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Improving the yield, processing quality and disease and pest resistance of potatoes by genotypic recurrent selection

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Abstract

This paper starts with a brief summary of potato germplasm collections, potato domestication, the introduction of the crop to Europe and its subsequent history, and potato breeding. It then describes a potato breeding programme which was started at the Scottish Crop Research Institute (SCRI) in 1991 with the aim of improving the yield, processing quality and disease and pest resistance of potatoes by genotypic recurrent selection. The initial germplasm was past introgressions from the Commonwealth Potato Collection. The programme made use of progeny tests developed at SCRI and has involved cycles of crossing, selection between progenies (full-sib families) and clonal selection within the selected families. In the fourth cycle we showed how new breeding objectives and germplasm could be accommodated whilst continuing to maintain the progress which was confirmed at the end of that cycle. The paper concludes with brief comments on a continuing need in Europe for new cultivars to increase potato usage in economically and environmentally sustainable ways.

Keywords

Commonwealth Potato Collection, introgression, population improvement, potato breeding, water and fertiliser use

Introduction

Wild relatives and genebanks

Recognition of Central and South America as the centres of origin and diversity of tuber-bearing *Solanum* species resulted in numerous collecting expeditions, from those pioneered by the Russians in the 1920s to the more recent ones in the 1990s. The collecting expeditions led to the establishment of a number of potato germplasm collections:

- World Collection at International Potato Center (CIP), Lima, Peru
- Commonwealth Potato Collection (CPC), Dundee, Scotland
- Dutch-German Potato Collection (CGN), Wageningen, The Netherlands
- Groß Lusewitz Potato Collection (GLKS), IPK, Groß Lusewitz, Germany
- Potato Collection of Vavilov Institute (VIR), St. Petersburg, Russia
- US Potato Genebank (NRSP-6), Sturgeon Bay, Wisconsin, USA
- Potato Collections in Argentina, Bolivia and Peru

At SCRI, since 1965, we have maintained the CPC, an extremely valuable germplasm collection dating back to 1938. It comprises 1500 accessions: two thirds wild species (80), one third cultivated potatoes (BRADSHAW and RAMSAY 2005).

Domestication

More than 7000 years ago, domestication took place in the Andes of southern Peru from the northern group of members of the *S. brevicaule* complex of species (SPOONER et al. 2005). The result of domestication was the diploid species *S. stenotomum* from which six other cultivated species were derived, including *S. tuberosum*, which became the most widely grown one in South America, and *S. phureja* which became the second most widely grown one. *S. tuberosum* is a tetraploid ($2n = 4x = 48$) species that displays tetrasomic inheritance (HAWKES 1990). The short-day adapted landrace populations of the Andes and the long-day adapted ones of coastal Chile are genetically distinct groups (RAKER and SPOONER 2002) that have been classified both as separate subspecies (*S. tuberosum* subsp. *andigena* and subsp. *tuberosum*) and as groups within *S. tuberosum* (Gp Andigena and Gp Tuberosum), along with the other cultivated potatoes (DODDS 1962). Initially the potato was a staple food; but after its introduction to Europe and North America it was selected for use as a table vegetable, for processed products (French fries, crisps) and for starch production.

Potato history in Europe

The potato was first introduced from South America into the Canary Islands around 1562, and from there to mainland Europe (HAWKES and FRANCISCO-ORTEGA 1993) in subsequent years. It now seems safest to assume that the early introductions of cultivated potatoes to Europe came from both the Andes and coastal Chile. Analysis of DNA from 49 herbarium specimens has confirmed the presence in Europe of Andean potatoes from around 1700 and Chilean potatoes from 1811 (AMES and SPOONER 2008). Key stages in its history in Europe were:

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- Introduced at end of 16th century.
- Initially a botanic curiosity.
- Potential as food crop first seen in Ireland at end of 17th century.
- The 18th century (the 1700s) saw the potato accepted as a foodstuff throughout Europe because of the need to overcome food shortages for military and economic development.
- French fries became a culinary item in France around 1800 and were introduced into England in the 1860s where they were soon sold with fish (fish and chips). Industrial production developed from the1950s.
- Potato chips (crisps) have a US origin dating back to 1853, but commercial production did not get underway until 1895. From the 1920s to the present day there have been many technical innovations.

Potato breeding

Potato breeding began in 1807 in England when Knight made the first recorded hybridizations between varieties by artificial pollination (KNIGHT 1807). It then flourished during the second half of the 19th century when many new cultivars were produced by farmers, hobby breeders and seedsmen, and has continued to the present day. The period since 1900 has seen the development of scientific breeding methods based on genetic principles. For example, this was the aim of the Scottish Plant Breeding Station (SPBS) which was founded in 1920.

Early on at SPBS it became apparent that the European potato lacked genes for resistance to what were, or became, major diseases and pests. Hence desirable genes were introgressed from the wild and cultivated species of Latin America; first for late blight resistance (*Phytophthora infestans* (Mont.) de Bary) from 1932, then for resistance to *potato virus Y* (PVY) and *potato virus X* (PVX), from 1941, and finally for resistance to potato cyst nematodes (PCN, *Globodera rostochiensis* and *G. pallida*) from 1952. Past introgressions were (BRADSHAW and RAMSAY 2005):

- Late blight resistance from *S. demissum*
- *Ny* gene for PVY resistance from *S. demissum*
- *Ny* gene for PVY resistance from *S. chacoense*
- *Ry* gene for PVY resistance from *S. stoloniferum*
- *Rx* gene for PVX resistance from *S. acaule*
- *Rx* gene for PVX resistance from *S. tuberosum* Gp Andigena
- *H1* gene for *G. rostochiensis* resistance from *S. tuberosum* Gp Andigena
- 'H3' *G. pallida* resistance from *S. tuberosum* Gp Andigena
- PCN resistance from *S. vernei*

Combining late blight resistance, virus resistance and two sources of PCN resistance

By 1990 cultivars and clones were available with resistances to late blight, viruses and potato cyst nematodes; but no systematic attempt had been made to combine them in a single cultivar, although parents for crossing had been chosen to complement one another for desirable characteristics.

Therefore, in 1991, a multitrait (MT) breeding programme was started at SCRI to combine quantitative resistances to late blight and the white potato cyst nematode (*G. pallida*) with commercial worth as judged by breeders through a visual assessment of tubers (breeders' preference) (BRADSHAW et al. 2003). Quantitative resistances were used because major gene resistance to late blight had not proved durable and major gene resistance to pathotype Pa2/3 of *G. pallida* had not been found. The parents with resistance to pathotype Pa2/3 of *G. pallida* also had either major gene (*H1*) or quantitative resistance to pathotype Ro1 of *G. rostochiensis*, the golden potato cyst nematode, pathotypes Pa2/3 and Ro1 being the ones present in Britain. Parents were also included with resistance to *potato leafroll virus*, *potato virus Y* and *potato virus X*, but time and resources did not permit direct selection for virus resistance in each generation (SOLOMON-BLACKBURN and BRADSHAW 2007). Such an overall combination of traits was, and still is, lacking in European potato cultivars, despite 50 years of breeding effort.

The breeding programme has made use of progeny tests developed at SCRI (BRADSHAW et al. 2003) and has involved cycles of crossing, selection between from 120 to 145 progenies (full-sib families), and clonal selection within the selected progenies. We have shown that the breeding scheme can operate on a three year cycle with limited within progeny selection, and on a five or six year cycle with more extensive within progeny selection. Six years are required when resistance to late blight is assessed in the tubers as well as the foliage. The more extensive within progeny selection is recommended once genes have been combined from sufficient parents to achieve one's objectives. Even so, these cycle lengths are much shorter than the time from making a cross to releasing a new cultivar which has averaged 13 years since 1975, a year longer than the target of 12 years (MACKAY 2005). This would be the cycle time if one waited for release of a cultivar before using it as a parent. Furthermore, we have previously shown that progeny testing provides a solution to the common but ineffective practice in potato breeding of intense visual selection of quantitative traits between seedlings in a glasshouse and spaced plants at a seed site (BRADSHAW and MACKAY 1994, BRADSHAW et al. 1998).

The yield increase after three cycles of indirect selection through breeders' visual preference was only modest because it was operating against a decrease which would occur in the absence of selection. A practical improvement in the scheme would be to increase the number of progenies assessed to over 200, given the moderate to high heritabilities of the progeny and clonal tests. But this would require a considerable effort because the success rate achieved with the potato pollinations was typical at just over 30%.

In the fourth cycle we showed how new breeding objectives and germplasm could be accommodated whilst continuing to maintain progress, something that is important in any long term breeding strategy. It was decided that clones emerging from the programme for use as parents in commercially funded breeding programmes would be of more value if they had improved processing quality, given that 50% of the British potato crop is now processed. Hence five SCRI cultivars with processing quality were added as parents together with three new blight resistant parents that were available from another project. Blight resistance could also be classified as a new breeding objective because of changes in the *P. infestans* population in Britain.

The new germplasm continued in the breeding scheme only if it was selected from the progeny tests which included existing germplasm. Thus 54 successful crosses were made in 2003 (cycle 4) in addition to the 68 from the 15 MT parents from cycle 3, but just six progenies were good enough to enter the breeding programme along with 19 from the 68 progenies. When the recurrent selection operates on a five or six year cycle to include clonal selection, potential new parents can be included for assessment, and these could include new cultivars selected from earlier cycles. Again, however, their progenies would survive only if superior to those from the most recent cycle. If, as a result, germplasm containing desirable genes failed to enter the breeding programme, then consideration should be given to introgression of the genes or improvement of the germplasm in a separate population improvement programme.

The 108 clones selected from cycle 4 were assessed in 2007 and 2008 and compared with Maris Piper, the most widely grown cultivar in Britain. These assessments confirmed that none of the original 36 parents combined late blight and *G. pallida* resistance whereas this was achieved with two of the 15 clones selected from the third cycle and 23 of the 108 clones selected from the fourth cycle. They had foliage blight scores greater than or equal to 5.5 (≤ 40% necrotic tissue) compared with a score of 2.5 (> 80% necrotic tissue) for susceptible cultivar Maris Piper, 25 days after infectors were placed in the spreader rows of the field trial. They had less than 22.5% of their tubers infected with tuber blight, compared with 45% for Maris Piper. They also had *G. pallida* scores of ≤ 3.08 (square root of cyst number) which was taken as the cut-off point for resistance because it was the highest score of the nine original parents with resistance. Among the 23 clones were 16 with an acceptable fry colour after storage at 10°C (score ≥ 4.5, on a 1 (dark) to 9 (light) scale), and of these, five were not significantly ($P > 0.05$) lower yielding than Maris Piper (yields > 15.66 kg/plot compared with 19.41).

Three of these were used as parents in commercially funded breeding programmes in 2008, together with a lower yielding one which molecular markers indicated had *S. tuberosum* Gp Andigena derived *G. pallida* resistance. Also used were four clones that proved more susceptible to tuber blight once these results were known in 2008. Three of these clones were relatively high yielding and one had good fry colour after cold storage at 4°C. It can therefore be concluded that good progress has been made in producing clones which combine resistances to late blight and potato cyst nematodes with improved yield and processing quality.

Future needs and prospects

There is a continuing need in Europe for new cultivars to increase potato usage in economically and environmentally sustainable ways. Economic benefits will come from cultivars that give higher yields of saleable product at less cost of production. However, it is not obvious that this can be achieved from crosses between modern cultivars, remembering that potatoes have a high harvest index. Yield heterosis (hybrid vigour) is seen in crosses of modern cultivars to long-day adapted populations of Gp Andigena and Gp Phureja/Stenotomum; but these populations need improving for other traits to have real impact because they are not as good as intensively selected Gp Tuberosum.

Environmental benefits will come from cultivars that have inbuilt resistance to pests and diseases, particularly to *G. pallida* and *P. infestans*. In England and Wales over 60% of potato fields are infested with *G. pallida* and 10 late blight sprays are normal practice as susceptible cultivars are widely grown. Whilst good progress is being made with resistance to PCN, durable resistance to late blight remains elusive. A new genotype of *P. infestans*, 'blue' 13_A2, has dramatically increased in Britain over the three years 2005 to 2007 to account for more than 70% of the population (COOKE et al. 2008). It is an aggressive metalaxyl resistant A2 mating type isolate which has overcome the resistance in cultivars Stirling and Torridon, two out of the best three parents used for blight resistance in 1991. Hence further new sources of resistance are desirable despite two of the 15 clones selected from cycle 3 and 23 of the 108 clones selected from cycle 4 having useful resistance to genotype 'blue' 13_A2 as well as to *G. pallida*. Resistance to *P. infestans* genotype blue_13 has been found in the CPC in accessions of *S. brachycarpum*, *S. bulbocastanum*, *S. capsicibaccatum*, *S. chacoense*, *S. commersonii*, *S. demissum*, *S. iopetalum*, *S. okadae*, *S. polyadenium*, *S. stoloniferum* and *S. verrucosum*; but it is not obvious if they will prove durable.

Environmental benefits will also come from new cultivars that can make better use of water and fertilisers (N and P). In Britain most potato growing is in nitrate vulnerable zones; potatoes occupy 2.5% of arable land but consume 8% of P-fertiliser and P enrichment of surface water is a problem; and half of the irrigation water applied in England goes on potatoes. With climate change there is likely to be competition for water resources between agricultural, industrial and domestic users. It is not yet clear if cultivated potatoes or wild species will provide the necessary germplasm for improvement in these traits, but our initial focus is on root architecture and its effect on water and mineral uptake and we are looking at the correlation between field and glasshouse grown potatoes.

Prospects are good for new cultivars that can be stored below 6°C without sweetening (reducing sugar production) and hence can be used out of storage for producing acceptable fried products. Such storage would result in a reduction in the use of sprout suppressants when compared with current storage at 6°C to 10°C. The use of such cultivars may also result in lower levels of acrylamide in fried products, current levels being perceived as a potential health risk.

Finally new cultivars, such as the Phureja cultivars released from SCRI since 2001, are likely to provide consumers with novel potato products and convenience foods and potatoes with improved flavour and nutritional and health benefits.

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