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Selection for yield and yield components in the early generations of a potato breeding programme

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Summary. A number of unselected potato (*Solanum tuberosum* L.) clones were grown at two locations (a seed site and a ware site) in three consecutive years. The repeatability of total yield and yield components in the first two clonal years was compared with the same characters recorded in the third clonal year. Selection for yield in the first clonal year was only marginally more effective than a random reduction in number of genotypes, while selection in the second clonal year appeared to be somewhat more effective as judged by performance in the third clonal year. The inefficiency of selection in the first clonal year was ascribed, at least in part, to the inaccuracy of yield assessment as well as the "carry-over" effect of the mother tubers. Correlations of total yield were higher between different years in the same location than between different locations. Selection under growing conditions suitable for production of seed tubers tended to result in selection of early maturing clones which would not necessarily be optimal for ware growing conditions.

Key words: *Solanum tuberosum* – Selection efficiency – Potato breeding – Yield – Yield components

Introduction

When breeding new cultivars of potatoes (*Solanum tuberosum* L.) most breeding schemes involve the growth and assessment of many thousands of different genotypes. In early generations each clone is grown in small plots (at first only a single plant) usually at only one location without replication.

In these generations yield or yield components will not be recorded, but clones will be selected or rejected by visual appraisal of commercial worth (Blomquist and Lauer 1962; Davies and Johnston 1974; Tai and Young 1984; Scholz 1986). Later in the breeding programme the number of surviving genotypes will be sufficiently few and the stocks sufficiently large to permit yield trials to determine the most productive clones. However, even in the earlier generations breeders are greatly influenced by tuber yield and yield components when visually assessing breeding material (Maris 1969; Tai 1975; Brown and Caligari 1986).

The first-year plants are grown from true seed. Breeders generally agree that selection at this stage is ineffective and simply provides tubers that are planted for assessment the following year (Pfeffer 1963; Anderson and Howard 1981; Tai and Young 1984). In many breeding programmes, however, numbers are reduced at this stage (for some examples see Brown et al. 1984). Selection by visual preference of individual clones in the first clonal year is no more effective than selection of seedlings from true seed (Brown et al. 1986) and also results in the loss of valuable clones (Maris 1964; Anderson and Howard 1981). The size of tubers produced by seedlings affects the yield of the first clonal year plants and, therefore, influences breeders when selecting this next generation (Blomquist and Lauer 1962; Brown et al. 1984; Brown and Caligari 1986).

It has been suggested, therefore, that selection by visual preference in the seedling and first clonal year is at best a random reduction in the number of genotypes. There are even some indications that early generation selection in potato breeding may have negative effects (Brown et al. 1986). Some breeding programmes are already changing their early generation methods because of results of recent research (as noted by Mackay 1986 and Thompson 1986).

This study was conducted to provide increased knowledge of the repeatability of yield and yield components in early clonal generations and give a better understanding of underlying problems of early generation selection.

Materials and methods

The genotypes examined were derived from eight crosses made prior to 1981. The crosses were representative of those

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normally screened in the commercial potato breeding programme at the Scottish Crop Research Institute (SCRI) and are the ones reported on by Brown et al. (1984) and Brown and Caligari (1986). In 1981, 200 seeds from each of the eight crosses were sown in seed pans in an aphid-proof greenhouse. In the spring of 1982, 25 clones from each cross were taken at random from the genotypes that had produced tubers. These clones were grown at two locations, Blythbank, Peeblesshire (BB) and the Murrays Farm, East Lothian (MURR), in three successive years. Each clone in each year was grown in plots at both locations, in two randomised blocks, if sufficient tubers were available. In the first clonal year (1982) each plot was a single plant, in the second clonal year (1983) three plants and in the third clonal year (1984) five plants. The seed tubers used in the second and third clonal years were from the plants grown at BB (a high grade seed site) the previous year and hence no problems of health were detected during the experiment. As virtually all the seed produced in a year was required for the next years' trial the different seed sizes produced from field-grown plants were distributed at random over sites and replicates.

Foliage maturity of clones was recorded each year at MURR by scoring all clones for leaf senescence on one day each year. Earlier senescing clones were given lower scores on a 1–9 scale. After harvest, total weight of tubers and number of tubers produced from each plot were recorded at each site and mean tuber weights calculated.

In field trials in the first and second clonal years six standard cultivars were grown amongst the 200 clones. Each standard cultivar was represented by four plots of appropriate size in each block at each site.

BB is the location used by the potato breeding department at SCRI for production of healthy seed stocks. It is, however, also the location where clonal assessments are carried out in the first two clonal years. MURR is used for yield trials of more advanced breeding material. The BB site is planted later and harvested earlier than the MURR site, to reduce the possible spread of aphid borne viruses. Hence BB has a much shorter growing season. It is also at an higher altitude and has a different soil type to MURR.

Results

Mean squares from the analysis of variance of total tuber weight, mean tuber weight and number of tubers per plant for the 200 clones grown at two locations in three consecutive years are presented in Table 1. The analyses are based on block means. Because in the first clonal year replication was confounded with tuber size, the three-way interaction was used as the basic error term (Brown and Caligari 1986). There were highly significant differences between clones and between years for all three characters examined. Due to the longer growing season, the MURR location produced significantly higher yields, with more and heavier tubers than the BB site. There were significant interactions between years and locations for all three characters, probably due to the relatively dry conditions in 1983 which affected the MURR location to a greater extent than the BB site. There were no significant interactions of clones with location, suggesting that the ranking of clones was consistent and selection could be practised at either site equally effectively. The clone by year interaction was not significant for total tuber weight, suggesting that yield selection in one year would produce similar results the next year. The number and mean weight of tubers, however, did not give consistent results over years and the clone by year interactions were significant.

The correlation coefficients between the three clonal generations are presented in Table 2 for the three characters. The main comparisons of interest are between the third clonal year and the two earlier generations. Even though yield data collected from two replicates of five plants may not be regarded as completely accurate, the yields from the third clonal year were considered the most accurate available in the study and yield of the first and second clonal year were compared with them as well as with each other. Coefficients for total tuber weight show that although the second clonal year correlated with the third more highly than the first clonal year did with the third, the estimates were not significantly different, accounting for 27% and 24% of the yield variation respectively. The performance of clones was, therefore, equally assessed in the first and second clonal generations, relative to

Table 1. Mean squares from the analysis of variance of total tuber weight, mean tuber weight and number of tubers for clones grown at two locations in three consecutive years

Source	df	Total tuber wt	Mean tuber wt ($\times 10^3$)	No. of tubers
Clones (C)	199	0.48***	5.20***	49.04***
Years (Y)	2	54.18***	156.50***	3,289.80***
Locations (L)	1	1.72***	73.30***	948.67***
C×Y	398	0.17	2.00**	26.79***
C×L	199	0.16	1.14	10.01
Y×L	2	17.59***	86.30***	701.87***
C×Y×L	398	0.11	1.20	8.52

** $P=0.01$–0.001; *** $P<0.001$

Table 2. Correlations between years for total tuber weight (TTW), mean tuber weight (MTW) and number of tubers per plant (TN) recorded in FCY (first clonal year), SCY (second clonal year) and TCY (third clonal year)

SCY	TTW	0.244***	
	MTW	0.478***	
	TN	−0.040	
TCY	TTW	0.493***	0.520***
	MTW	0.397***	0.604***
	TN	0.327***	0.318***
		FCY	SCY

*** $P<0.001$

Table 3. Correlations for total tuber weight (TTW), mean tuber weight (MTW) and number of tubers per plant (TN) between two different locations (BB and MURR) in the third clonal year (TCY) compared with first and second clonal years (FCY and SCY)

		FCY		SCY	
		BB	MURR	BB	MURR
BB – TCY	TTW	0.39***	0.22**	0.65***	0.38***
	MTW	0.31***	0.21**	0.54***	0.37***
	TN	0.34***	0.21**	0.39***	0.11
MURR – TCY	TTW	0.37***	0.45***	0.28***	0.36***
	MTW	0.31***	0.40***	0.45***	0.46***
	TN	0.31***	0.21**	0.34***	0.21**

** $P = 0.01–0.001$; *** $P < 0.001$

Table 4. Correlations between foliage maturity (averaged over 3 years) and yield characters recorded at BB and MURR in the first, second and third clonal years (FCY, SCY and TCY)

		Total tuber wt	Mean tuber wt	No. of tubers
BB	– 1982 (FCY)	– 0.08	– 0.20**	0.19*
	– 1983 (SCY)	– 0.23**	0.06	– 0.10
	– 1984 (TCY)	– 0.05	– 0.18*	0.21**
MURR	– 1982 (FCY)	0.21**	0.03	0.21**
	– 1983 (SCY)	0.04	0.03	0.08
	– 1984 (TCY)	0.38***	0.10	0.21**

* $P = 0.05–0.01$; ** $P = 0.01–0.001$; *** $P < 0.001$

the third. However, selection for yield was not very successful in either the first or second clonal generations with nearly 75% of the variation being left unaccounted for in both cases. Turning to mean tuber weight, the correlation of the second and third years, accounted for 36% of the variation. This was much better than the correlation between the first and third generation, which accounted for only 16% of the variation. The latter was even lower than the correlation of the first with second year. For the second component of yield, number of tubers per plant, the correlations between third and first as well as third and second years were again very similar, as they were for total tuber weight.

In the first and second clonal year, five cultivars were grown as standards, each being represented by four plots in each block at each location. With these standard cultivars in the first clonal year the error sum of squares accounted for 21%, 58% and 50% of the total sum of squares for total tuber weight, mean tuber weight and number of tubers per plant, respectively. In the second clonal year the comparable figures were 14.4%, 14.9% and 16.5%. When the standard cultivars were grown as three-plant plots (SCY), the error sum of squares accounted for a much smaller proportion of the total sum of squares than in the single-plant plots, as might be expected (Caligari et al. 1985).

Since growing conditions for seed production at BB, differ from those where potatoes are grown for ware at MURR, it is questionable whether selection under these conditions would produce genotypes which will perform to a high standard at a ware site. This relationship was studied by correlating the results from the third clonal year with those from the previous two for the two sites separately (Table 3). For all three characters, the correlations were generally larger, although usually not greatly so, within sites as opposed to between sites. In fact, of the 12 sets, 10 show this relationship while two, involving tuber number, show a slight reverse trend.

Although the differences are not large there are effects due to the site of selection. These may be due to the shorter growing season at BB and be a reflection of foliage maturity. Maturity (measured on a 1–9 scale of increasing lateness) was correlated with yield and the two yield components (Table 4). For total yield and mean tuber weight, at BB there tended to be negative correlations; i.e., earlier maturity was associated with higher yield and greater tuber weight. At MURR, on the other hand, the reverse was true and higher yields tended to be associated with later maturity. The number of tubers per plant showed a positive relationship at both sites, with higher numbers being produced by later maturing clones.

Discussion

Correlations for total tuber weight, mean tuber weight and number of tubers per plant between successive years of a potato breeding scheme were positive and significant. Selection for these characters would therefore appear to be possible in either the first or second clonal year. Caution should be used, however, in the degree of confidence placed in this selection process since only about 25% of the variation can be accounted for by the correlation between the yield of successive generations.

In this experiment, yield data were recorded but no genotypes were discarded. It was therefore possible to simulate selection at various selection intensities. Selection would normally have been carried out at the end of each of the three years. To examine the efficiency of selection at these stages, the relationship between the number of selected and rejected clones can be studied for the years taken in pairs. For example, the material in the first year (FCY) can be divided into two categories, selected and rejected, depending on set criteria. The second year clones (SCY) can then be selected on the same or different criteria. From this it can be asked what proportion of clones that were selected in SCY were a) selected in FCY and b) rejected in FCY. The ratio of these proportions will be termed the selection ratio and is –

Year 1	Selected (w)		Rejected (x)	
Year 2	Selected (y)	Rejected (w−y)	Selected (z)	Rejected (x−z)

$$\text{Selection ratio} = (y/w)/(z/x)$$

If the selection ratio is equal to zero, then either there were no repeat selections made in the second year, or there were no clones selected in the second year that had been discarded in the first. A selection ratio less than 1.0 indicates that a higher proportion of clones were selected from the clones that were discarded in the first year than from those selected in the first year. Selection ratios equal to 1.0 indicate that there was no association between the selections in the two years and selection ratios greater than 1.0 show that selection was effective, with increasing values of selection ratio indicating increasing efficiency.

The selection ratios of the 200 clones selected on total tuber weight at different selection intensities in the first and second clonal years are shown in Table 5. Irrespective of the proportion retained in the second clonal year there is a general increase in the selection ratios as the percentage of clones retained in the first clonal year increases. When 99% of the first clonal year clones are retained sampling variation plays a large part and the selection ratios are either 0.0 or almost 1.0. The highest selection ratio was obtained by selecting 90% of the first clonal year genotypes and 50% in the second clonal year. Selection at this level may however not justify the effort involved in discarding only 10% of the first clonal year genotypes. When larger proportions of first clonal year genotypes are discarded the selection ratios are reduced to just above 1.0. From this it would appear that moderate to high selection intensities would not give a significant improvement over random reduction. Similar results are seen for the selection intensities in the second and third years but the ratios tend to be higher.

The selection ratios suggest that selection for total tuber weight was more effective between the second and third clonal years than between the first and second clonal years. The inefficiency of selection at the single-plant stage was due, at least in part, to the inaccuracy of yield assessment on a single plant basis at

Table 5. Selection ratios (for definition see text) of 200 clones for total tuber weight at different selection intensities (i.e. % of clones retained). The upper figures show the ratios for selection in the first year followed by the second, while the lower figures show selection in the second followed by the third

Selection intensity in year 2							
99%	1.0	1.0	1.0	1.0	1.0	1.1	1.0
	1.0	1.0	1.0	1.0	1.0	1.1	1.0
90%	1.1	1.1	1.1	1.1	1.2	1.5	0.9
	1.1	1.1	1.1	1.2	1.4	2.3	0.0
75%	1.3	1.4	1.3	1.2	1.4	2.2	0.0
	1.3	1.2	1.4	1.7	2.0	5.2	0.0
50%	1.3	1.6	1.7	1.4	2.0	5.2	0.0
	1.3	1.7	1.9	2.3	3.3	0.0	0.0
25%	0.0	1.4	1.7	1.4	2.0	2.6	0.0
	2.7	2.4	2.4	7.4	8.0	0.0	0.0
10%	0.0	1.4	1.8	0.9	1.0	2.1	0.0
	3.5	1.5	2.4	18.6	6.2	0.0	0.0
1%	0.0	0.0	1.5	0.5	0.7	0.0	0.0
	0.0	0.0	5.9	0.0	0.0	0.0	0.0
Selection intensity in year 1	1%	10%	25%	50%	75%	90%	99%

the level of replication used. This finding is the same as that of Brown et al. (1986) when they examined the efficiency of visual preference scores. This suggests that the inefficiency of selection by visual appraisal is not merely a reflection of its subjective nature since the objectively assessed yield characters in this study show similar effects.

Selection for yield and yield components appears to be more effective in the second clonal generation. Selection at the 50% level of intensity in the second clonal generation resulted in selected clones being almost 19 times more likely to be amongst the top 10% yielding in the third clonal year, than the discarded clones. More intense selection for yield in the second clonal year would appear to be counter-productive.

Selection under growing conditions of a seed production site (BB) resulted in the selection of early maturing clones (see also Simmonds 1969) which would not necessarily be suited to ware growing conditions.

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