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J. E. Bradshaw · M. F. B. Dale · G. R. Mackay

Use of mid-parent values and progeny tests to increase the efficiency of potato breeding for combined processing quality and disease and pest resistance

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Abstract A potato breeding strategy is presented which avoids the common but ineffective practice of intense early-generation visual selection between seedlings in a glasshouse and spaced plants at a seed site. Once pair crosses have been made, progeny tests are used to discard whole progenies before starting conventional within-progeny selection at the unreplicated small-plot stage. Clones are also visually selected from the best progenies for use as parents in the next cycle of crosses whilst they are multiplied to provide enough tubers for assessment of their yield and quality. Mid-parent values, as well as progeny tests, are then used to select between the resultant crosses. Material from other breeding programmes can be included in the parental assessments and used in the next cycle of crosses if superior. Finally, in seeking new cultivars, the number of clones on which to practise selection is increased by sowing more true seed of the best progenies, but without selection until the small-plot stage. Traits considered are resistance to late blight [*Phytophthora infestans* (Mont.) de Bary] and to the white potato cyst nematode [*Globodera pallida* (Stone)], fry colour and tuber yield and appearance, as visually assessed by breeders. The theoretical superiority of the strategy for seeking new cultivars lies in being able to practise between-cross selection for a number of economically important traits within 1 or 2 years of making crosses, something that is not possible on individuals as seedlings in the glasshouse or spaced plants at the seed site. This also means that full-sib family selection can be operated on a 3-year cycle, an improvement on current practice of clonal selection on what is often at least a nine-year cycle. New cultivars can be sought with more confidence from the best progenies in each cycle, and modern methods of rapid multiplication used to reduce the number of clonal generations required to find the best clones.

Keywords Potato breeding · Multi-trait selection · Progeny tests · Mid-parent values · Index selection

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J. E. Bradshaw (✉) · M. F. B. Dale · G. R. Mackay
Scottish Crop Research Institute,
Invergowrie, Dundee DD2 5DA, Scotland
e-mail: jbrads@scri.sari.ac.uk
Fax: +44-1382-568587

Introduction

Potato breeding has traditionally involved making crosses between pairs of parents with complementary features. The aim has been to generate genetical variation on which to practise phenotypic selection for clones with as many desirable characteristics as possible for release as new cultivars. Since the middle of the 19th century, many cultivars have been produced world-wide, with the 1999 World Catalogue of Potato Varieties (Hamester and Hils 1999) listing nearly 2,000 cultivars from 100 countries. Nevertheless, there is a continuing need for new improved cultivars and, in the UK, the priority is to combine high levels of durable disease and pest resistance with acceptable yields and the quality demanded by processors and supermarkets (Bradshaw et al. 1998a).

Bradshaw and Mackay (1994) cited the Scottish Crop Research Institute (SCRI) programme prior to 1982 as typical of potato breeding world-wide in that it used intense visual selection of seedlings and spaced plants which several independent reviews concluded were ineffective (Tai and Young 1984; Caligari 1992; Tarn et al. 1992; Bradshaw and Mackay 1994). Research at SCRI not only confirmed the ineffectiveness of visual selection of individual clones (Brown et al. 1984, 1987a) but also demonstrated that seedling progeny evaluation by breeders' visual preference scores could be used to reject entire crosses on the grounds that they were less likely than others to contain clones of commercial worth (Brown et al. 1987b,1988; Bradshaw et al. 1998b). Furthermore, it was shown that having practised this selection between crosses, visual selection within crosses became effective at the small-plot stage, with correlated responses for faster emergence, earlier maturity, higher yield and greater

regularity of tuber shape (Bradshaw et al. 1998b). However, greater overall benefits from selection first between and then within crosses were expected from subsequently sowing more seed of the best crosses (resowings) to increase their population size, and from simultaneously selecting for other traits in choosing those crosses (Bradshaw et al. 1998b). Therefore, at SCRI, the use of seedling progeny tests has been extended to incorporate selection for quantitative resistances to late blight [*Phytophthora infestans* (Mont.) de Bary] and the white potato cyst nematode [*Globodera pallida* (Stone)] as well as selection for visual preference (Bradshaw et al. 1995), and a tuber progeny test for fry colour has been used to identify the most promising crosses for processing (Mackay et al. 1997). Furthermore, all of these progeny tests have been used in a breeding programme set up in 1991 to combine quantitative resistances to late blight and the white potato cyst nematode (pcn) with commercially acceptable tuber yield and quality, but including parents with resistance to potato leaf roll luteovirus (PLRV), potato Y potyvirus (PVY) and potato X potexvirus (PVX) (Bradshaw et al. 1999). Multi-trait (MT) full-sib recurrent selection has been practised on a 3-year cycle with new cultivars sought from resowings of the best crosses (progenies) in each cycle.

This paper presents the results of breeding experiments from the third cycle of the MT programme involving the assessment of parents as well as progenies and discusses how they can be used to improve the efficiency of potato breeding for combined processing quality and disease and pest resistance. The strategy advocated is a compromise between the high-cross-number with small-progeny-size strategy of simple theory, in which no information on the parents is available (Wricke and Weber 1986), and the low-cross-number with large-progeny-size one advocated by Witcombe and Virk (2001) from more realistic theoretical and practical arguments.

Materials and methods

The multi-trait breeding programme

Thirty-nine parents were used to initiate the MT breeding programme at SCRI in 1991 (Bradshaw et al. 1999). They comprised ten parents with field resistance to late blight derived from *S. demissum*; 12 with resistance to the white potato cyst nematode of which six had resistance derived from *S. vernei*, four from *S. tuberosum* subsp. *andigena*, and two from both these sources; 14 with virus resistance derived from a number of sources including *S. demissum*; and three additional parents with good fry colour. In order to combine desirable genes from the 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 (A×B, A×C and B×C). Then, in 1997, crosses were attempted between the 27 progenies selected from the 1995 seedling and 1996 tuber progeny tests, and 154 out of 351 combinations were achieved. The 108 parents used in the 1997 crosses comprised from one to nine clones from each of the 27 progenies and resulted in a new set of 192 progenies (full-sib families) for testing. The numbers of tubers of parents and true seeds of progenies determined the extent of their use in the breeding experiments described in this paper.

Use of seedling progeny tests and mid-parent values of crosses already made to select between crosses

When a breeding programme continues with another round of crosses (recurrent selection), the breeder faces the dilemma of whether to wait until potential parents have been assessed for all important traits or to make crosses at random between clones which have been visually selected from the best progenies. A compromise is to do the latter while assessing the clones used as parents, and then to use mid-parent values as well as progeny tests to select between the crosses actually made. This combined use of progeny tests and mid-parent values is illustrated with the 96 progenies which were included in all of the 1998 seedling progeny tests and whose 62 parents were multiplied in four-plant plots in 1997 and assessed in a yield trial at Gourdie Farm, Dundee, in 1998. Some of the 62 parents were used only once, whereas one clone was a parent in 21 crosses. The seedling progeny tests were those for commercial worth of tubers [breeders' preference (bp)], foliage blight (fb), tuber blight (tb) and pcn. Fry colour (fry) was chosen to illustrate the use of mid-parent values because it cannot be reliably assessed on tubers from seedlings, but a high correlation of 0.86 between mid-parent values and offspring means had been found by Bradshaw et al. (2000). Smith's (1936) discriminant function for plant selection was used to calculate an index score for each progeny. The economic weights for bp, fb, tb, pcn and fry in phenotypic standard deviation units were in the ratio 1:½:½:1:1 so that foliage and tuber blight combined had the same weight as the other traits.

Use of tuber progeny tests to select between crosses

As fry colour and other economically important traits can be assessed in tuber progeny trials, there is scope for further selection between crosses when the tubers from the seedling progeny test for breeders' preference are planted as tuber progenies at seed and ware sites as described by Bradshaw et al. (2000). This is illustrated with the 36 progenies which were chosen from the 145 in the 1998 seedling progeny tests for bp, fb and pcn. They were grown in a tuber progeny trial with two replicates of 15 tubers of each progeny at SCRI's high-grade seed site (Blythbank Farm, near West Linton, Scotland) in 1999 and assessed for fry. The parents of 30 out of the 36 progenies were assessed for fry in the 1998 yield trial and hence mid-parent values and progeny means were compared for these progenies.

Correlation of bp scores between glasshouse and four-plant plots for clones within crosses

It was mentioned in the introduction that once visual selection has been practised between crosses, it appears that selection within crosses becomes effective at the first small plot stage. Hence it was decided to omit the spaced plants (singles) generation when 14 progenies (including average and worst as controls) from which to seek new cultivars were chosen from the 122 in the 1998 seedling progeny tests for bp, fb, tb and pcn (Bradshaw et al. 1999). In 1999, an average of 185 true seeds (range: 131–213) from each of the 14 progenies were sown in a glasshouse (resowings) to provide around 2,400 clones for visual assessment in four-plant plots at SCRI's high grade seed site in 2000. This allowed the correlation for breeders' visual preference between clones in the glasshouse and in the four-plant plots to be determined for each progeny.

Parental assessment in yield trial

The 1998 yield trial had a randomised complete block design with two replicates and five-plant plots and was handled as described for a similar ware trial grown in 1995 (Bradshaw et al. 1998b). It was planted on 4 May and harvested on 21 September. The produce of each plot were kept in a potato store at ambient temperature. Two tubers were taken from each plot and stored at 10 °C from 16 November to 22 January 1999. Then each tuber was cut in half and a 2-mm-thick slice taken and fried in vegetable oil at 175 °C in a thermostatically-controlled chip fryer until all of the water had boiled off (bubbling ceased). Colour was assessed on a 1–9 scale by comparison with a standardised colour chart (1 = extremely dark to 9 = extremely pale), where 5 and above is an acceptably light colour (Mackay and Dale 1990).

Progeny tests

All of the progeny tests had randomised complete block designs with two replicates (Bradshaw et al. 1995). The bp test was sown on 25 March 1998 and the tubers scored on a 1–9 scale of increasing preference from 17 September to 28 September 1998 by two breeders who each scored both replicates. The mean of the 18 seedlings of each progeny in each replicate was calculated for each breeder and then averaged over the two breeders to give the data used for analysis.

The fb test was sown on 23 April 1998 (two samples of 25 seeds of each progeny), inoculated on 28 May 1998 and scored 1 week later on a 1–4 scale of increasing resistance. An equal mixture of races 1,2,3,4,6,7 and 1,3,4,7,10,11 of *P. infestans* was chosen for the test to overcome the R genes thought to be present in the progenies.

The tb test was sown on 22 July 1998 and harvested and inoculated on 28 October 1998 with the same races as in the fb test. There were 16 seedlings of each progeny in each replicate, giving a maximum of 32 tubers in each sample as two tubers were taken from each seedling where possible. The numbers of infected tubers in the samples were recorded from 10 November to 12 November 1998, and the percentage of infected tubers in each sample was calculated. The percentages were converted to degrees by the variance – stabilising angular transformation before further analysis of the data.

The pcn test was sown in mid-April 1998 (two samples of 25 seeds of each progeny) and the root balls examined by eye and the cysts counted on 22 June and 23 June 1998. The variance-stabilizing square root transformation was performed before further analysis of the data. Pathotype Pa2/3 was used in the test.

The tuber progeny test for fry was planted at Blythbank Farm on 20 May 1999 and harvested on 8 September 1999 when progeny bulks (one tuber per plant) of each plot (15 plants) were taken for storage at 10 °C from 21 September to 19 January 2000. The fry colour of each tuber was determined as described in the previous section, and the mean of the 15 scores for each plot used in the subsequent analysis.

Smith's discriminant function

In order to select between crosses, an index score (I) was calculated for each progeny from the formula $I = b^1x$, where x is a column vector of the phenotypic deviations of the progeny means (over replicates) and mid-parent values of all traits under consideration from their population means and b is a column vector of weights calculated using Smith's (1936) discriminant function for plant selection, i.e. $b = P^{-1} Ga$.

The genotypic (G) variance-covariance matrix was estimated by subtracting the environmental (E) variance-covariance matrix from the phenotypic (P) one for the 96 progenies assessed for all traits. As all of the tests used different samples of seed of the progenies and were independent of each other, all of the environmental covariances were zero. The environmental variances (divided by the number of replicates) were estimated from the 96 progenies present in all tests to avoid any possible bias from including other progenies. The environmental variance for the mid-parent values was estimated as the mean square for replicates × mid-parent values, divided by the number of replicates, in an analysis of variance in which the mid-parent values of the 96 progenies were calculated for each replicate separately. Hence, the broad-sense heritability of mid-parent values $[(V_{P(MP)} - V_{E(MP)})/V_{P(MP)}]$ does reflect their repeatability, despite the parents being unequally represented in the progeny (i.e. successful crosses). The heritability of progeny means was estimated as $(V_P - V_E)/V_P$ where V_P and V_E are the phenotypic and environmental variances of progeny means.

The economic weights (a) were expressed in phenotypic standard deviation units i.e. $a = 1/\sqrt{V_P}$.

The predicted superiority (R) of resowings of the best progenies was estimated as $R = Gb \cdot \Delta I/\sigma_I^2$, where ΔI is the mean of the progenies selected for resowing minus the mean of all progenies, and σ_I^2 is the variance of I (Lin 1978).

All calculations were done using GENSTAT 5 Release 3 (Genstat 5 Committee 1993).

Resowings of 14 progenies from the 1998 progeny tests

True seed was sown on 24 March and 25 March 1999 and the resulting seedlings transplanted on 23 April into 12.5-cm square pots arranged in a honeycomb grid of pots and spaces on a glasshouse bench in 14 blocks, one for each progeny. The soil was removed from the pots on 24 August and the tubers independently scored on 31 August by two breeders on a 1–9 scale of increasing preference. Four tubers from each pot were put into bags and kept in a dark store at 6 °C from 1 September until 10 April 2000. They were then chitted in a glasshouse, planted by hand at Blythbank Farm on 15 May 2000 and handled as described by Bradshaw et al. (1998b) for four-plant plots under a high-grade seed regime. All clones from a progeny were grown together in a block, but with a different randomisation to that used in the glasshouse. The progenies were harvested from 31 August to 5 September and the tubers from each plot placed in wooden boxes and scored by the same two breeders as in the glasshouse. Both breeders scored progenies 1 and 2; then one breeder did progenies 4, 6, 8, 9, 10 and 14, and the other breeder progenies 3, 5, 7, 11, 12 and 13. Visual assessments were made on a 1 (poor) to 9 (excellent) scale of yield, tuber size, regularity of tuber shape (appearance) and resistance to growth cracking as an aid to determining overall preference on the same scale.

Results

Use of seedling progeny tests and mid-parent values of crosses already made to select between crosses

The key determinants of the selection index used to select between 96 crosses in 1998 are shown in Table 1. The index takes account of the range of heritabilities from 0.878 for fry down to 0.408 for fb, the small but favourable correlation between fb and tb and the small but unfavourable ones between pcn and both fb and tb.

The index scores for the 96 families ranged from 3.992 to –3.138, with a mean of zero, variance of 2.261 and standard deviation of 1.504. However, it is their ranks which are of interest, and the top 12 are shown in Table 2, along with their scores for each trait, to give an insight into how one trait is balanced against another. Thus, all 12 progenies had a better than average score for bp, and likewise ten for fry, ten for pcn, nine for tb and just five

Table 1 Construction of selection index[a] from the results of the 1998 progeny tests for breeders' preference (bp), foliage blight (fb), tuber blight (tb) and the white potato cyst nematode (pcn), and the mid-parent values for fry colour (fry) from 1998 yield trial where high values are desirable for bp, fb and fry and low ones for tb and pcn

	bp (1–9 scale)	fb (1–4 scale)	tb (ang)	pcn (square root no. cysts)	fry (1–9 scale)
Genotypic variance–covariance matrix (G)					
bp	0.10134				
fb	0.03107	0.09284			
tb	–1.02897	–1.99796	124.65756		
pcn	–0.04232	0.21622	–5.38881	2.84095	
fry	0.00365	–0.00619	–0.01992	–0.07566	0.34651
Phenotypic variance – covariance matrix (P)					
bp	0.15814				
fb	0.03107	0.22739			
tb	–1.02897	–1.99796	149.28256		
pcn	–0.04232	0.21622	–5.38881	3.86095	
fry	0.00365	–0.00619	–0.01992	–0.07566	0.39461
Phenotypic correlations (*r*)					
fb	0.164				
tb	–0.212	–0.343			
pcn	–0.054	0.231	–0.224		
fry	0.015	–0.021	–0.003	–0.061	
Heritability of progeny means/mid-parent values	0.641	0.408	0.835	0.736	0.878
Progeny test mean/mean of mid-parent values	3.978	1.766	31.75	7.917	4.017
Economic weights (a)	2.515	1.049	–0.0409	–0.509	1.592
Selection index weights (b)	1.782	0.356	–0.0428	–0.350	1.424

[a] Index I = 1.782 (bp–3.978) + 0.356 (fb–1.766) – 0.0428 (tb–31.75) – 0.350 (pcn–7.917) + 1.424 (fry–4.017)

Table 2 Selection index scores for 12 best progenies assessed in 1998 progeny tests and yield trial for fry colour (positive values are desirable for bp, fb and fry and negative ones for tb and pcn), and predicted consequence of resowing best 12 progenies

Progeny	Rank	Index score	bp − $\overline{\text{bp}}$	fb − $\overline{\text{fb}}$	tb − $\overline{\text{tb}}$	pcn − $\overline{\text{pcn}}$	fry − $\overline{\text{fry}}$
97MT198	1	3.992	0.050	–0.016	–2.77	–2.257	2.108
97MT14	2	3.359	0.162	0.734	2.53	–1.797	1.608
97MT200	3	3.351	0.537	0.484	–19.91	–1.447	0.608
97MT190	4	2.969	0.867	–0.266	–9.54	–1.722	0.358
97MT52	5	2.790	0.510	0.484	–3.16	–3.047	0.358
97MT17	6	2.690	0.525	–0.016	–10.51	–0.257	0.858
97MT106	7	2.574	0.270	–0.266	–26.57	–2.062	0.233
97MT199	8	2.221	0.455	1.234	–15.53	1.598	0.608
97MT191	9	2.036	0.635	–0.266	18.23	–3.122	0.483
97MT168	10	1.980	0.744	0.734	–22.01	0.478	–0.267
97MT15	11	1.613	0.172	–0.016	6.50	–1.057	0.858
97MT130	12	1.579	0.470	–0.016	–1.20	–3.082	–0.267
standard error of difference	–	–	0.337	0.519	7.018	1.428	0.310
Predicted response to selecting top 12	–	2.596	0.294	0.103	–6.91	–0.998	0.603

for fb, although a further four were only just below average. The balance is also seen in the predicted responses to sowing more seed of the best 12 progenies. The greatest (increase as percentage of mean) impact is predicted for tb (despite being given less weight), followed by fry and pcn, then bp and fb, and this is approximately in order of decreasing heritability.

In the MT programme, the 12 progenies actually chosen for resowing were selected from the 122 assessed for bp, fb, tb and pcn on the basis of an index in which fb and tb were each given half the weight of bp and pcn. Eight out of the 12 were included in the 96 under consideration in this section and, of these, seven were selected when fry was included in the index. In contrast, the progenies ranked 1 and 2 in Table 2 made these positions because of their fry score and ranked only 20 and 18, respectively, when fry was not considered. There were a few other minor changes.

Use of tuber progeny tests to select between crosses

There were statistically significant differences ($P < 0.001$) in fry between the 36 progenies grown at the seed site in

Table 3 Correlation for breeders' preference scores between clones within crosses in glasshouse and in four-plant plots at high-grade seed site and percentage of variance in latter that can be accounted for by visual assessments of yield, regularity of tuber shape and growth cracks

Progeny	Numbers of clones	Correlation (*r*) between glasshouse and seed site	Percentage of variation in preference scores at seed site accounted for by yield, shape and growth cracks	Breeder
1 97MT52	194	0.092NS	84.4	JEB & MFBD
2 97MT168	209	0.229**	83.3	JEB & MFBD
3 97MT17	187	0.107*	73.9	MFBD
4 97MT19	121	0.206**	83.0	JEB
5 97MT30	162	0.161*	80.4	MFBD
6 97MT34	122	0.370***	88.9	JEB
7 97MT36	175	0.356***	73.2	MFBD
8 97MT101	186	0.363***	89.1	JEB
9 97MT106	200	0.212**	84.9	JEB
10 97MT130	145	0.206**	84.9	JEB
11 97MT146	199	0.181**	85.9	MFBD
12 97MT187	199	0.196**	81.5	MFBD
13 97MT190	186	0.234**	77.7	MFBD
14 97MT200	202	0.193**	78.6	JEB

***P<0.001, **P=0.01–0.001, *P=0.05–0.01, NS = not significant

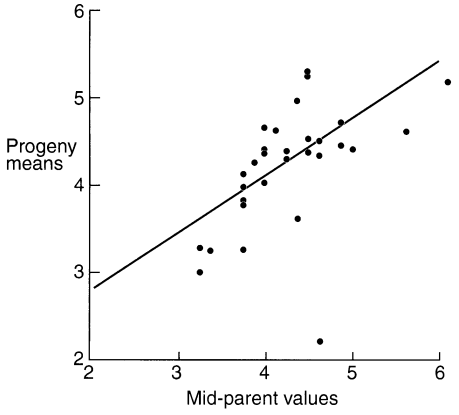

Fig. 1 Fry colour on a 1 (dark) to 9 (light) scale of parents grown at ware site in 1998 and 30 progenies grown at seed site in 1999

1999. The progeny means ranged from 2.19 (poor) to 5.28 (good) and had a broad-sense heritability of 0.765. The parents of 30 out of the 36 progenies were assessed for fry in the 1998 yield trial and hence mid-parent values and progeny means can be compared for these progenies. There was a moderate correlation of $r = 0.534$ ($P < 0.01$) which rose to $r = 0.708$ ($P < 0.001$) when an outlier (progeny with lowest mean) was omitted (Fig. 1). The top two mid-parent values were 6.125 and 5.625 for the parents of 97MT198 and 97MT14, respectively, and these progenies were highly ranked at positions 3 and 8 out of 30 in 1999. As noted in the previous section, they would only have been selected for resowings if the mid-parent values for fry had been included in the selection index. Six of the top eight progenies for fry colour in 1999 were included in the 96 progenies considered in the previous section and, on their selection index scores, were ranked 24, 1, 5, 30, 35 and 2. Thus, typically advancing between a quarter and a third of the seedling progenies (down to ranks 24–32) to the seed site on the basis of the index would have included four or five of these six progenies.

Correlation of bp scores between the glasshouse and four-plant plots for clones within crosses

Of the 2,589 seedlings raised in the glasshouse, 2,562 produced tubers and were planted at the high-grade seed site and, of these, 2,487 also produced tubers and were scored at harvest. The correlations for bp between the assessments in the glasshouse and in the four-plant plots are shown in Table 3. Although both breeders (J.E. Bradshaw and M.F.B. Dale) scored all of the clones in the glasshouse, there was a division of labour for 12 of the progenies at the high-grade seed site. Hence, the correlations with the glasshouse preference scores are shown for the individual breeder who scored the four-plant plots. There was good within-progeny agreement between the breeders in the glasshouse ($r = 0.668$, averaged over progenies) and also for the two progenies they both scored at the seed site ($r = 0.729$). Although all but one of the correlations between glasshouse and seed site were statistically significant (Table 3), their magnitudes were low, ranging from 0.092 to 0.370 with an average value of 0.226. The multiple linear regressions of bp scores for progenies at the seed site onto the visual assessments of the same material for yield, size, regularity of shape and growth cracks confirmed that from 73.9% to 89.1% of the variation in preference scores could be accounted for by variation in yield, regularity of shape and growth cracks. Size, which is a component of yield, made a negligible additional contribution.

Discussion

A breeding strategy can be developed from the results presented in this paper that avoids the common but ineffective practice of intense early-generation visual selection between seedlings in the glasshouse and spaced plants at a seed site. The main features of the strategy are as follows and include both novel and standard practice. Potential parents are assessed at the start of the breeding programme and mid-parent values used to predict the mean performance of crosses and, hence, which crosses should be made. As some of the crosses actually made will be superior to others, progeny tests are then used to discard whole progenies before starting within-progeny selection at the small-plot stage. Clones are visually selected from the best progenies for use as parents in the next cycle of crosses while they are multiplied to provide enough tubers for assessment of their yield and quality. Mid-parent values as well as progeny tests are then used to select between the crosses actually made and hence choose progenies from which to seek new cultivars and parents for the next round of crossing. Material from other breeding programmes can be included in the parental assessments and used in the next cycle of crosses if superior. Finally, in seeking new cultivars, the number of clones on which to practise selection is increased by sowing more true seed of the best progenies (resowings), but without selection until the small-plot stage.

Mid-parent values are used to predict progeny means in order to choose which crosses to make and also to complement progeny tests in selecting between those actually made. The first use should be standard practice in breeding programmes because of its impact on eventual success and how quickly this can be achieved, but it is not always done. The accuracy of the predictions should be checked by inclusion of a random sample of crosses for assessment of offspring on mid-parent regressions. It would also be advantageous to predict the amount of genetical variation within crosses as those combining high variances with high means would be the best ones from which to seek new cultivars. However, both Bradshaw et al. (1998b) for potatoes and Utz et al. (2001) for winter wheat crosses concluded that only the parental means can be recommended for predicting the usefulness of crosses. The second use of mid-parent values aims to save time by allowing crosses to be made before assessing parents for traits for which progeny tests are either unavailable or unreliable. The same philosophy applies in the accelerated recurrent selection schemes proposed by Mackay et al. (1999).

Combining mid-parent values for fry colour with seedling progeny tests for late blight, pcn and bp is particularly attractive in potato breeding programmes aimed at combining disease and pest resistance with processing quality. Progenies can be chosen for resowings within a year of making crosses without having to either delay 1 year to do a tuber progeny test for fry colour or risk losing good progenies for fry as happened with the 12 progenies selected in the MT programme on the basis of seedling progeny tests. Should the subsequent tuber progeny test reveal any major adverse departures from expectations, then the progenies concerned need not be advanced from the glasshouse to the field. There was, for example, one such outlier in the fry data in Fig. 1. When this outlier was excluded from the data, a moderate correlation of 0.71 was found for the mid-parent values and offspring means, which were assessed in different years. An even higher correlation of 0.86 was found by Bradshaw et al. (2000) in a diallel set of crosses involving 15 of the 39 parents used to start the MT programme and in which the parents and progenies were assessed in the same trial. Hence, the use of mid-parent values for fry is justified.

The predicted responses to sowing more seed of the best progenies are shown in Table 2 and confirm that only modest responses can be expected for individual traits when selecting for a number of traits. Had enough seed been secured of all 192 progenies (a realistic target), and enough tubers of all 108 parents, then 12 out of all 192 progenies rather than 12 out of 96 would have been selected and the intensity of selection increased accordingly. Selecting fewer than 12 progenies would start to run the risks associated with a narrow genetic base. Nevertheless, the clones assessed in small plots at the seed site should show worthwhile improvements in quality and disease resistance over a population selected solely but ineffectively for visual preference. This should result in less testing and selection being required in later generations and hence allow fewer clonal generations to cultivar release, with promising clones rapidly multiplied through modern methods of micropropagation.

The number of years from crossing required for the resowings to reach the small plot stage is the same as in the traditional visual selection scheme if the resowings are progressed straight from the glasshouse to small plots without going through single-spaced plants at the seed site. The use of well-separated 12.5-cm pots rather than tightly packed 10-cm ones resulted in larger tubers and prevented problems arising from stolons growing into neighbouring pots. The average correlation for bp between clones within crosses in the glasshouse and four-plant plots was low ($r = 0.226$). Hence, little would be gained from raising more seedlings in the glasshouse than required for the four-plant plots unless selection could be introduced for other highly heritable traits. The corollary of this is that molecular-marker-assisted selection for a number of traits is expected to have the greatest impact at this stage in the breeding programme, provided the markers and desired genes are tightly linked. Nevertheless, the principle remains that progeny sizes for resowings should be determined by the predicted effectiveness of within-cross selection and the number of clones that can be handled in unreplicated small plots and in yield trials. Bradshaw and Mackay (1994) quoted figures from the SCRI programme prior to 1982 of 4,000 four-plant plots at the seed site and 1,000 clones in the first year of replicated yield trials at a ware site as typical of potato breeding world-wide. The number grown in

four-plant plots in this paper was less, namely 2,487, but realistic.

As already mentioned, the progenies selected for the resowings can also be planted the next year as tuber progenies at seed and ware sites by using the tubers from the seedling progeny test for bp. This not only allows confirmation of their performance for fry colour and other traits not assessed in the seedling progeny tests but also provides clones for use as parents in the next cycle of crossing. Full-sib family recurrent selection can, therefore, be operated on a 3-year cycle, with new cultivars produced every cycle. This is in marked contrast to many current breeding programmes where breeders wait 9 years or more to acquire what they regard as sufficient information on selected clones to warrant using them in another cycle of crossing and selection (Bradshaw and Mackay 1994). The parents used in the new cycle of crosses are multiplied in small (four-plant) plots in the year of crossing to provide seed for yield trials the following year and hence mid-parent values for all traits assessed. Some can then be multiplied further and assessed as potential cultivars.

Finally, further gains in efficiency can be expected from advances in potato genomics which will allow parents to be chosen on the basis of gene content, crosses to be made between parents with desirable complementary gene contents and clones which combine these genes to be selected in the seedling generation in the glasshouse for rapid multiplication as new cultivars.

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