

Applied potato genetics and breeding: the way ahead for potato breeding

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Introduction The principal cultivated potato (*Solanum tuberosum*) is a tetraploid species ($2n = 4x = 48$) which was introduced into Europe, and thence the rest of the world, from the Andes of South America in the late 16th century. By the end of the 18th century, it had been adapted to long-day conditions through selection by its early cultivators for earlier-tubering, higher-yielding clones. These were derived from seedlings from naturally occurring berries, the consequence of uncontrolled, largely self-pollination.

Potato breeding in the modern sense began in 1807 in England, when Knight made deliberate hybridisations between different varieties by artificial pollination, and flourished during the second half of the 19th century when many new cultivars were produced by farmers and hobby breeders.

However, it was the rediscovery, in 1900, of Mendel's 1865 paper on Experiments in Plant Hybridization that marked the birth of modern genetics, and opened the way to crop improvement by scientific breeding methods based on a sound knowledge of the inheritance of economically important traits. The development of such methods for potatoes was one of the challenges which faced scientists at the Scottish Plant Breeding Station (SPBS) on its foundation in 1921, and one which now faces the members of the newly-formed Applied Potato Genetics and Breeding Research Unit at SCRI.

This article reviews the way ahead for potato improvement at SCRI, in terms of the needs of the British Potato Industry, the germplasm available to breeders, the possibilities for modifying existing cultivars by genetic transformation and the technologies available for enabling faster, more efficient, and novel breeding

strategies based on genotypic selection. It is concerned with producing improved cultivars for clonal propagation by tubers, and not with ones for propagation by True Potato Seed (TPS). This is because SCRI breeders are sceptical about the place of TPS in the highly developed markets of Europe and North America, whilst acknowledging that there is much interest throughout the tropics in TPS as a means of avoiding some of the disease problems associated with the maintenance of vegetative stocks.



Priorities for potato improvement In Britain, 150,000 hectares of potatoes are grown for ware each year, primarily from seed-tubers produced in Scotland (15,000 hectares). Approximately 30 per cent of the crop is for processing (French fries and crisps) and 70 per cent for table use, mainly through supermarkets.

Seasonal fluctuations in supply require storage of tubers for long periods in order to ensure continuity of supply.

Today, as never before, the commercial success of new cultivars is heavily dependent on meeting the quality requirements of processors and supermarkets, and this is a trend that is likely to continue. Hence, the priorities shown in Table 1 reflect our recent discussions with these important end-users, an assessment of disease priorities in northern Europe, and the potential for increased seed exports to southern Europe and N. Africa. The majority of today's most popular cultivars are susceptible to a range of pests and diseases which have to be controlled by the widespread use of chemicals, such as fungicides for late blight, nematicides for cyst nematodes and insecticides for aphid-transmitted virus diseases. This is particularly true of cultivars for processing, where old ones such as Russet Burbank and new disease-susceptible ones such as Shepody are increasing in area. However, chemical control is

1 Cultivars with the processing quality demanded by the manufacturers of crisps (chips) and French fries.

Whilst many traits are important, particularly adequate dry matter content and fry colour, major thrust is still:

- resistance to low temperature sweetening (and hence dark, bitter-tasting, fry products) so that tubers can be stored at 2°C to 4°C to control the development of diseases, weight loss and sprouting in store, with reduced reliance on sprout inhibiting chemicals.

2 Cultivars with the table quality demanded by supermarkets.

Again, many traits are important: tubers must be resistant to after-cooking-blackening, then:

- attractive skin finish paramount
- flavour and texture as judged by taste panels
- low levels of glycoalkaloids
- special purpose cultivars e.g. salad and punnet types

3 Combining quality with durable resistance to pests and diseases

Priorities for resistance:

- potato cyst nematodes, particularly *G. pallida* - the most serious pest problem in UK
- late blight (in foliage and tubers) - world-wide problem, concern about new blight populations
- blackleg and powdery scab - common criticisms of Scottish seed
- blemish diseases^(a) - supermarkets want good skin finish
- storage diseases^(b) - less important now, but cannot ignore
- viruses:

PLRV	}	- most serious worldwide
PVY		
TRV	}	- cause of spraing in tubers, particularly those of some important processing varieties
PMTV		
PVX		- less important now

4 Cultivars with potential for seed export to southern Europe and N. Africa

- resistance to warm temperature diseases and pests e.g. early blight, *Fusarium* dry rots, *Verticillium* wilt and potato tuber moth
- resistance to abiotic stresses e.g. heat, cold, drought, salinity

^(a)silver scurf, black dot, black scurf, skinspot

^(b)gangrene, dry rot

Table 1 Priorities for potato improvement.

expensive, not always effective, and raises environmental and food safety concerns, particularly over large-scale insecticide use and pesticide residues in tubers for human consumption. Hence, cultivars with higher levels of disease and pest resistance are highly desirable, but they must retain the marketable yield and quality required for a modern cultivar to be successful.

Although Britain does not have a potato starch industry, it is worth mentioning that the potential variation in the chemical and physical structure of starch is immense and, hence, there is tremendous scope to produce novel starch for use both in the food and non-food market sectors. Plant breeding and biotechnology have a major rôle to play in generating new starches, as already seen in The Netherlands with the development of amylose-free potatoes by genetic modification of the starch variety, Karnico¹. Amylose production was completely suppressed by antisense, RNA-mediated inhibition of granule-bound starch synthase, an approach made possible by the identification of an amylose-free mutant produced by techniques associated with conventional breeding.

It may also be possible to engineer the tuber synthesis of commercial quantities of fructans from sucrose for use in the food industry, or modify potatoes to produce and store novel compounds such as pharmaceuticals². Finally, it might be worth considering improvements in the nutritional value of what is already a highly nutritious food, by correcting its methionine and cysteine deficiency with genes encoding proteins rich in these amino acids.

Germplasm for potato improvement At the beginning of the 20th century, progress in potato breeding was being impeded by a narrow genetic base tracing back to the few original introductions of *S. tuberosum* subsp. *andigena* from South America to Europe in the latter part of the 16th century, limited further casual introductions in the 17th and 18th centuries, and a single cross with a Chilean *Tuberosum* (*S. tuberosum* subsp. *tuberosum*) in the 19th century (Fig. 1).

Furthermore, it is believed that relatively few of the 228 wild tuber-bearing taxonomic species of the genus *Solanum* were involved in the early domestication process in the Andes - probably just several closely related and inter-fertile members of series *Tuberosa*. Compared with the wild species, cultivated potatoes also evolved under a very limited range of environmental conditions in cool temperate regions. As a

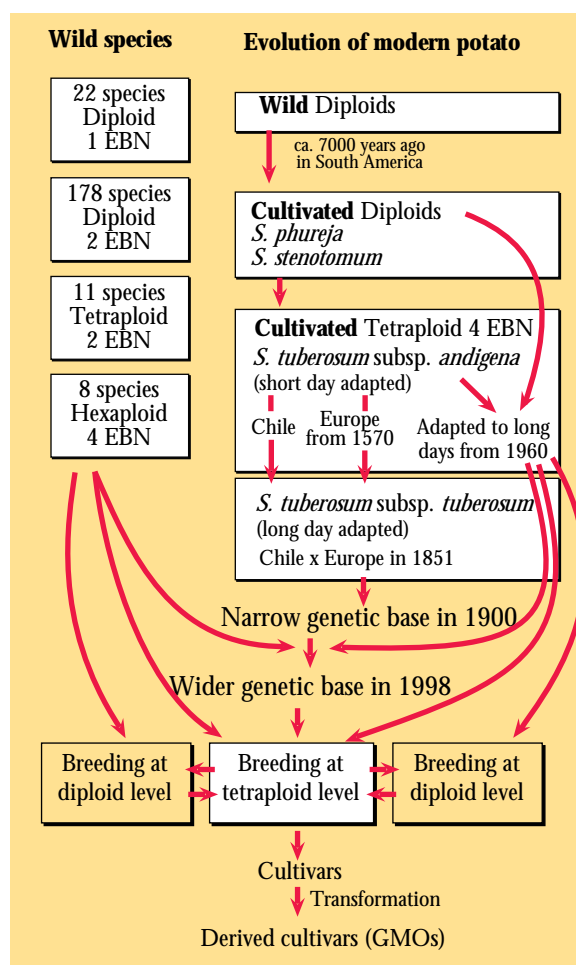


Figure 1 Germplasm for potato improvement.

consequence, they were often unable to resist the attacks of pests and diseases occurring over the much wider range of conditions in which they eventually became cultivated.

During the 20th century, the genetic base of the European potato (*S. tuberosum* subsp. *tuberosum*) has been widened in a number of ways, as shown in Figure 1. At SPBS/SCRI, high levels of resistance to viruses PVX and PVY, to cyst nematodes and to late blight have been introgressed from wild and cultivated species, and have proved sufficiently durable to remain useful today, with the exception of R gene resistance to late blight. However, it is hoped that the high levels of field resistance achieved in the SCRI-bred cultivars, Torridon and Stirling, will prove more durable, despite also being derived from relatively few accessions of *S. demissum*. Encouragingly, recent unpublished results from an experiment in CIP's Global Initiative on Late Blight³ have confirmed that Torridon and Stirling are highly resistant in a wide range of environments.

Nevertheless, as insurance against lack of durability in the longer term, new sources of resistance to late blight are being evaluated from *S. papita* and *S. verrucosum*, and to cyst nematodes from *S. boliviense*, *S. kurtzianum* and *S. sparsipilum*.

SCRI also has long-day adapted populations of *S. tuberosum* subsp. *andigena* (Neotuberosum) and *S. phureja*/*S. stenotomum* derived from accessions of the Commonwealth Potato Collection (CPC) through the work of Simmonds, Glendinning and Carroll in the 1960s (see Bradshaw & Mackay⁴ for brief review). Experience has shown, however, that it is relatively easy to introgress desirable genes from short-day adapted *S. tuberosum* subsp. *andigena* into clones capable of becoming commercially successful cultivars, and hence the long-day adapted *S. phureja*/*S. stenotomum* (also referred to as *S. tuberosum* Group Phureja/Stenotomum) material looks set to have a greater impact than Neotuberosum. It appears to be a good source of resistance to *Erwinia* soft rot and blackleg, powdery scab and skin spot, as well as having interesting cooking qualities. Indeed, although this adapted diploid population has only 60 to 70 per cent of the yield of tetraploid cultivars, there is interest in it as a speciality vegetable and MRS Ltd entered a commercially-promising clone into National List Trials in 1998.

Finally, clones resistant to low temperature sweetening, including one which became cv. Brodick, and others with simply inherited resistance to PLRV multiplication, have been identified in SCRI's tetraploid breeding material.

In planning future breeding work, a balance needs to be kept between making use of the genetical variation already available in *S. tuberosum* subsp. *tuberosum*, utilising long-day adapted *S. tuberosum* subsp. *andigena* and *S. phureja*/*S. stenotomum*, and locating and introgressing new genes from wild and cultivated species. During the 20th century, samples of many of these species have been collected and held in international germplasm collections such as the CPC, which is kept at SCRI in true seed form and contains representatives of 81 species. The use of molecular marker technology to study the genetic differences and similarities among this germplasm, should assist breeders to make more rational decisions on its utilisation, and should also help to establish core collections of germplasm for detailed evaluation. Although there is scope for further understanding of species relationships, it would appear that breeders can introgress genes from virtually any potato species into *S. tubero-*

sum [by manipulating effective ploidy as determined by endosperm balance number (EBN) or by embryo rescue] and somatic fusion may widen opportunities still further. As many wild species are diploids which readily cross with dihaploids (2 sets of chromosomes) of *S. tuberosum* (both 2EBN), there is scope for breeding at the diploid level before returning to the tetraploid level, but the optimum amount is still a matter for debate and further genetical research.

Genetically modified potatoes Today, the genetic improvement of existing cultivars with specific genes is a reality, made possible because the potato has proved amenable to *Agrobacterium tumefaciens* Ti plasmid-mediated genetic transformation, although a major research effort is always required to isolate, clone and incorporate a desired gene into the Ti plasmid. The first such derived commercial cultivar was Monsanto's NewLeaf™ Russet Burbank with Bt (*Bacillus thuringiensis*) resistance to Colorado beetle, which was granted registration in the USA in 1995. NewLeaf Plus™, with the addition of replicase-mediated resistance to PLRV, is set to follow this year. In

Europe, the first transgenic potato in agriculture is almost certain to be a Dutch amylose-free starch cultivar, as mentioned earlier. However, whether or not SCRI becomes actively involved in releasing genetically modified cultivars, as opposed to doing transgenic research, will probably be determined more by who owns the relevant patents and intellectual property than by what is biologically feasible and desirable.

In the meantime, three main thrusts to work on genetically modified potatoes can be discerned. 1) The molecular cloning of natural resistance genes and their transfer into well-adapted but susceptible cultivars is being pursued in a number of laboratories world-wide. 2) The search for novel forms of genetically-engineered resistance to pests and diseases constitutes a major effort at SCRI and elsewhere. SCRI virologists have demonstrated the effectiveness of coat protein-mediated resistance to PLRV and PMTV, and others have done the same for PVX and PVY. Genes coding for lytic enzymes from bacteria and insects are being evaluated at a number of laboratories world-wide as a way to achieve transgenic resistance to a

Further research and development required:

Anther (microspore) culture

- may prove better than inducer pollinations for dihaploid and monohaploid production of any genotype in large numbers for breeding and genetics at diploid and monoploid level

Disease and quality tests

- need ones that breeders can use on the few tubers available early in breeding programme but which truly reflect field and processing performance

Genetic (molecular) markers

- for marker-assisted-selection, tracking introgression, identifying sexual and somatic hybrids, fingerprinting new cultivars for identification, prerequisite of map-based cloning, assessing biodiversity in germplasm collections, choosing parents that complement one another genotypically

Micropropagation

- to increase rate of multiplication and hence availability of new cultivars, and controls for experiments - fairly routine but some recalcitrant genotypes

Progeny testing

- to identify best parents and crosses - very useful, but not yet available for all economically important traits e.g. blackleg and powdery scab

Protoplast fusion

- still has a place as a way to overcome barriers to sexual hybridisation with wild species and for limited chromosome transfer, but genotype-dependent, and barriers can be overcome by manipulating ploidy levels etc.

Transformation (*Agrobacterium*) and regeneration

- for production of transgenic potatoes - still some difficult cultivars - and there are limits to size of DNA in vector

Table 2 Enabling technologies for potato improvement.

number of bacteria and fungi, and a whole range of novel strategies can be anticipated, along with increased understanding of the biochemical basis of host-pathogen interactions. However, it is too early to say which will be successful in providing high levels of durable resistance. 3) Transgenic approaches at SCRI and elsewhere have also provided new ways of understanding and manipulating carbohydrate metabolism aimed at developing genetically in-built resistance to low temperature sweetening caused by an accumulation of glucose and fructose. There are a number of encouraging examples where about a 50 per cent reduction in sugar content can be achieved through modulating single genes, but it appears that the more extensive reductions which are needed will require the concerted regulation of more than one gene. This in turn will require multiple transformation or appropriate new vectors (Howard Davies, personal communication).

It would appear that the genetic modification of existing and future cultivars will have a major place in agriculture, provided that the general public is satisfied by adequate scientific evidence that it is safe to release transgenic potatoes into the environment, and that it will be safe to eat their tubers. This will require the conventional skills of plant breeders to test and trial such material, as well as ensuring its agronomic suitability.

Enabling technologies for potato improvement The strategies and methods for achieving the breeding objectives outlined earlier, depend on the enabling technologies available, as well as the germplasm; and so will the rate of progress. The key technologies now being used, or under development, are listed in Table 2 and deserve further comment.

Many modern aspects of potato improvement have developed from the amenability of the potato to tissue culture techniques. These include the ability to infect many types of potato tissue with *Agrobacterium tumefaciens* for transformation, regeneration of plants from culture, rapid methods of micro-propagation, anther culture and protoplast fusion. However, some of these techniques are still genotype-dependent, and there is certainly scope for further increases in efficiency.

Rapid progress in potato breeding requires the correct choice of parents and crosses, and efficient selection procedures. At SCRI, the development, validation and use of seedling and tuber progeny tests for disease resistance and quality traits have proved of immense value in selecting the most promising progenies for

further breeding at the earliest opportunity, as well as for using biometrical methods to study the inheritance of quantitative traits and to identify the best parents for future breeding. Such research has already led to the submission of three clones for National Listing within 6 years of crossing (Ann. Rep. 1996/97, 40-45). Likewise, the development of reliable tests on clones has enabled the most promising ones to be identified in the selected progenies, and multiplied for evaluation as potential new cultivars. The two most important traits for which we still require reliable progeny tests are blackleg and powdery scab resistance. This is because it has proved difficult so far to get symptom expression of these diseases under glasshouse conditions, and success in field trials is weather-dependent.

It can be seen in Table 2 that many applications are envisaged for molecular marker technology, including molecular-marker-assisted selection strategies for the introgression of desirable genes from wild species and for breeding at the diploid and tetraploid level. These strategies should avoid the problems associated with selection for the many economically important traits which are substantially modified by environmental factors or which can only be detected in special tests, for example, virus resistance. The proviso is that there has to be tight linkage between the markers and the desired (or undesired) genes, the ideal being markers within the desired genes. In the longer term, locating the genes underlying quantitative traits through their linkage to molecular markers, should have a big impact on determining breeding strategies and methods, because one will know the number of genes involved, their chromosomal locations, and the magnitudes and natures of their actions.

Concluding remarks Although this article has looked at the way ahead at SCRI, many of the objectives, strategies and methods are relevant to potato breeding world-wide. Hence, one further way ahead is likely to be increased participation in international collaboration on what is, after all, the fourth most important food crop in the world after wheat, maize and rice.

References

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