The potato

M. T. Jackson

The potato produces more edible energy and protein per hectare and per unit of time than probably any other crop. Originating in the Andes, its cultivation is now widespread. Rapid technological progress is stimulating production in non-traditional environments

The potato, *Solanum tuberosum* ssp. *tuberosum*, is the most important root crop grown in the world today. Annual production has been estimated at 285 million tonnes, and the potato is the fourth most important crop after wheat, maize, and rice. Although the potato originated in the Andes of South America, it has achieved its greatest exploitation in the industrialised countries of the northern hemisphere. This is really quite remarkable since it was introduced into Europe only about 400 years ago, and it did not become an important crop plant here until the 18th century.

It is a member of the family Solanaceae, as are the tomato, pepper, eggplant, and tobacco. Unlike other solanaceous plants, potatoes reproduce both sexually and asexually through tubers. The tuber is an underground stem, much enlarged and modified as a food storage organ, with minute scale-like leaves and buds (the 'eyes'). Tubers arise as swellings between the terminal bud and the penultimate expanding internode of underground stems or stolons.

The potato is adapted to temperate climates. In the tropics of South America it is an indigenous crop of the cool temperate zones of the high altitudes in the Andes (2000-3800 m). Here, however, it is adapted to a short-day photoperiod of approximately 13 hours, under which it tuberises. In the northern hemisphere, the potato underwent intense selection and adaptation to a daylength of up to 17 hours, and in the process became differentiated from its Andean progenitor, *S. tuberosum* ssp. *andigena*.

The potato gene pool

Solanum tuberosum is a tetraploid plant with a somatic chromosome number of $2n = 48$. The genetic base of varieties selected in the northern hemisphere is rather narrow, but in South America, and particularly in Peru and Bolivia, there are eight other cultivated species (table 1) represented by several thousand distinct genotypes, some of which are shown in figure 1. These cultivated forms represent a classical polyploid series with diploids, triploids, tetraploids and pentaploids. In addition to the cultivated species, there are almost 200 wild tuber-bearing species, all classified in the genus *Solanum* Section *Petota*. Within Section *Petota*, there are 18 taxonomic groups or series, but by far the largest is Series Tuberosa, which contains all the cultivated forms and the majority of the wild species. Wild potatoes range in ploidy from diploid to hexaploid.

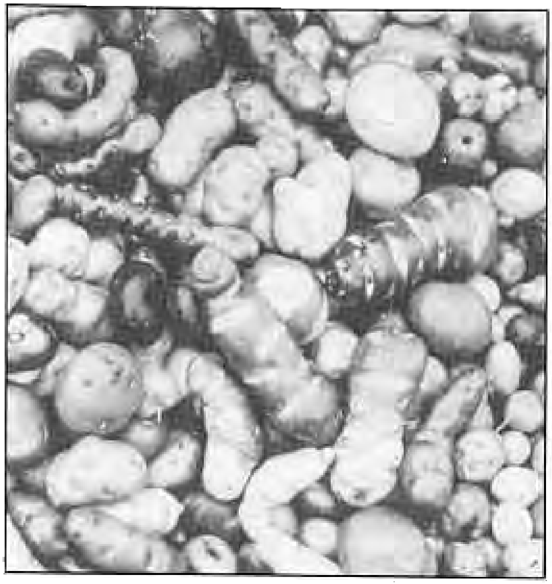

Figure 1. Tubers of primitive potato varieties from Peru. (Source: Ford-Lloyd, B. V. and Jackson, M. T. (1986) Plant genetic resources. *London: Edward Arnold.)*

Table 1 The cultivated species of potatoes

Species	Ploidy	Distribution
S. stenotomum	2×	Central Peru and Bolivia
S. goniocalyx	2×	Central Peru and Bolivia
S. phureja	2×	Venezuela to northern Peru
S. × *ajanhuiri*	2×	Southern Peru to northern Bolivia
S. × *juzepczukii*	3×	Central Peru and Bolivia
S. × *chaucha*	3×	Central Peru and Bolivia
S. tuberosum		
ssp. *andigena*	4×	Venezuela to northern Argentina
ssp. *tuberosum*	4×	Chile/worldwide
S. curtilobum	5×	Central Peru and Bolivia

Potatoes are found from Colorado in the United States, through Mexico and Central America, and down through the Andes of South America, as far south as 45 °S. They are adapted to a diverse range of environments from sea level on the coast of Peru to the high Andes at over 4000 m, although most species are plants of medium to high altitudes. They extend through a wide range of plant communities, including the scrub and cactus deserts of Mexico, the southern United States, Peru, Bolivia and Argentina, and the high rainfall mountain and cloud forests of the eastern Andean slopes, Mexico, and Central America. Species which grow at altitudes over 3500 m exhibit frost tolerance. Some are found as weeds of cultivation in maize and potato fields.

Most diploid species are outbreeders, controlled by a one-locus S-allele gametophytic incompatibility system, which breaks down in the tetraploid species. Tetraploids are self-fertile, and in the field most true seeds are produced as a result of self pollination. This leads to rapid inbreeding depression. However some outcrossing does occur, as potatoes are pollinated by bumble bees. The triploid and pentaploid forms are virtually sterile. Many European and North American varieties flower only sparsely, but the primitive varieties found in South America flower abundantly and produce much true seed.

Considerable genetic heterozygosity is locked-up in potato clones; as a result of this combination of sexual and asexual reproduction seedling progenies are heterogeneous. Clonal propagation ensures uniformity, and is exploited in commercial potato production.

History

All the evidence points to South America as the source of the potato. At the time of the Spanish conquest in South America during the early 16th century the potato was clearly an ancient cultivated plant. The exact origin of cultivated potatoes may never be known, but through research on primitive varieties and wild species, potato scientists have discovered some evidence of their evolution. During domestication, there was selection for short stolons, for loss of bitter glycoalkaloids in the tubers, and for large, brightly coloured tubers. Archaeological information concerning the antiquity of the crop comes from ceramics in the form of potatoes found in burial sites on the northern coast of Peru, and relating to the Mochica, Chimu, and Inca cultures from about the fourth century AD. Actual tuber remains have been identified from some sites in Peru, based on comparisons of starch and cell structures in fresh and preserved tubers, and have been radiocarbon-dated at about 8000 years old.

The potato was introduced into southern Spain in the late 16th century, in about AD 1570. The Russian botanists, Juzepczuk and Bukasov, claimed that the potato was brought to Europe from Chile, and that it would have been adapted to the long days of Europe right from the time of its introduction. This explanation seems straightforward, but the English potato scientists Dr Redcliffe Salaman and Professor Jack Hawkes have cited considerable contrary historical and geographical evidence. By the time of the introduction of the potato into Spain, Chile had not been conquered by the Spanish. Instead, they believe the first potatoes came from Colombia. Drawings of the potato in early herbals are very similar to the Andean forms, ssp. *andigena*. At first the potato was only a botanical curiosity in Europe, and did not become an important crop until the mid-18th century. Linnaeus described *S. tuberosum* in about 1750, after the potato had undergone almost two centuries of adaptation to long-day conditions.

Production and consumption

The potato is a relatively staple part of the diet of European and North American people. It is also a very important food of the highland populations in the Andean countries of South America, particularly Peru and Bolivia. In these countries the per capita consumption is as high as 95 kg per annum, mostly as fresh potatoes. In Europe and North America, per capita consumption is also very high, but here a considerable proportion of potatoes are processed, for canning, frozen french fries, crisps, and for starch production, amongst other products.

Most potatoes are produced in Europe and North America (table 2). Here, the production of ware potatoes (i.e. for consumption) is sustained by sophisticated programmes of seed tuber production. The regular availability of healthy seed tubers, and efficient and timely disease and pest control, ensure that high yields are consistently achieved. In the Netherlands, for instance, yields are as high as

Table 2 The ten largest potato producing countries in 1980. (Source: World Potato Facts, International Potato Center 1982)

Country	Production (1000 t)	Area (1000 ha)	Yield (t ha^{-1})
USSR	66 900	6 933	9.6
Poland	26 400	2 336	11.3
USA	13 653	468	29.2
China	12 500	1 460	8.6
German DR	8 568	519	16.5
India	8 306	693	12.0
France	7 485	254	29.5
Germany FR	6 694	260	25.7
UK	6 327	205	30.8
Netherlands	6 267	173	36.3

$36\,t\,ha^{-1}$, and yields in the UK are in excess of $30\,t\,ha^{-1}$. The world's largest producer, the Soviet Union, has average yields of only $10\,t\,ha^{-1}$. In many developing countries yields are lower still, due principally to the poor quality of seed potatoes which are used to produce commercial potato crops. Because conditions in many tropical countries are not favourable for seed multiplication, farmers often have to import expensive seed tubers each year from Western Europe or North America. It is common for peasant farmers to save the smallest tubers from a commercial ware crop as seed tubers for the next planting. Moreover, they often cannot afford to use fertilizers at the correct rate, nor control pests and diseases. As a result, the potato crop never reaches its full potential in the field and yields are often pitifully low.

In Great Britain, ten varieties account for 78 per cent of the production, and one of these, cv King Edward still maintains its popularity after eight decades (table 3). Potatoes are classed as first early, second early, or maincrop varieties. Early potatoes are harvested before the end of July, and have tubers that are relatively small in size with thin skins. Yields may be quite low, but because of consumer demand, prices are generally high. Maincrop varieties are harvested from September onwards, and tubers are larger, skins are thicker and their storage potential is greater than early potatoes. Most ware potatoes are produced in the east of England, in Lincolnshire, Norfolk, and Cambridgeshire. Most seed potatoes are produced in Scotland.

In the industrialized nations, the crop is now almost completely mechanized, from planting to harvesting, grading, packing, and storage. In contrast, the production of potatoes in many developing countries is relatively unsophisticated. There is much use of manual labour and draught animals for ploughing, planting, and earthing-up the rows during growth of the crop. Potatoes are generally harvested by hand. In many parts of Peru, the peasant farmers still use the traditional footplough or 'chaqui taclla' (figure 2). It is also common to see several different varieties growing together in the same field. These may even belong to different species. In southern Peru, potatoes are still grown on ancient terraces constructed by the Incas (figure 3).

Table 3 The top ten potato varieties grown in Great Britain in 1984. (Source: Potato Marketing Board)

Variety	Type	Area (%)	Yield ($t\,ha^{-1}$)
Maris Piper	maincrop	15.9	47.3
Desiree	maincrop	12.9	42.8
Wilja	second early	10.0	43.0
Record	maincrop	9.5	40.1
Pentland Crown	maincrop	7.5	43.5
Pentland Squire	maincrop	6.5	41.8
Pentland Dell	maincrop	4.3	46.2
Estima	second early	3.7	43.2
Pentland Javelin	first early	3.5	—
King Edward	maincrop	3.3	42.7
Other varieties	all types	22.0	—

Figure 2. Peasant farmers using the Andean footplough near Huanuco in central Peru. Potatoes can be seen growing on the far hillside.

Figure 3. Ancient terraces in Cuyo-Cuyo in southern Peru, used for growing potatoes and other minor tuber crops.

Many people continue to view the potato as a northern-latitude crop, important only in the industrialized countries. In fact, the potato has migrated rapidly into tropical and subtropical areas where it is now grown extensively. In developing regions over the last two decades potato production has increased sharply, the rate being nearly twice that of the total food production and substantially higher than that of most other major food crops. Potato production has increased most rapidly in countries such as China, India, and Indonesia, and Asia now accounts for 84 per cent of the 91 million tonnes of potatoes produced in developing countries.

Potato production is expanding for several reasons. One is that the potato crop produces more edible energy and protein per hectare and per unit of time than practically any other crop. This is particularly important for small subsistence farmers who can fit the potato into their multiple-cropping systems. Other reasons include strong consumer demand for potatoes and the high profitability of commercial crops. Rapid technological progress with potatoes is stimulating expansion of production in non-traditional environments in these countries.

Diseases and pests

The potato is affected by more than 100 diseases caused by fungi, bacteria, viruses, and mycoplasmas, although fortunately only a few of these are major pathogens in any one potato growing area. Many are restricted to the centre of diversity of the potato in the Andes. Several insect and nematode pests of potato have become established worldwide.

It has been estimated that worldwide losses of potato yield through disease are 30 per cent. They affect the emergence, development, and vigour of the crop in the field. Fungal diseases, such as late blight (*Phytophthora infestans*), which attack the foliage, reduce yield because the growth of the tubers is dependent on the functioning leaf area. Seed tubers may decay before planting or rot in the soil due to disease, and some fungal and bacterial diseases cause wilting and the premature death of plants. Plants can become systemically infected with virus diseases, and plant vigour is affected as plants become stunted due to decreases in internode length and mottling of the foliage. Other viruses may rapidly kill the plant, through near complete defoliation, as occurs with strains of potato virus Y (PVY). The control of potato viruses is particularly important in the production of seed tubers. Nematodes attack the root system, decreasing the efficiency of plant growth and development. In some situations, storage losses due to diseases and insect pests can be serious.

All aspects of potato diseases and pests cannot be described in this article. However, it is interesting to highlight the impact which potato diseases and pests can have on socio-economic development. Late blight was the disease responsible for the Irish Potato Famine in the mid-1840s. The starvation and deaths which resulted, and the emigration which followed, decimated the Irish population. Late blight remains the most important potato disease globally. In the UK the disease rarely becomes serious, but in many tropical countries, favourable conditions for the development of late blight epidemics occur all year round, even when the growth of the crop is at an early stage. Without proper control, which many peasant farmers cannot afford, the disease rapidly destroys the foliage.

Bacterial wilt, caused by *Pseudomonas solanacearum*, is found in warmer climates in tropical and subtropical countries. It has rendered large areas useless for the cultivation of high value crops such as potato, tomato, eggplants, and tobacco, as well as bananas, because it persists for many years in the soil.

The potato cyst nematode (*Globodera* spp.) is one of the few pests of the potato to have spread with the crop after its introduction into Europe from South America. In the UK it is estimated to cause a 10 per cent loss of yield.

Genetic conservation and utilization

The first potato collecting missions to the Andes were made in the 1920s by Russian botanists under the direction of N. I. Vavilov. The UK has also been involved in germplasm collection, primarily through the work of Professor Jack Hawkes and his colleagues at the University of Birmingham. It is indeed fortunate that collection of potato germplasm was initiated before loss of diversity, or genetic erosion as it is often called, had become too serious in many regions of the Andes. Moreover, genetic conservation of this crop received further stimulus with the foundation of the International Potato Center (CIP) in Peru in 1972, and the formation of the World Potato Collection. Since 1973, collecting missions have travelled throughout the Andes and have 'captured' most of the primitive varieties of potatoes now grown by peasant farmers. In the World Potato Collection, the identification of duplicate clones has reduced the size of the collection from about 15 000 accessions to about 5000 clones, which are propagated annually (figure 4). The collection is being transferred gradually to *in vitro* storage.

The World Collection also contains about 100 wild species represented by some 1500 accessions. Several of these species are new to science, and others, once thought to have become extinct, or only known as dried herbarium specimens, have been rediscovered. The most important collection of wild species is at Sturgeon Bay, Wisconsin, in the USA, and other collections are located at the Scottish Crop Research Institute, Edinburgh (the Commonwealth Potato Collection), and in West Germany. A large working collection of about 120 wild species and cultivars is held under licence from MAFF at the University of Birmingham, and is used for pre-breeding and taxonomic research.

In the UK, the principal breeding programmes are located at the Scottish Crop Research Institute, and the Plant Breeding Institute, Cambridge. Potato breeding priorities are influenced by the requirements of the processing industry, and the need to improve potato quality, but resistance to late blight, viruses and cyst nematodes remains important.

Undoubtedly the potato is one of the best examples of germplasm utilization in plant breeding, and this contrasts with the situation in other major crops where the wild species genepool is much smaller. Crossability relationships between cultivated and wild species have been determined, and this information is used by potato breeders to assess the chances of success of inter-specific hybridization before the costly process of germplasm utilization actually begins.

Perhaps the earliest utilization of a wild species was the transfer of resistance to late blight from the wild Mexican hexaploid species, *S. demissum*, which was used for many years as a source of R-gene race specific resistance. Nowadays, breeders are using sources of horizontal or field resistance which has been found in both wild species and primitive tetraploid varieties from South America, and which seems to be a more durable type of resistance.

A particular success story in germplasm utilization is the incorporation of resistance to bacterial wilt from the diploid cultigen *S. phureja*. This resistance was discovered in a germplasm collection in Colombia in the late 1960s, and has been used to breed wilt-resistant varieties, which also have resistance to late blight. Such varieties are beginning to have a major impact in the warm tropics, in Peru, Central America, Rwanda and Burundi, and in the Philippines.

Resistance to PVX and PVY has been found in two tetraploid wild species, *S. acaule* and *S. stoloniferum;* the former species is also a source of frost-tolerance genes. *S. vernei*, a diploid from northwest Argentina, closely related to *S. tuberosum*, is the species commonly used for resistance to the cyst nematodes. Although the use of wild species presents breeders with some problems, such as long stolons and high glycoalkaloid content for instance, which must be eliminated by a protracted programme of backcrossing, the incorporation of genetic resistances cannot be stressed too highly. In doing so, the potato has the potential to become a crop of the small, peasant farmer in the developing world.

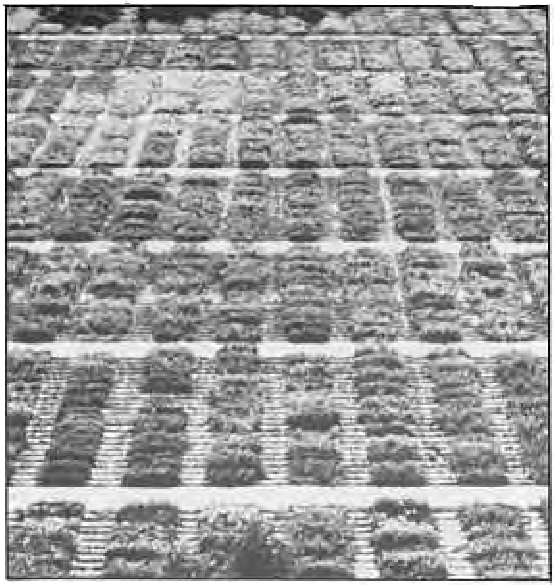

Figure 4. Part of the World Potato Collection of the International Potato Center, planted at Huancayo, central Peru, at 3000 m. (Source: International Potato Center.)

Potatoes and biotechnology

The application of biotechnological strategies offers considerable promise in several ways for potato improvement. Tissue culture methods have been used in recent years for the rapid propagation of potatoes. Meristem culture is used to eliminate virus and other tuber-borne diseases from varieties which have undergone severe degeneration. Another aspect concerns the routine application of tissue culture for the conservation of germplasm, by growth on minimal media, which slows down the growth of cultures, with the advantages that this brings in terms of less-frequent subculturing.

Even though diversity exists in primitive cultivars and wild species, there has been recent interest amongst potato breeders in somaclonal variation for varietal improvement. The plants regenerated from leaf mesophyll protoplasts of several potato varieties have shown diverse variation patterns, and it is hoped to select variants which are essentially the same as the mother plants, but which manifest an improved quality, say for disease resistance. For instance, Shepard and his co-workers in the United States have successfully produced over 1000 somaclones of the variety Russet Burbank. These showed considerable variation in terms of compactness of growth habit, maturity date, and tuber uniformity. Five somaclones were more resistant than Russet Burbank to early blight toxin, and four of these showed increased resistance to the fungus in the field. In the UK, work at the Plant Breeding Institute and Rothamsted Experimental Station, Harpenden has led to the production of several thousand somaclones from mesophyll-derived protoplasts or explants. Results from disease tests indicate that some somaclones from Maris Piper and Feltwell may be more resistant to PVY or PLRV than their respective parents, and resistance to common scab (*Streptomyces scabies*) has also been detected in somaclones.

While this approach is very much a 'shot in the dark', it does have considerable potential, although it is much too early to predict what the final outcome will be. For the utilization of exotic germplasm, two techniques namely protoplast fusion and embryo culture, may well prove to be useful. Protoplast fusion offers the potential for somatic hybridization between species. Somatic hybridization has not been applied practically to date, but problems associated with the combination of two genomes which would result from protoplast fusion, such as sterility, will probably be of less significance in potatoes because of vegetative propagation. Screening for disease resistance, tolerance of heavy metals, or herbicide resistance, for example, might be achieved more efficiently through protoplasts, because of the chance of applying a selective pressure directly during the *in vitro* phase. This approach has been used with pathogens which attack their hosts by toxins, including the late blight pathogen and several *Fusarium* species.

In many crosses involving distantly related species, hybrid embryos fail to develop for one reason or another. In cases where post-fertilization breakdown is the main cause of cross incompatibility, embryo culture is appropriate, whereby embryos are excised from developing seeds before abortion occurs, and cultured on nutrient agar. Embryo culture has already shown much promise for the transfer of virus resistance from *S. etuberosum*. Rapid multiplication techniques can accelerate the breeding cycle by increasing the amount of seed tubers available for testing and distribution. Another way in which this can be achieved is by using disease screening techniques which are rapid and highly sensitive. Disease indexing of virus diseases using the molecular technique of nucleic acid hybridization (or 'dot blotting') may well revolutionize screening for these diseases in potato breeding and radically shorten the breeding cycle. 'Dot blotting' relies on identifying the homology between labelled DNA from a virus and extracts from a plant. A positive reaction indicates the presence of the disease. It has been calculated that the screening of 1000 plants could be achieved in as little as four days. To date most success has been achieved with probes to potato spindle tuber viroid (PSTV), but at the Plant Breeding Institute, probes to common viruses have been made and will soon be used routinely in testing breeding materials.

The potential of genetic transformation has been demonstrated in potatoes using *Agrobacterium tumefaciens* as a vector. Research at Rothamsted Experimental Station in this field is still at an early stage.

True potato seed

An exciting new alternative strategy to the use of seed tubers for potato production involves the utilization of true potato seed (TPS), which is the product of sexual fertilization. Many of the problems associated with tuber seed, especially virus diseases and costly transportation and storage are eliminated. The idea of using TPS for producing potatoes is not new. Potato scientists use TPS in breeding research to develop new varieties. During the past decade, farmers in the People's Republic of China have successfully grown potatoes from TPS. Research at the International Potato Center and other institutes has concentrated on the development of appropriate technologies for use of TPS as an alternative to the traditional seed tuber.

There has been more progress in the agronomic research related to TPS than in breeding. In Peru and the United States, scientists are evaluating TPS progenies produced through open pollination in the field or through controlled hybridization. Research in the UK on TPS is being carried out at the University of Birmingham, in collaboration with the Plant Breeding Institute and the International Potato Center, and is funded by the Overseas Development Administration. Scientists are attempting to produce TPS at the diploid level through inbreeding. These international collaborative efforts are all aimed at producing a low-cost food for the small-scale farmer in the developing world.

An international dimension

International collaboration in potato research has increased since 1972 when the Consultative Group on International Agricultural Research (CGIAR) established the International Potato Center in Lima, Peru. Since its inception, CIP has acted as a catalyst for the improvement and greater utilization of the potato in the food systems of developing countries. The CIP programme has three major dimensions, namely *(i)* ten 'research thrusts' which are cross-disciplinary; *(ii)* contracted research projects in institutes and universities in both the developed and developing countries; and *(iii)* regional research and training in seven regions of the world, ensuring rapid and efficient transfer of technology between CIP and national programmes.

A central feature of CIP's programme is the exploitation of diversity in the World Potato Collection. Disease and pest resistant potatoes have been identified, and utilized by CIP breeders to produce segregating genetic materials, which are distributed to developing countries, for testing under local conditions. Preliminary screening of germplasm is carried out in Peru at locations on the coast, in the high Andes, and in hot and humid sites on the eastern slopes of the Andes. Needless to say, potatoes exported from Peru are produced under strict quarantine from plants which have been tested and certified free from diseases and pests.

Another important aspect of CIP's programme is seed production technology for developing countries. Rapid multiplication techniques allow national programmes to produce large quantities of seed from a few tubers of valuable clones. In Vietnam, for instance, farmers have even adapted tissue culture techniques for use in their own homes, using unsophisticated equipment.

Research on potato storage has had an impact in Central America and Southeast Asia. Diffuse light stores are being used by peasant farmers to store seed tubers. Under these conditions, the light compensates for the relatively high temperatures in tropical conditions, with the consequence that the seed tubers are preserved in a much better condition, have short sturdy sprouts, and grow much more vigorously when planted.

The socio-economics programme evaluates the problems associated with the adoption of technology by farmers, and the importance and growth of the potato in developing market economies. Social scientists – economists, sociologists, and anthropologists – work alongside the biological scientists to identify production constraints, and to generate and evaluate technology alternatives.

Through the Regional Research and Training Programme, scientists throughout the world act as an interface to put CIP's research results where they can be most effective, and to help colleagues located at CIP headquarters in Peru become familiar with production constraints in other parts of the world, so that the research can respond to such challenges. An important feature of the responsibilities of the regional scientists is training. Trained personnel can receive and adapt technology, and improve potato production in their own countries.

The importance of the potato in many countries is reflected in the existence of several scientific associations dedicated to potatoes alone. In Europe, the European Association for Potato Research meets in plenary session every three years and promotes research and development of the potato in all its aspects. Section meetings on more specialized themes are held at more regular intervals. A journal, *Potato Research*, is published four times a year, accepting papers in English, German, or French. The North American counterpart is the Potato Association of America, which meets annually. Its journal, the *American Potato Journal* is published monthly. There is also an association in Latin America, and one in India.

Further reading

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