Applied potato genetics and breeding: potato improvement by multitrait genotypic recurrent selection

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Introduction Today, in Britain, the most widely grown potato (*Solanum tuberosum* subsp. *tuberosum*) 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 [*Phytophthora infestans* (Mont) de Bary], nematicides for potato cyst nematodes (PCN), and insecticides for aphid-transmitted virus diseases. However, chemical control is 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, new cultivars with higher levels of disease and pest resistance are highly desirable but, for commercial success, they must have acceptable marketable yields and meet the quality requirements of processors and supermarkets (Ann. Rep. 1997/98, 76-80).

Therefore, in 1991, we set up an experimental breeding programme designed to combine quantitative resistances to late blight and the white potato cyst nematode [*Globodera pallida* (Stone)] with commercially acceptable tuber yields and quality. Such resistances were available in *S. tuberosum* germplasm held at SCRI as a result of past breeding and introgression from wild and short day-adapted cultivated species, but had not been incorporated into widely grown cultivars. We decided to concentrate on quantitative field resistance to late blight because it has proved more durable than dominant R-gene resistance, which the fungus can readily overcome. We also decided to select for resistance in the tubers as well as in the foliage because the one does not guarantee the other and susceptible tubers can be infected by spores produced over a relatively long period of time from the slowly spreading sporulating lesions of a leaf-resistant cultivar. Whilst cultivars with major gene resistance (H1) to the common UK pathotype (Ro1) of the golden potato cyst nematode (*G. rostochiensis*) were being widely grown, only quantitative resistance was available to the common UK pathotype (Pa 2/3) of *G. pallida* (Ann. Rep. 1995, 30-34). It was also thought desirable to include in the breeding programme parents with virus resistance, particularly to Potato Leaf Roll Luteovirus (PLRV) and Potato Y Potyvirus (PVY). However, it was not possible to select for virus resistance during the programme, although the products of this research will be assessed for their resistance.

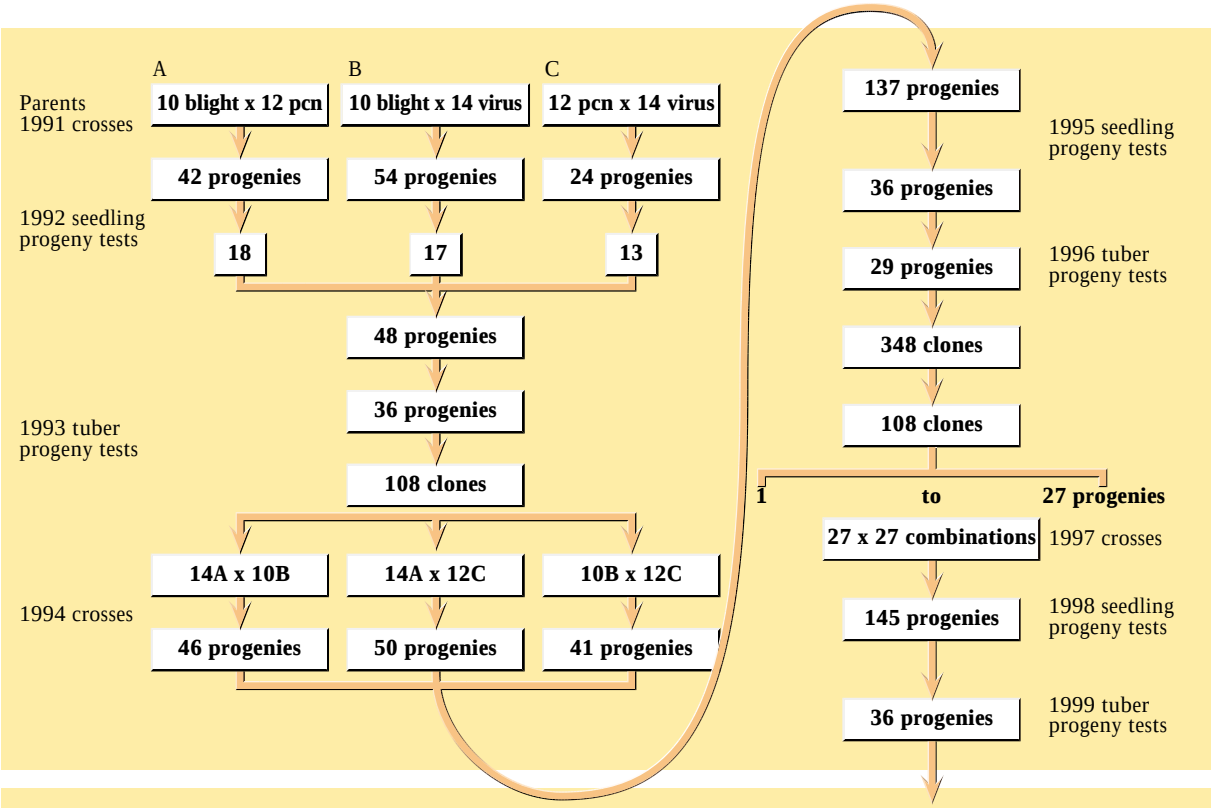

Figure 1 Multitrait genotypic recurrent selection programme.

The breeding programme had important research objectives because it was designed to use the seedling and tuber progeny tests developed at SCRI (see Bradshaw & Mackay[1] for review) for the first time in a multitrait genotypic recurrent selection programme. In genetical terms, the aim was to increase the frequency of desirable genes in the breeding material over a number of generations of recurrent selection, and in each generation to seek the best genotypes available for multiplication as new cultivars or parental material for future use. Clearly the shorter each cycle in years, the faster the overall rate of progress. In practice, we found that we could operate on a three-year cycle (Fig. 1) comprising crossing, seedling progeny tests, and tuber progeny tests each cycle.

Outline of the programme In order to combine desirable genes from three sets of parents, pair crosses were made in 1991 between the blight and PCN resisters (set A), the blight and virus resisters (set B), and the PCN and virus resisters (set C), followed in 1994 by crosses between progenies from different sets (AxB, AxC and BxC). Then, in 1997, crosses were attempted between the 27 progenies selected from the progeny tests. The overall success rate for crossing in 1991, 1994 and 1997 was 28%, 32% and 41% of desired combinations, figures that were typical for tetraploid potatoes.

In the 1992 seedling progeny tests, any progenies that were below average for breeders' visual assessment of tubers for commercial worth (breeders' preference) were eliminated, together with any that were below average for foliage blight and pcn resistance in set A, foliage blight resistance in set B, and PCN resistance in set C. In contrast, in 1995 and 1998, the best progenies were selected for further evaluation on the basis of a selection index, in which the breeders' preference, PCN and foliage blight scores in standard deviation units from their overall means were weighted by their heritabilities. Any progenies that subsequently proved too susceptible to tuber blight were also eliminated.

The best seedling progenies were grown in the field as tuber progenies at our high grade seed site (Blythbank Farm, Peeblesshire) in 1993 and 1996, and the same will happen in 1999. In 1993, two breeders visually selected the most attractive looking clone in each of three replicates for each of the 36 progenies to give 108 clones for the next round of crossing, as well as for evaluation as new cultivars. In 1996, a slightly different approach was taken. At harvest, the six most attractive looking clones from each of the two replicates of the 29 progenies were selected and tested for

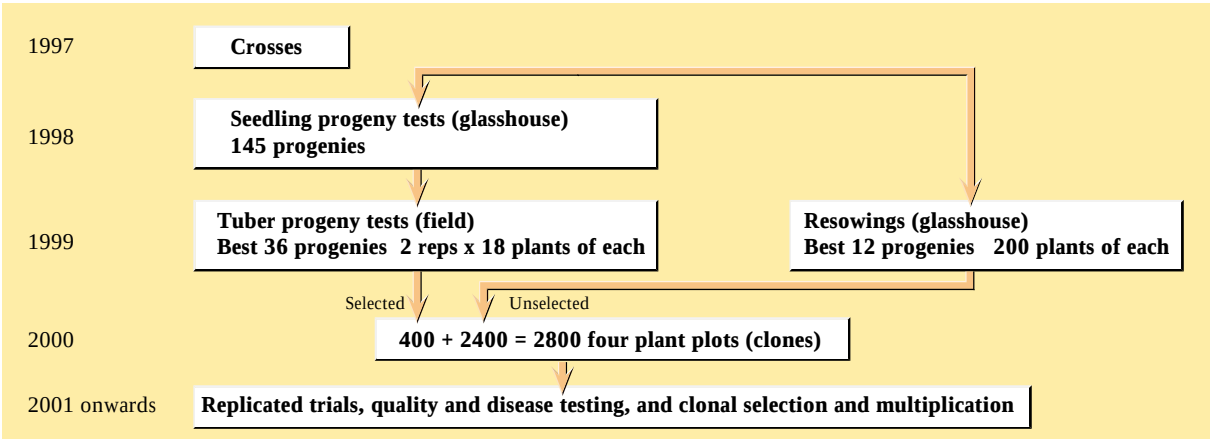

Figure 2 Cultivar production.

PCN resistance from 30 January to 16 April 1997. The 108 most resistant clones (cyst counts <40% of control cultivar Desiree) were then used as parents for the next round of crossing, as well as for evaluation as new cultivars. In 1999, after harvest, a tuber progeny test for fry colour is going to be introduced into the programme, as has already been successfully done in our targeted and accelerated breeding of potatoes for processing quality (Ann. Rep. 1996/97, 40-45). In other words, the multitrait breeding programme is an evolving research project.

More plants have been raised from the best crosses of each cycle to provide further clones for evaluation as potential cultivars. This year (1999), for example, 200 true seeds from each of 12 of the best progenies from the 1998 seedling progeny tests have been sown in a glasshouse (resowings) to provide up to 2,400 clones for visual assessment in four-plant plots at our seed farm in the year 2000 (Fig. 2). The selected clones will then enter a multistage multiplication and selection programme involving replicated yield trials and quality and disease testing, as described by Bradshaw and Mackay[1], in order to provide potential cultivars to private companies for multisite trials and submission to National List Trials.

Progress to date An indication of our progress to date is given by the results of the 1998 seedling progeny tests (Fig. 3). There was enough seed for two replicates of 25 seeds of 145 progenies for each of the breeders' preference, PCN and foliage blight progeny tests, and of 122 progenies for the tuber blight progeny test. Breeders' preference is the only progeny test where individual clones (2 x 18) within progenies are assessed and a mean taken. This is done by at least two breeders on a 1 to 9 scale of increasing preference, where 3 or less is unacceptable and 5 or more is acceptable, with 4 borderline.

The broad sense heritabilities (h^2_B, proportion of variation which was genetical) ranged from 0.39 for foliage blight to 0.82 for tuber blight, and were similar to those found in 1992 and 1995, except for foliage blight, which was slightly lower (0.55 in 1992 and 0.63 in 1995). The highest correlation between traits was the one between resistance to foliage blight and resistance to tuber blight, which was statistically significant (P<0.1%) but small in magnitude (r=0.35), and underlined the need to select for resistance to both in a breeding programme.

The 12 progenies selected for resowings in 1999 were chosen using a selection index based on Smith's[2] discriminant function for plant selection with relative

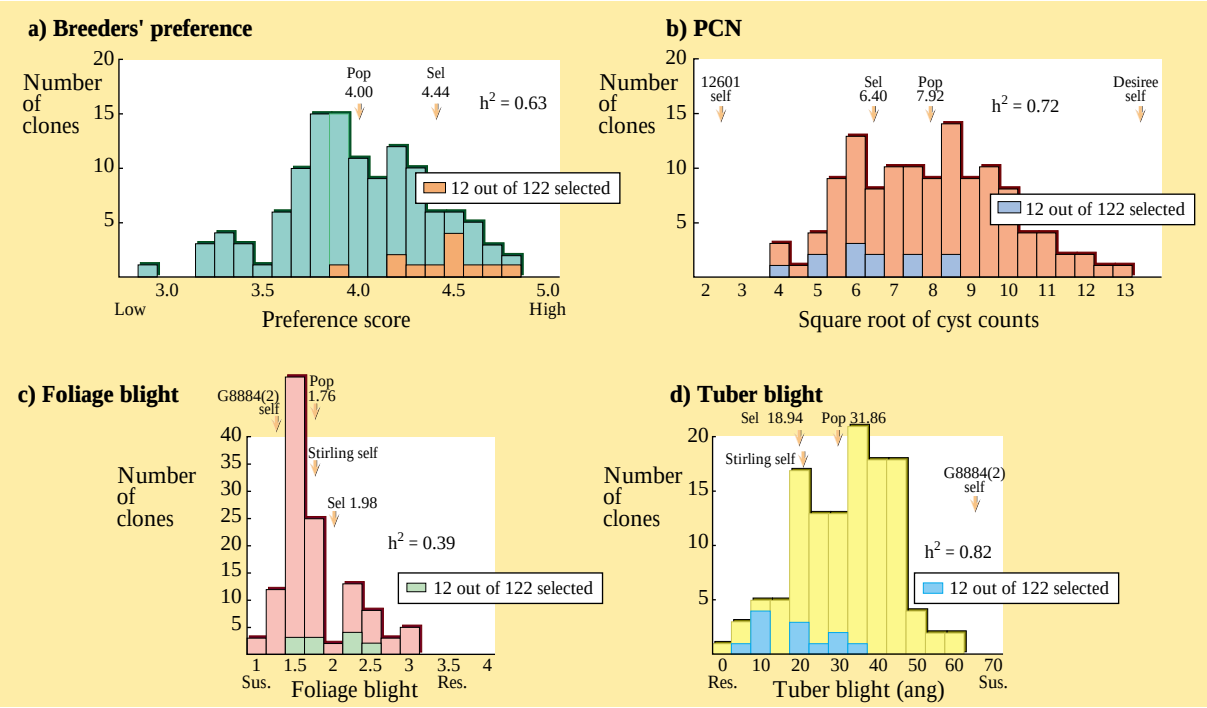

Figure 3 1998 progeny tests for a) breeders' preference; b) PCN; c) foliage blight; d) tuber blight.

economic weights in phenotypic standard deviation units of 1:1:½:½ for the four traits, so that foliage and tuber blight together were given a similar weight to breeders' preference and pcn. The mean of the 12 progenies was 4.44 for breeders' preference (individual clones:<4 reject, ≥5 definitely select); 6.40 for PCN, which was closer to the resistant than the susceptible control; 1.98 for foliage blight, which was better than the resistant control; and 18.94 for tuber blight, which was as good as the resistant control. Hence, in seeking new cultivars and parents from these progenies, there is a good chance of finding clones that are better than these means for all four traits, but it remains to be seen if they are as good as the best of the original parents for individual traits. This critical assessment will come in the year 2001, when the best clones from the 12 progenies are compared with the parents used in the original crosses.

Diallel analysis of variation in population The genetical variation in the multitrait breeding population has been evaluated through a 15 x 15 diallel set of crosses, including selfs and some reciprocal crosses, made in 1992[3] and subsequently assessed in seedling and tuber progeny tests. Five male fertile parents were chosen from each of the three sets of parents used in 1991. The large amount of GCA (General Combining Ability) variation found for breeders'preference, PCN, foliage blight and tuber blight was indicative of much additive genetic variance in the population. Furthermore, the only statistically significant ($P<0.05$) correlation between GCAs for different traits was a favourable one ($r=0.56$) between foliage and tuber resistance to late blight. It was concluded that prospects were good for simultaneously improving all four traits over a number of generations of multitrait genotypic recurrent selection. It was also concluded that the variation due to SCA (Specific Combining Ability), which was found for breeders' preference and tuber blight, could be exploited in selecting the best crosses for cultivar production. The assessment of other economically important traits, including yield and fry colour, was done on tuber progenies at our high grade seed site from 1994 to 1996, and in replicated ware trials in 1995 and 1996. Fry colour had the highest narrow sense heritability ($h_n^2 = 0.90$), measured as twice the GCA variance divided by the phenotypic variance (i.e. observed variation) of progeny means. Therefore, the 36 tuber progenies being evaluated in the breeding programme in 1999 will be selected for this important processing characteristic, as already mentioned. Emergence, maturity, yield, dry matter content and dormancy were identified as other traits that would respond to progeny (i.e. full-sib family) selection.

Future possibilities Although the diallel analyses provided valuable information about the genetic varia-

tion present in the multitrait programme for traits displaying continuous variation, they did not provide any clues as to the number of genes segregating, their chromosomal locations, or what they do. Therefore, two of the crosses from the diallel were chosen for a more detailed genetical analysis using molecular markers in collaboration with Robbie Waugh and his colleagues in the Potato Genomics Unit and with Christine Hackett in BioSS. AFLP markers have already been identified which are associated with resistance to foliage blight in cv. Stirling, resistance to *G. pallida* in clone 12601ab1 (ex. *S. tuberosum* subsp. *andigena*) and resistance to *G. pallida* in clone 12288af23 (ex. *S. vernei*), and which account for between 20% and 34% of the phenotypic variation. Hence, we can start to explore whether or not molecular marker assisted selection can improve the efficiency of the multitrait breeding programme, both for selecting parents for the next round of crossing, and for identifying superior genotypes within the best progenies at an earlier stage than could otherwise be done.

As the European potato is a tetraploid, which displays tetrasomic inheritance, it is also worth exploring whether or not faster progress is possible by haploidisation to the diploid level, followed by recurrent selection at the diploid level, before polyploidisation back to the tetraploid level for cultivar production. However, this will have to await the outcome of current research on microspore embryogenesis, because a much larger number of both male and female fertile dihaploids are required than has proved possible by the standard *S. phureja* inducer method.

References

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