tuber seed is the costliest potato production input in these countries, and use of poor-quality seed results in serious losses. Viruses are a major cause of this reduced yield. Quarantine restrictions on imported seed often seriously reduce the interchange of potentially valuable and more appropriate germ plasm.

Potato leaf roll virus (PLRV) and potato virus Y (PVY) have been identified as the most important diseases affecting the potato in developing countries, and CIP has given these viruses top research priority. Potato virus X (PVX) and potato spindle tuber viroid (PSTV) are also important. An intensive screening of CIP's germ plasm collection, using seedling screening techniques developed at CIP, is producing valuable breeding material with resistance to PLRV, PVY, and PVX and to insect vectors of potato viruses. Twelve countries are participating in international regional trials for virus resistance.

Several previously unknown viruses have been identified and characterized in Peru: Andean potato latent virus, wild potato mosaic virus, Andean potato mottle virus, and potato virus T. A strain of PVX that does not cause symptoms on *Gomphrena globosa* has also been found in the Andes.

The existence of these new viruses and of other potato pathogens unknown outside the Andes has meant that CIP has had to take extreme precautions in distributing the germ plasm they develop to other countries. Serology, electron microscopy, and, recently, enzyme-linked immunosorbent assay (ELISA) have been adopted to test for viruses in leaf samples, tubers, and plantlets derived from meristem culture in order to insure distribution of virusfree material. Polyacrylamide gel electrophoresis is being used to detect PSTV.

Certified Seed Programs

A major obstacle to increasing potato production in developing countries, especially those in the tropics, is the lack of potato seed certification programs such as those in Europe, Canada, Japan, and the United States. Few developing countries have the technology, facilities, isolated areas, climatic conditions, and socioeconomic development needed for a successful program of potato seed certification. Potato seed used in developing countries ranges from native cultivars in the Andes that have never had the "benefit" of a certification program to seed produced by relatively sophisticated programs. Many developing countries in the tropics depend entirely on costly seed imported from temperate countries and often plant poorly adapted cultivars suited for temperate latitudes. In addition, massive importations of seed carry the risk of bringing in new, potentially destructive pathogens.

Most developing countries with cool climates and somewhat isolated potato-growing areas attempt to develop seed certification programs modeled after those in developed countries. Their success varies greatly. Lack of a successful program can mean that new, promising cultivars may never be used because seed is not available from a temperate country that exports seed. It can also mean that expensive imported seed is used in succeeding years until it "runs out" and becomes so diseased that yield is seriously reduced.

A recent innovation in overcoming this stumbling block in potato production is the use of true seed rather than asexual propagation with tubers. The potato is highly heterozygous, and each plant arising from true seed differs from every other plant. Many agronomic problems have to be solved before the use of true seed can become widespread and economically feasible in developing countries. Scientists at CIP believe these problems can be solved and that those caused by heterozygosity can be minimized through breeding. Tubers are the costliest input in potato production in developing countries, and the use of true seed might reduce costs to a level similar to that of the cereal crops. CIP (3) has estimated true seed at 5% or less of total production costs, compared with as much as 60% for tuber seed. The sheer bulk of tuber seed means that considerable energy is used for transportation, harvesting, and storage. The use of true seed could have a major impact on diseases because almost all pathogens (except PSTV) carried in tuber seed would be eliminated.

CIP scientists who visited the People's Republic of China reported that in 1977, 2.5 t of true seed were produced in Inner Mongolia and shipped to farmers in southern China for both multiplication of tuber seed and direct planting for production of consumer potatoes (3).

Whether the many technical problems associated with making widespread use of true seed in developing countries a reality can be solved is unknown, but the approach is well worth the research effort needed, as conventional systems of certified seed production may never be of great benefit to small farmers in tropical countries.

The Challenge

The challenge is great for those engaged in potato disease research aimed at increasing potato production in developing countries. The numerous urgent problems and the lack of reliable information on disease losses make establishment of research priorities difficult. Socioeconomic factors usually are beyond the control of researchers, but poor understanding of these factors may lead to unrealistic, uneconomic, and inappropriate recommendations in many developing countries. In addition to the simplistic goal of increasing potato production, a major goal should be to improve the nutrition, economic conditions, and quality of life of small farmers. Paradoxically, increasing production may often be achieved most efficiently by allocating scarce national resources to the large, efficient farmers. A major challenge is to design research that will increase potato production and simultaneously improve the lot of small farmers. It is encouraging to note that CIP has a socioeconomic unit that includes two agricultural economists and an anthropologist.

CIP is making a major effort to develop technology for potato production in the hot, humid tropics. In most tropical developing countries, the potato has been primarily a rich man's food. CIP has made considerable progress in selecting cultivars adapted to the hot, humid tropics and in developing technology that can bring the high production and balanced protein and calories of the potato to populations who need them. Because plant pathogens may be the principal obstacle to success of this effort, a major challenge to pathologists will be to conduct research to control these pathogens in this new environment for potatoes. How well potatoes can compete in the future with root crops, such as cassava, sweet potatoes, true yams (*Dioscorea* spp.), *Colocasia* sp., and *Xanthosoma* sp., that are well adapted to the hot, humid tropics is to be determined.

The research in developing countries on potatoes will benefit not only the economies and small farmers of those countries but also potato production in the developed countries of the world. For example, knowledge of the potential for variation of *P. infestans* changed the direction and emphasis in breeding programs around the world. Valuable germ plasm with disease resistance, as yet unutilized, can be maintained and identified in the tropics before pathogens arrive in developed countries. If the humanistic goals of sharing scientific research with developing countries is not enough to encourage support for international potato disease research, enlightened self-interest should be.

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