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Early-generation selection between and within pair crosses in a potato (*Solanum tuberosum* subsp. *tuberosum*) breeding programme

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Abstract In 1992, 72 seedlings from each of 198 pair crosses were grown in a glasshouse, and the tubers produced by each plant were visually assessed on a 1–9 scale of increasing preference. Three groups of four progenies with high, medium and low mean scores were chosen to progress, without selection via tuber progenies and four-plant plots at a high-grade seed site, to replicated yield trials in the third clonal generation. The three groups maintained their high, medium and low scores for visual preference over the three clonal generations and also had high, medium and low scores in the second and third clonal generations for yield, size and appearance of tubers, all of which were components of visual preference. The three groups were predicted to have 13.6%, 1.8% and 0.2% of their clones exceeding the mean of 13 control cultivars for visual preference in the replicated trials, and 12.1%, 4.9% and 1.4% for yield, and 56.8%, 37.1% and 14.8% for appearance. The experiment confirmed that selection for visual preference within crosses in the seedling and first clonal generations is very ineffective, but that worthwhile progress can be made from selection in the second clonal generation, with correlated responses for faster emergence, earlier maturity, higher yield and greater regularity of shape (appearance). Combining selection of the high group of progenies with selection in the second clonal generation of the best 34 out of the 120 clones in this group, produced a response in visual preference in the third clonal generation of 1.00 compared with a maximum possible of 1.74. Ways of achieving further improvements in early-generation selection are discussed.

Key words Potato breeding · Family selection · Cross prediction · Breeders' visual preference · Within-family selection

Introduction

Potato breeding worldwide has traditionally involved making crosses between pairs of parents with complementary features based on phenotype in order to generate genetical variation on which to practise phenotypic selection over a number of vegetative generations, the aim being to identify clones with as many desirable characteristics as possible for release as new cultivars. The programme at the Scottish Crop Research Institute (SCRI) before 1982 was typical in its handling of the early generations (Bradshaw and Mackay 1994). Visual selection reduced the number of potential cultivars from 100,000 in the seedling generation (SG) in the glasshouse to 40,000 spaced plants at a high-grade seed site in the first clonal generation (FCG), then to 4,000 four-plant plots at the seed site in the second clonal generation (SCG) and finally to 1,000 clones in replicated yield trials at a ware site in the third clonal generation (TCG). Several independent reviews concluded that such intense early-generation visual selection was very ineffective (Tai and Young 1984; Caligari 1992; Tarn et al. 1992; Bradshaw and Mackay 1994). However, research at SCRI not only confirmed the ineffectiveness of visual selection of individual clones (Brown et al. 1984; Brown et al. 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; Brown et al. 1988). Mild clonal selection within the remaining crosses could then be practised in the first and second clonal generations to achieve the same target of 1,000 clones for

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replicated yield trials, but with a much improved frequency of superior clones. If necessary, the population sizes of the best crosses could be increased by sowing more true seed (resowings) of each. Recently, Simmonds (1996) reviewed the critical points for the effective exploitation of such a family selection scheme with the objective of encouraging the appropriate use of family selection in plant breeding.

This paper evaluates the effectiveness of early-generation family selection in the SCRI potato breeding programme following its transfer from Pentlandfield near Edinburgh to Invergowrie near Dundee, and hence its likely general applicability, and then goes on to determine the stage at which within-family selection becomes effective. Throughout the experiment, the material was scored by those staff who would normally do so at each stage in the potato breeding research programme at SCRI.

Materials and methods

The 12 crosses chosen for the experiment

In 1992, the progenies from 198 pair crosses (i.e. full-sib families) were grown in a glasshouse progeny test and visually assessed by four breeders (see below). Four progenies with a high mean score (in top 14), four with an intermediate score (ranked between 100 and 117 inclusive), and four with a low score (in bottom 14), were chosen to progress to replicated yield trials in the third clonal generation with evaluation but without selection. In choosing each set of four progenies, an effort was made to include a range of within-progeny variation (one high, two intermediate, and one low phenotypic standard deviation for visual preference). The 12 crosses were all aimed at combining disease and pest resistance with acceptable yield and quality. Their codes will be seen in Table 3 (B – late blight, P – potato cyst nematodes, V – virus, and MT – multitrait disease and pest resistance, i.e. B, P and V).

Seedling progeny test in glasshouse (SG)

Four batches of 25 seeds of each of the progenies were sown in 10-cm square pots and placed under a mist unit in a randomised complete block design (RCB). Replicates 1 and 2 were sown on 7 and 8 April and replicates 3 and 4 on 14 and 15 April. After 4 weeks, 18 randomly chosen seedlings from each pot were transplanted into 10-cm square pots, which were arranged on a glasshouse bench in the same RCB design in two rows of nine (from front to centre of bench). Fisons Levington F2 peat/sand compost was used for both seed and seedlings. The seedlings were grown to maturity and the senesced foliage removed on 26 August. The pots were covered with polythene to prevent surface tubers greening while the compost dried out. By 4 September, the compost had been removed from each pot and the tubers returned to the empty pots. Between 11 and 16 September, the tubers in each pot were independently assessed by two breeders on a 1–9 scale of increasing preference, as described by Brown et al. (1988). JEB scored replicates 1 and 2, MFBD did 3 and 4, GELS did 1 and 4 and his assistant did 2 and 3. All 864 clones (18 clones × 4 replicates × 12 progenies) chosen for the experiment were given a unique number and stored in the dark at 6°C from 5 November 1992 to 30 March 1993. They were then moved to a glasshouse ready for planting at SCRI's high-grade seed site.

Tuber progenies at high-grade seed site (FCG)

The 12 progenies were grown at SCRI's high-grade seed site (Blythbank Farm, West Linton, Peeblesshire) in 1993 in an RCB design in the same four replicates as in the glasshouse. However, new randomisations were used for progenies within replicates and clones within plots. Each plot comprised a single drill of 18 plants (clones) at 50 cm spacing, with 75 cm between drills.

The trial was planted by hand on 5 May. The fertiliser applied, and the use of aphicides, herbicides and fungicides (for late blight control) were standard for seed potatoes in Scotland. The desiccant Reglone was applied at half the recommended rate on 10 August to make it easier to dig the experiment by hand on 3 September. The same day, two breeders (JEB and MFBD) independently assessed the produce of all plants on a 1–9 scale of increasing preference. The tubers were kept in a potato store at Blythbank until planting the following year.

Four-plant plots at high-grade seed site (SCG)

The clones were grown in four-plant plots at Blythbank Farm in 1994 in the same four replicates as the previous year, but with complete individual randomisation of clones within replicates.

The trial was planted by hand on 11 May and handled as in 1993, except that tubers were 37.5 cm apart within the single-drill plots and there were gaps (2 m) between plots to allow machine harvesting. Reglone was applied on 10 August, and the trial was burnt down with acid on 16 August. The trial was harvested on 30 and 31 August and the produce of plots placed in wooden boxes and scored independently in the field by two breeders (JEB and MFBD). They made visual assessments on a 1 (low)–9 (high) scale of yield, tuber size, regularity of shape (appearance) and resistance to growth cracking as an aid to determining overall preference on the same scale, as well as recording tuber shape on a 1–4 scale for round, oval, long oval and extra long oval. In order to keep the experiment to a manageable size, it was continued with two of the four replicates by keeping all of the clones from replicates 1 and 4 in store for trial in 1995. Selected clones from the other two replicates continued in the breeding programme but will not be considered further in this paper.

Replicated trials at ware site (TCG)

Two replicated yield trials were grown at a ware site (Gourdie Farm, Dundee) in 1995, one for each of the unselected replicates from 1994. Each trial had an RCB design with two replicates and single-drill plots of five tubers spaced 45 cm apart with 75 cm between drills. Gaps (2 m) were left at the ends of the drills to allow machine harvesting. Tubers were brought from the Blythbank potato store early in February and placed in open brown paper bags in mid-March ready for planting, which took place on 18 April. The drills were covered the same day.

Cultural details

Fertiliser was incorporated into the soil on 4 April to supply 147, 147 and 220.5 kg ha^{-1} of N, P_2O_5 and K_2O, respectively.

Stomp 400 SC (pendimethalin) herbicide at 3.3 l ha^{-1} and Lexone 70 DF (metribuzin) at 0.5 kg ha^{-1} were applied for weed control on 1 May, followed by Gramoxone 100 (paraquat) at 3 l ha^{-1} on 16 May.

Aphids were controlled by spraying with Aphox (pirimicarb) at 280 g ha^{-1} on six occasions from 12 June until 11 August. Late blight (*Phytophthora infestans*) was controlled with fungicide sprays: Dithane 945 (mancozeb) at 1.7 kg ha^{-1} on five occasions (with the Aphox) from 12 June until 28 July, followed by Super-Tin 4L (fentin hydroxide) at 560 ml ha^{-1} on 11 and 23 August.

Scoring and harvesting

Emergence was scored on a 1 (none)–9 (all 5 plants in a drill well established) scale on 29 May.

Maturity was scored on a 1 (all 5 plants dead—early maturity)–9 (all plants still green – late maturity) scale on 16 August.

The trials were burnt down with one application of sulphuric acid on 25 August.

Harvesting was done on 18 September with a single-row digger. The tubers from the 5 plants in each drill were placed in a net bag, taken into a potato store and the following assessments made between 28 November and 6 December. The weights of bags (kg) were recorded automatically by an Avery balance connected to an Epson HX-20 portable computer. Visual assessments were made by DT on a 1 (low)–9 (high) scale for tuber size, regularity of shape (appearance), resistance to growth cracking, resistance to sprouting and resistance to common scab. Three large tubers from each plot were cut open to check for internal defects (incipient hollow heart, hollow heart, internal necrosis and flecking) and the plot given an internal condition score on a 1 (all three tubers with severe defect such as hollow heart)–9 (no defects) scale. The plots were then independently given an overall preference score by DT and RNW on a 1–9 scale of increasing preference, which took account of yield but not internal condition, so that it was comparable to earlier generation scores. Two tubers from each plot were steamed for 45 min and scored for sloughing (1 severe disintegration to 9 none) before being cut open. After-cooking blackening was scored 4–5 h later (1 completely black to 9 none).

Lastly, on 21 and 22 February 1996 all of the plots were given a final score for sprouting (1 extensive to 9 none) and keeping quality (1 tubers very soft to 9 tubers still hard).

Statistical analyses

Analyses of variance and multiple regression and correlation analyses were all done using Genstat 5 Release 3 (Genstat 5 Committee 1993). In order to analyse the variation between clones within crosses (progenies), having first removed variation due to replicates or trials, we saved either the appropriate residuals (clones unreplicated) or effects (clones replicated) from the analyses of variance. The 12 crosses were carefully chosen and, hence, regarded as fixed effects, whereas the clones within families were considered a random sample of possible clones.

The heritability (h^2) of the differences between clones within crosses in the replicated trials was estimated from the components of variance for clones (σ_c^2) and replicates × clones interactions (σ_{rc}^2):

$$h^2 = \sigma_c^2/(\sigma_c^2 + \tfrac{1}{2}\sigma_{rc}^2)$$

These components of variance were also used to calculate an upper limit for a correlation (r) between assessments made on unreplicated plots and those made as the mean of two replicates:

$$r = \sigma_c^2/[(\sigma_c^2 + \sigma_{rc}^2)(\sigma_c^2 + \tfrac{1}{2}\sigma_{rc}^2)]^{1/2}$$

The response (R) in clonal generation Y to selection in clonal generation X can be determined from the intensity of selection (i) and either the regression of Y on X (b_{YX}) and the square root of the phenotypic variance for clones in generation X, or the correlation between X and Y (r_{XY}) and the square root of the phenotypic variance for clones in generation Y:

$$R = ib_{YX}\sigma_X = ir_{XY}\sigma_Y$$

Hence, the response in the third clonal generation to within progeny selection in an earlier generation was estimated from:

$$R = ir(\sigma_c^2 + \tfrac{1}{2}\sigma_{rc}^2)^{1/2}$$

where r was the correlation between clones in the replicated yield trials and in the earlier generation of interest. Direct and correlated responses to selection were estimated by using correlations between the same trait in both generations and between different traits.

Finally, the information from the replicated trials on the mean ($\bar{X}$) and genotypic variance (σ_c^2) of the clones in each cross was used to predict the proportion of clones expected to exceed a given target (T). A normal distribution was assumed so that the proportion could be calculated from the normal probability integral corresponding to the value $(T - \bar{X})/\sigma_c$ (Fisher and Yates 1963).

Results

Missing clones

As the experiment progressed, the number of clones missing at harvest increased from 21 out of 864 in the seedling progeny test, through 113 in the tuber progeny test, to 146 in the four-plant plots. Finally, 95 out of 432 clones were missing in the replicated trials, the number varying over progenies from 1 to 14 out of 36. There were, however, sufficient clones remaining in each progeny for a realistic assessment of progeny means and variances, and the average number of clones per progeny in the high, medium and low groups was 30, 28.5 and 25.75 (SED = 2.905).

Different scorers

For traits where clones were scored by more than one breeder, the mean score for each clone was used as the most accurate evaluation of the clone available. For visual preference the correlation between scorers was 0.683 in the seedling generation (average of four combinations of scorers), 0.798 in the first clonal generation, 0.790 in the second clonal generation and 0.738 in the replicated trials. In the second clonal generation, the correlation for yield was 0.898, for size 0.854, for regularity of shape 0.613, for shape 0.707 and for growth cracks 0.637.

Visual preference

Multiple regression analyses revealed that, in the four-plant plots, 87.8% and 82.2% of the variation over all clones in JEB's and MFBD's preference scores could be accounted for by their visual assessments of yield and regularity of shape (appearance), with size and growth cracks accounting for a further 0.6% for JEB and 4.0% for MFBD. As yield and appearance were correlated ($r = 0.618$ and 0.545 for JEB's and MFBD's assessments, respectively), it would be misleading to say that one accounts for more variation than the other. In the replicated trials, 70.9% of the variation over all plots in DT's preference scores were accounted for by yield, appearance and size, with growth cracks accounting for a further 0.8%, whereas for RNW, 75.6% of the variation in his preference scores were accounted for by yield and size, with appearance and growth cracks accounting for a further 1.7%. Yield and appearance were uncorrelated ($r = 0.021$), whereas yield and size were correlated ($r = 0.555$).

Differences between the high, medium and low progenies

Analyses of variance revealed that there were statistically significant differences between the 12 progenies for all traits except internal condition, there being very few internal defects in any progeny (overall mean 8.62). There was also only a low level of growth cracking and of sloughing. It is also worth noting for later discussion that, for visual preference, the correlations between the means of the 12 progenies in the seedling generation and in the first, second and third clonal generations were 0.875, 0.889 and 0.865.

The variation was partitioned into differences between and within the three groups of progenies chosen for their high, medium and low preference scores in the seedling generation. The differences between the three groups are shown in Table 1. They maintained their high, medium and low scores for visual preference over the three clonal generations. The low overall mean score of 2.55 in the replicated trials reflected low yields due to little rainfall during June, July and early August 1995. The three groups also had high, medium and low scores for yield, size and appearance in the four-plant plots and replicated trials, all three traits being components of visual preference, and likewise for emergence (high = rapid) and maturity (high = late) in the replicated trials. Group scores were in the reverse direction for resistance to scab and to sprouting, and for keeping quality. There were no significant differences between groups for sloughing or for after-cooking blackening, and those for shape (round to extra long oval) in the four-plant plots were not associated with the preference scores.

Variation between clones within the 12 crosses

The analyses of variance revealed that there were statistically significant differences ($P < 0.001$) between clones within crosses for all of the traits assessed in the replicated trials (Table 2). Furthermore, for all traits,

Table 1 Differences between three groups of four crosses chosen for their high, medium and low visual preference scores in the seedling generation

Trait	Group				Significance		
	High	Medium	Low	SED	Between groups (B)	Within groups (W)	B > W
Seedling generation							
Visual preference	5.19	4.52	3.76	0.106	***	NS	***
First clonal generation							
Visual preference	4.58	4.36	2.96	0.130	***	**	***
Second clonal generation							
Visual yield	4.11	3.62	3.12	0.100	***	***	*
Visual size	3.95	3.53	3.09	0.079	***	***	NS
Visual appearance	4.28	3.92	3.28	0.073	***	**	***
Visual shape	2.07	1.74	1.90	0.045	***	***	NS
Visual growth cracks	8.88	8.94	8.89	0.046	NS	**	NS
Visual preference	3.86	3.29	2.56	0.100	***	***	**
Replicated trials							
Emergence	4.57	4.14	3.72	0.190	**	**	NS
Maturity	5.95	5.40	4.26	0.189	***	***	NS
Yield (kg/plot)	5.86	4.85	3.87	0.291	***	NS	**
Visual size	4.44	3.67	3.45	0.165	***	**	NS
Visual appearance	4.32	3.92	3.33	0.154	***	NS	**
Visual growth cracks	8.94	8.98	8.79	0.064	*	NS	NS
Scab	3.84	4.57	4.81	0.189	***	NS	*
Sloughing	8.38	8.30	8.28	0.137	NS	**	NS
After-cooking blackening	4.75	4.84	4.64	0.126	NS	*	NS
Sprouting 1	4.47	5.63	6.67	0.265	***	***	NS
Sprouting 2	3.23	3.97	5.14	0.256	***	**	*
Keeping quality	3.43	4.47	5.68	0.181	***	***	**
Visual preference	3.10	2.52	2.02	0.150	***	NS	**

***$P < 0.001$, **$P = 0.01$–0.001, *$P = 0.05$–0.01, NS $P > 0.05$

Table 2 Components of variance (σ^2_{rc} replicates × clones, σ^2_c clones) and heritability (h^2 for two replicates) for clones within crosses in replicated trials, and correlations with visual preference in four-plant plots

	σ^2_{rc}	σ^2_c	h^2 for $r = 2$	Correlations with visual preference in four-plant plots		Correlated response to selection[a]
				JEB	MFBD	
Emergence	0.862	1.336	0.76	0.343	0.340	0.577
Maturity	0.351	1.833	0.91	– 0.329	– 0.367	– 0.627
Yield	1.418	2.221	0.76	0.417	0.339	0.822
Visual size	0.489	0.847	0.78	0.099	0.149	0.165
Visual appearance	0.426	0.664	0.76	0.260	0.337	0.355
Visual growth cracks	0.170	0.147	0.63	– 0.030	– 0.028	– 0.018
Scab	1.140	1.440	0.72	– 0.090	– 0.119	– 0.188
Internal condition	0.939	0.403	0.46	0.097	0.146	0.144
Sloughing	0.993	0.556	0.53	– 0.156	– 0.158	– 0.205
After-cooking blackening	0.294	0.260	0.64	0.169	0.176	0.140
Sprouting 1	1.257	2.885	0.82	– 0.082	– 0.014	– 0.114
Sprouting 2	1.275	2.102	0.77	– 0.156	– 0.135	– 0.306
Keeping quality	0.870	1.350	0.76	– 0.025	– 0.015	– 0.034
Visual preference	0.265	0.436	0.77	0.423	0.419	0.403

[a] Response in replicated trials to selection for visual preference in four-plant plots based on mean of JEB and MFBD correlations and proportion selected of 0.25

this variation was greater than that between the 12 progenies; for example, by a factor of 1.87 for visual preference. The heritability of the differences between clones (mean of two replicates) ranged from 0.46 for internal condition to 0.91 for maturity.

The correlations between the traits assessed in the replicated trials and the visual preference scores in the four-plant plots are shown separately for the two breeders (Table 2) because they would normally each score half of the four-plant plots to save time. It can be seen that the two sets of correlations were very similar. Interest centres on their magnitudes and not their statistical significances because, with 311 degrees of freedom, a value as low as 0.111 would still be significant at the 5% level. The highest correlations were for visual preference followed by yield, early maturity (i.e. negative correlation), emergence and visual appearance. The values of 0.423 and 0.419 for visual preference fell short of the estimated maximum value of 0.69.

The correlations between four-plant plots and replicated trials for yield were 0.437 (JEB) and 0.455 (MFBD) compared with an estimated maximum of 0.68, for size 0.246 and 0.243 (maximum 0.70), for appearance 0.382 and 0.419 (maximum 0.68), and for growth cracks 0.331 and 0.107 (maximum 0.54). Hence, all of the correlations of trait with trait were higher than those of trait with visual preference in the four-plant plots but lower than their maximum possible value.

The correlations between the traits assessed in the replicated trials and the visual preference scores in the first clonal generation (JEB, MFBD and their mean) and seedling generation (GELS) were also examined. For the first clonal generation, there was good agreement between the two breeders who work sometimes together and sometimes independently in this generation. All of the correlations were extremely low with the highest values (mean of two breeders) of 0.121, 0.121 and 0.119 for maturity, visual size and visual preference. Likewise in the seedling generation for the person who normally harvests the material, all of the correlations were extremely low with the highest value of 0.151 for visual preference followed by 0.148, 0.127 and 0.119 for visual size, yield and maturity.

The correlations were also used to predict the response in the replicated trials to selection between clones within progenies within replicates in earlier clonal generations. For visual preference in the seedling, first and second clonal generation (average of JEB and MFBD correlations), the predicted responses were 0.114i, 0.090i and 0.317i, where i is the intensity of selection. The proportion selected in the second clonal generation is usually between 0.25 and 0.33, for which i is 1.271 and 1.097, thus giving a predicted response of between 0.403 and 0.348. Even if the proportions selected in the seedling and first clonal generation were as low as 0.10 ($i = 1.755$), the responses in the third clonal generation of 0.200 and 0.157 would still be less than that for selection in the second clonal generation, and the same would be true of 0.01 ($i = 2.665$) selected, with responses of 0.304 and 0.239.

The correlated responses in the third clonal generation to selection for visual preference in the second clonal generation are shown in the final column of Table 2. They are based on the average of the JEB and MFBD correlations shown in the previous two columns and an intensity of selection of $i = 1.271$ (0.25 selected). The largest predicted correlated responses are for faster emergence, earlier maturity, higher yield and greater regularity of shape (appearance).

Proportion of clones from each cross expected to exceed a given target

The information from the replicated trials on the mean and genotypic variance of the clones in each cross was used to predict the proportion of clones expected to exceed a given target. The results are shown in Table 3 for visual preference, yield and visual appearance. These traits were considered to be the ones of most interest in the context of this experiment because visual preference was the selection criterion in the early generations, and visual preference was largely determined by yield and visual appearance in the four-plant plots. The targets chosen as appropriate were the means of the 13 controls included in the replicated trials: 3.97 for visual preference, 7.49 kg/plot for yield, and 4.15 for visual appearance. Clones below these averages would almost certainly be rejected in a practical breeding programme.

Although the variances of the 12 crosses differed for all three traits, the differences resulted in only relatively minor changes to the rankings of the crosses based on their means alone. The changes were greatest for yield, for which the target value was furthest from the highest mean. Furthermore, the correlation for visual preference between σ_c and the phenotypic standard deviations originally used to choose the 12 progenies was low and non-significant ($r = 0.205$, $P > 0.05$).

The original three groups of four crosses with high, medium and low preference scores in the seedling generation were predicted to have 136, 18 and 2 clones per 1,000 exceeding the target for visual preference in the replicated trials; 121, 49 and 14 exceeding the target for yield; and 568, 371 and 148 exceeding the target for appearance.

Finally, one can have confidence that the overall conclusions on within cross selection will apply to the crosses in the high group as their average genotypic variances for all three traits were similar to the values in Table 2.

Table 3 Proportion of clones from each cross expected to exceed a given target (T)

Cross	σ^2_{rc}	σ^2_c	h^2	Mean	% > T
Visual preference					T = 3.97
91P28	0.378	0.412**	0.69	3.44	20.3
91MT40	0.206	0.677***	0.87	3.12	15.2
91MT129	0.233	0.406***	0.78	2.62	1.7
90B16	0.322	0.592***	0.79	3.24	17.1
				3.10	**13.6**
91MT9	0.384	0.295**	0.61	2.73	1.1
86P25	0.270	0.818***	0.86	2.38	3.9
86V3	0.236	0.216**	0.65	2.82	0.7
91MT24	0.372	0.700***	0.79	2.16	1.5
				2.52	**1.8**
91MT1	0.154	0.159**	0.67	1.82	0.0
91P23	0.131	0.562***	0.90	2.18	0.8
91MT66	0.128	0.364***	0.85	2.08	0.1
86V29	0.187	0.171**	0.65	2.01	0.0
				2.02	**0.2**
Yield					T = 7.49
91P28	1.706	1.956**	0.70	6.25	18.7
91MT40	1.134	1.807***	0.76	5.77	10.0
91MT129	2.077	1.031*	0.50	5.83	5.1
90B16	0.985	3.276***	0.87	5.59	14.7
				5.86	**12.1**
91MT9	1.524	1.352**	0.64	5.51	4.5
86P25	2.625	4.011**	0.75	4.75	8.5
86V3	1.912	0.582^{NS}	0.38	5.24	0.2
91MT24	1.131	5.578***	0.91	3.86	6.2
				4.84	**4.9**
91MT1	1.389	2.215***	0.76	4.11	1.2
91P23	0.392	3.236***	0.94	4.43	4.5
91MT66	0.855	1.284**	0.75	3.05	0.0
86V29	1.078	1.015**	0.65	3.86	0.0
				3.86	**1.4**
Appearance					T = 4.15
91P28	0.607	0.978***	0.76	4.35	57.9
91MT40	0.608	0.589**	0.66	4.03	43.6
91MT129	0.663	0.308*	0.48	4.17	51.6
90B16	0.450	0.805***	0.78	4.73	74.2
				4.32	**56.8**
91MT9	0.385	0.603***	0.76	3.93	39.0
86P25	0.195	1.105***	0.92	3.76	35.6
86V3	0.222	0.335***	0.75	3.50	13.1
91MT24	0.462	1.184***	0.84	4.44	60.6
				3.91	**37.1**
91MT1	0.222	0.922***	0.89	3.28	18.1
91P23	0.203	0.443***	0.81	3.19	7.5
91MT66	0.677	0.301^{NS}	0.47	3.81	26.8
86V29	0.270	0.528***	0.80	3.06	6.7
				3.33	**14.8**

***$P < 0.001$, **$P = 0.01$–0.001, *$P = 0.05$–0.01, NS $P > 0.05$

Response to selection for visual preference between and within crosses

The mean of the 337 clones in replicated trials for visual preference was 2.57 compared with 3.08 for the 120 clones in the group of four crosses with a high score in the seedling generation and compared with 3.57 for the 34 clones out of the 120 with a score of 5 or more in the four-plant plots (mean of two breeders). The mean of the top 34 clones in the replicated trials was 4.31. In other words, between cross selection in the seedling generation combined with within cross selection in the second clonal generation achieved a response in the third clonal generation of 1.00 (57%) compared with a maximum possible response of 1.74. The predicted response from the means in Table 3 (3.10–2.55 = 0.55) and selection in the second clonal generation ($0.317i = 0.317 \times 1.202 = 0.38$) was 0.93, a value close to the observed response of 1.00. Between cross selection in the seedling generation combined with within cross selection in the first rather than the second clonal generation was less effective with a mean of 3.41 for the

24 clones out of the 120 with a score of 5.75 or more in the tuber progenies (mean of two breeders).

Finally, it is of interest for later discussion to compare the response to individual clonal selection with cross (family) selection, despite the 12 crosses not being a random sample of the 198 originally assessed. The correlations between the third clonal generation and the seedling, first and second clonal generations were 0.865, 0.743 and 0.782 for the crosses and 0.432, 0.351 and 0.549 for the clones. The phenotypic standard deviations in the third clonal generation were 0.528 and 0.912 for crosses and clones, respectively. Assuming the same intensity of selection, the ratios of the responses in the third clonal generation to cross and clonal selection (i.e. family/individual) in the seedling, first and second clonal generations were 1.16, 1.23 and 0.82. In other words, cross selection was superior in the seedling and first clonal generations but not in the second clonal generation. As a consequence, selecting clones in the seedling generation with scores ≥ 5.5 (127 clones) followed by those in the four-plant plots with scores ≥ 4.75 (30 clones) resulted in means in the replicated trials of 3.00 (for the 127 clones) and 3.47 (30 clones), values slightly less than those above of 3.08 and 3.57. Again, selection in the seedling generation followed by selection in the first rather than the second clonal generation was less effective with a mean of 3.21 for the 27 clones out of the 127 with a score of 5.75 or more in the tuber progenies.

Discussion

As potato breeders seek new cultivars from crosses between pairs of parents with complementary features, one might expect most of the variation they exploit to exist within the crosses they make. However, in practice, breeders commonly find that differences occur between crosses, as happened in this experiment for all traits examined except internal condition. This is partly because breeders often make speculative crosses on the basis of the reputed characteristics of potential parents rather than their actual performance in extensive replicated trials and partly because specific combining ability does occur for many traits (see Bradshaw and Mackay 1994) and is, by definition, only manifest once crosses have been made and assessed. As Simmonds (1996) points out, outstanding new cultivars nearly always emerge from exceptionally good parental combinations.

The experiment confirmed the conclusions of earlier work done at SCRI that seedling progeny evaluations by breeders' visual preference scores can be used to reject entire crosses on the grounds that they are less likely than others to contain clones of commercial worth. For example, selecting the group of four 'high' crosses was predicted to give 13.6% of clones exceeding a target score of 3.97 for visual preference (Table 3), a gain of 1.42 on a 1–9 scale over the mean of all clones of 2.55.

Although the experiment was done and analysed in a slightly different way to previous work, some direct comparisons can be made. The correlations between scorers for visual preference in the seedling, first clonal and second clonal generations were 0.683, 0.798 and 0.790 compared with 0.645, 0.738 and 0.795 in the previous experiment (Brown et al. 1987a). The correlations between the means of the 12 progenies (over all replicates and scorers) in the seedling generation and in the first, second and third clonal generations were 0.875, 0.889 and 0.865. With eight crosses, Brown et al. (1987b) had found values of 0.743 and 0.602 between seedling and first and second clonal generations, respectively, and later, with 52 crosses (Brown et al. 1988), values of 0.70 and 0.71. Although none of these sets of crosses were random samples, Brown et al. (1988) found that the correlation between seedling and first clonal generation for their complete set of 191 crosses (0.65) was similar to that for the 52 crosses (0.70) chosen to cover the range of seedling preference scores. Yield was an important component of visual preference in the second (correlation averaged over scorers = 0.839) and third (0.720) clonal generations, just as Brown and Caligari (1986) had found it to be in the seedling (0.648) and first clonal generation (0.493). Likewise, Neele et al. (1991) found that tuber yield was the principal component of plant appearance (equivalent to visual preference) in an experiment with 600 clones from 20 progenies over the first two clonal generations. Brown and Caligari (1986) also found an association between the weight of tuber planted in the first clonal generation and the resulting yield, and expressed concern about a possible carry-over effect between clonal generations inflating the true genetical correlation. However, in this experiment (as in Brown et al. 1988), the correlation between seedling and successive clonal generations did not decline, and the differences in visual preference in the seedling generation were reflected in yield differences in the replicated trials.

In theory, the best criterion for choosing the most promising crosses is the proportion of clones expected to exceed the required target. However, this criterion requires not only an estimate of the mean of each cross but also one of the genetical variation within each cross, and this is not available in the early generations when clones are unreplicated. Furthermore, for visual preference, there was virtually no correlation ($r = 0.205$) between the phenotypic variation in the seedling generation and the genotypic variation in the third clonal generation. Fortunately, the results from the third clonal generation showed that an adequate choice could be made from the cross means alone. The means had a larger influence on the predicted proportion than the variances, although the importance of the latter did increase with that of the target over the highest mean. Caligari and Brown (1986) found that, for visual preference, the square root of the phenotypic variance added increasingly to the accuracy as the target value increased but was not a major component in the prediction, and hence the mean alone gave adequate predictions. Furthermore, Brown et al. (1988) found that the mean preference score was a slightly better predictor of superior crosses over generations than the mean and within progeny phenotypic variance.

The good agreement with the earlier work done at SCRI is particularly encouraging as the latter was done before the SCRI potato breeding programme was transferred from Edinburgh to Dundee. Hence, in this experiment, a new seedling glasshouse with mobile benches and capillary matting was used instead of irrigation through sand beds on fixed benches, and the replicated ware trials were done at Gourdie Farm, Dundee instead of the Murrays Farm in East Lothian. Furthermore, six of the eight staff involved in the experiment were new. It is, therefore, reasonable to expect similar potato breeding programmes elsewhere to benefit from adopting the use of family selection, but this needs to be checked in any new situation. For example, Gopal (1997) determined the effectiveness of progeny selection where seedlings were raised in the field under short days and found lower correlations of 0.60 and 0.53 for general impression between seedlings and the first and second clonal generations, respectively. Furthermore, Tai and Young (1984) found that, whilst the heritabilities of cross means for eight seedling traits were considerably greater than for individual seedlings, the phenotypic variances of the latter were much larger than the former. As a consequence, the predicted responses to individual selection were greater than those for family selection. In contrast, in this experiment the predicted responses to family selection for visual preference in the seedling and first clonal generations were greater than those for individual selection (ratios 1.16 and 1.23, respectively). These were only modest improvements because individual selection does result in the best families contributing the most clones to the next generation. However, greater overall benefits from family selection are expected from subsequently sowing more seed of the best families to increase their population size and from simultaneously selecting for other traits in choosing those families. For example, 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).

Having identified the best crosses, one is still left with the problem of exploiting the variation within them, which, in this experiment, was greater than the variation between crosses. Neele et al. (1989) also found more variation at a late harvest for plant appearance (equivalent to visual preference) within than between 20 crosses similar to those used in commercial breeding in The Netherlands (ratio was 1.88 compared with 1.87 in this experiment).

All of the traits assessed in the replicated trials had a moderate to high within cross heritability. Hence, it should be relatively easy to identify superior clones in this and later stages of a potato breeding programme. However, as the number of clones entering replicated yield trials is usually only a modest number in plant breeding terms, it is essential that as many as possible are acceptable for visual preference so that they can be selected for worthwhile improvements in other traits such as after-cooking blackening, sloughing, internal condition, resistance to scab and resistance to sprouting and keeping quality.

The experiment confirmed that selection for visual preference within crosses in the seedling and first clonal generation is very ineffective, as previously reported by others (Tai and Young 1984; Brown et al. 1984, 1987a; Maris 1988). Indeed, having practised between family selection in these generations, it can be argued that there will be little loss of progress if virtually all of the clones from the best families are taken forward to the second clonal generation. This is partly because individuals in the seedling and first clonal generations are unreplicated so that the environmental contribution to the phenotypic variance cannot be reduced by replication and partly because of genotype × environment interactions over seedling and clonal generations. A seedling in a glasshouse and a spaced plant at a seed site are in very different environments to those found in commercial ware production. If resources allowed more clones to be assessed as four-plant plots, this could be achieved by raising more seedlings of the best crosses in the glasshouse and harvesting four tubers from each plant. The use of well-separated 12.5-cm pots rather than tightly packed 10-cm ones should result in larger tubers and prevent problems arising from stolons growing into neighbouring pots, as occurred at a low frequency in this experiment.

Selection was more effective in the four-plant plots, although the responses were less than expected from predictions based on the variation between similar-sized plots (5-plant) in the replicated trials, and this can be attributed to genotype x scorer and genotype × environment interactions. As well as any site and season differences between Blythbank in 1994 and Gourdie in 1995, the growing season at the seed site was deliberately shorter than at the ware site. One consequence of this was that within family selection for visual preference in the second clonal year resulted in higher yields with earlier maturity, whereas between family selection in the seedling generation resulted in higher yields with later maturity, something which may or may not be desirable in any particular breeding programme.

As the correlated responses to selection for visual preference in the second clonal generation were less than the direct responses for its components, there would appear to be scope for altering the consequences of selection for visual preference by changing the subjective weightings given to its components. However, Neele et al. (1991) concluded that selection for visual preference (their plant appearance) could not be improved upon by independently selecting for its components, which, in their material, were tuber yield, stolon length and tuber appearance. This supports the earlier conclusions of Maris (1988) that selection for individual components of visual preference (his general impression) was usually no more reliable than visual preference itself.

The experiment has demonstrated that combining between cross (family) selection for visual preference in the seedling generation with within cross (family) selection in the second clonal generation is better than combining it with within cross selection in the first clonal generation and can achieve a worthwhile response in the third clonal generation. Selecting the group of high progenies followed by the 34 clones with a score of 5 or more in the four-plant plots produced a response of 1.00 in the replicated trials compared with a prediction of 0.93 and a value of 1.74 for the 34 best clones in those trials (i.e. a realised response of 57%). Further improvements in the overall efficiency of early generation selection are likely to come from the introduction of within cross selection for traits with a higher heritability than visual preference; for example, disease and pest resistance (Plaisted et al. 1984; Swiezynski 1984; Lacey et al. 1987). Assessment of tubers from the seedling generation for resistance to potato cyst nematodes and from the first and second clonal generations for cooking and processing quality is worth pursuing as these tests can be done over winter between generations.

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