Theor Appl Genet (1997) 95 : 307–311

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Progeny selection for agronomic characters in early generations of a potato breeding programme

Received: 8 January 1997 / Accepted: 28 February 1997

Abstract Repeatabilities of progeny means, and the univariate cross prediction method were used to study the effectiveness of progeny selection for agronomically important characters in early generations of potato (*Solanum tuberosum* L.) breeding. The study was based on 90 progenies (72 crosses + 18 selfs) evaluated for three successive generations, i.e. seedling, first clonal and second clonal generations. Repeatabilities of progeny means were measured as correlation coefficients between generations. In the univariate cross prediction method, progeny means and within-progeny standard deviations were used to calculate the proportions of clones exceeding the target values, and correlation coefficients between generations for predicted and observed proportions of clones, were calculated. Population means varied from generation to generation. Correlation coefficients between generations for progeny means for most of the characters were significant, but moderate. These were higher than the correlation coefficients between predicted and observed proportions of clones exceeding the target values. The possibility of using progeny means as a selection parameter to reduce the number of genotypes to be examined in later stages by rejecting the poor crosses in seedling generation is discussed.

Key words Potato breeding · Early-generation selection · Progeny selection · Cross prediction · *Solanum tuberosum*

Introduction

The efficiency of individual clone selection in early stages of potato (*Solanum tuberosum* L.) breeding has been reported to be low to very low for most of the characters, for example, tuber yield and its components (Brown et al. 1984; Caligari et al. 1986; Maris 1988; Neele et al. 1991b; Gopal et al. 1992). A poor selection efficiency for individual genotypes in early generations shifted the attention of the breeders to progeny selection (Simmonds 1979, 1996) in an attempt to somehow reduce the number of genotypes to be examined in later stages. However, very little information is available on the efficiency of progeny selection in potato (Caligari and Brown 1986; Brown et al. 1987a; Maris 1988), and that confined to only a few characters, and the results have been conflicting. Further, in these studies, the potato crop was grown under long days (as in temperate regions) and seedlings raised in glasshouses. The study presented here reports the effectiveness of progeny selection in a potato crop grown under short days (as in sub-tropical regions) where seedlings were raised in the field.

Communicated by H. C. Becker

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Materials and methods

A random sample of 22 potato genotypes representing advance-generation clones, germplasm accessions, and exotic and Indian varieties, generally used as parents, was drawn from the National Potato Breeding Programme at the Central Potato Research Institute, Shimla. Twenty of these genotypes, AB455, E4451, F1277, JE812, JH222 (Kufri Jawahar), JN1501, JR465, JTH/C107, MS78-46, MS78-56, MS79-34, MS80-758, MS81-152, MS82-638, MS84-1169, PJ376 (Kufri Ashoka), RG1197, SLB/K23, CP1710 (Kerr Pondy) and CP2132 (Tollocan), belonged to *Solanum tuberosum* ssp. *tuberosum* and 2, EX/A680-16 and EX/A723, to ssp. *andigena*. The genotypes were grown and crossed during the summer (May–August) of 1992 at the Central Potato Research Station, Kufri (32°N, 77°E, 2500 m above sea level) in a 18 × 4 (females × males) NC II mating design using CP1710, CP2132, EX/A680-16 and EX/A723 as males because of their high pollen fertility and broad genetic base. The genotypes were also selfed, but 4 genotypes, AB455, E4451, F1277 and JR465, did not set any self seed.

The 90 progenies (72 crosses + 18 selfs) thus generated were evaluated in the field at the Punjab Agricultural University, Ludhiana (31°N, 75°E, 230 m above see level) during the autumns

(October–January) of 1993 to 1996 for three successive generations, i.e. seedling generation (SG), first clonal generation (FCG) and second clonal generation (SCG). In SG, there were two replications with each progeny represented by 60 randomly selected seedlings. At harvest, three tubers per seedling for each of the 50 randomly selected genotypes per progeny were retained and used to form three replications (one tuber per genotype per replication) of FCG. The same procedure was adopted to form material for SCG in which each progeny was represented by 40 genotypes and six replications. All experiments were laid out in completely randomised block design in short rows of 5 tubers each at the recommended intra- and inter-row distances of 20 cm and 60 cm, respectively. The crop was harvested at maturity. Normal manurial and cultural schedules were followed.

Characters recorded

Data were recorded in the three generations for ten characters (Table 2) on all 90 progenies. Plant vigour was recorded at full growth (80 days after sowing) and all other characters at maturity (120 days after sowing). Data for tuber yield, tuber number, average tuber weight and general impression were recorded on an individual plant basis, and for the remaining characters, on a plot basis.

Statistical methods

Two methods (1) repeatability of progeny means and (2) univariate cross prediction – were used to study the effectiveness of progeny selection.

1) Repeatability of progeny means: simple correlation coefficients were computed between generations for progeny means of various characters following the analysis of variance.
2) Univariate cross prediction: within-progeny standard deviations for each of the 90 progenies were calculated for the four characters, tuber yield, tuber number, average tuber weight and general impression. Means and standard deviations were used to calculate the proportion of lines (clones) expected to transgress particular target values following the method of Jinks and Pooni (1976). For this, the mean performance (rounded to the nearest integer) of the best-performing progeny in a generation was set as the target value (Table 1). The probabilities were estimated as the sum of the normal probability integral corresponding to the value $(T - \bar{x})/\sigma$ or $(\bar{x} - T)/\sigma$, depending on whether the predictions were for values greater than (or equal to) or less than (or equal to) the target value, T. Statistical tables were used to find the percentage of clones expected to exceed the target values at the estimated probabilities. Simple correlation coefficients were calculated between generations for the predicted and observed proportions of clones exceeding the target values for various characters.

Table 1 Mean performance of the best performing progeny in a generation used as target value

Character	Target values in different generations		
	Seedling	First clonal	Second clonal
Tuber yield (g/plant)	160	260	470
Tuber number (per plant)	20	13	15
Average tuber weight (g)	13	30	55
General impression (1 = very high to 5 = very poor)	2	2	2

Results

Analysis of variance showed significant genotypic differences among progenies for various characters in three generations studied. Population means averaged over progenies and coefficient of variation (CV) for various characters for successive generations are presented in Table 2. Population means improved for major characters of economic importance, i.e. tuber yield, average tuber weight and general impression, as the generations advanced. Plant vigour was higher in the clonal generations than in the seedling generation. Population means for tuber number, tuber colour and uniformity in tuber colour, tuber shape and tuber weight were more or less constant over the generations. However, tubers were longer in SCG than in SG and FCG. The coefficient of variation (CV) showed that maximum variation was for uniformity in tuber shape followed by tuber colour and uniformity in tuber weight, whereas minimum variation was for general impression followed by average tuber weight and number of tubers, respectively, in all the generations. There was negligible change in the magnitude of the CV over the generations for various characters.

Repeatabilities of progeny means

Correlation coefficients for means of 90 progenies between three successive generations (Table 3) showed that most of the correlations were significant. However, magnitudes of the correlations varied for characters and among the generations. Correlations between two immediate generations (i.e. SG vs. FCG and FCG vs. SCG) were higher than between two distant generations (i.e. SG vs. SCG).

For tuber yield, correlation coefficients between SG and SCG were low ($r = 0.34$), whereas those between SG and FCG and between FCG and SCG were moderate ($r = 0.56$ and 0.50, respectively). For tuber number and average tuber weight, correlation coefficients were in general of low magnitudes.

For general impression, plant vigour and tuber shape, all correlation coefficients were of moderate magnitudes (Table 3). Tuber colour and uniformity in tuber colour in SG were highly correlated with those in FCG ($r = 0.81$, 0.92, respectively). Other correlation coefficients for these characters were of moderate magnitudes. Correlation coefficients for uniformity in tuber shape and uniformity in tuber weight between SG and FCG were moderate, whereas those between SG and SCG and between FCG and SCG were of low magnitudes (Table 3).

Univariate cross prediction

Correlation coefficients between generations for predicted and observed proportions of clones exceeding

Table 2 Population means and coefficient of variation (CV) for various characters in three successive generations

Character	Seedling generation			First clonal generation			Second clonal generation		
	Mean	±SE	CV	Mean	±SE	CV	Mean	±SE	CV
Tuber yield (g/plant)	75.25	1.28	14.46	134.39	2.03	12.79	299.40	5.56	19.59
Tuber number (per plant)	8.83	0.13	12.55	7.25	0.01	11.21	8.50	0.13	15.52
Average tuber weight (g)	8.29	0.11	11.37	20.62	0.20	8.38	38.43	0.44	10.72
General impression (1 = very high to 5 = very poor)	3.24	0.07	5.80	2.85	0.06	5.29	2.58	0.03	6.45
Plant vigour (1 = very high to 5 = very poor)	2.35	0.06	19.95	1.98	0.04	17.69	2.00	0.04	14.36
Tuber colour (1 = white to 5 = purple)	1.38	0.05	29.32	1.34	0.05	32.99	1.42	0.06	31.45
Tuber shape (1 = round to 4 = long-oblong)	2.72	0.08	24.13	2.83	0.05	20.43	3.34	0.06	24.66
Uniformity in tuber colour (1 = high to 3 = poor)	2.40	0.05	18.46	2.38	0.07	16.47	2.49	0.04	13.50
Uniformity in tuber shape (1 = high to 3 = poor)	1.51	0.07	41.25	1.44	0.05	38.76	1.56	0.07	42.00
Uniformity in tuber weight (1 = high to 3 = poor)	2.01	0.07	28.40	1.90	0.07	29.51	1.98	0.07	30.70

Table 3 Correlation coefficients for progeny means of various characters between three successive generations, based on 90 progenies (*SG* seedling generation, *FCG* first clonal generation, *SCG* second clonal generation)

Character	SG vs. FCG	FCG vs. SCG	SG vs. SCG
Tuber yield	0.56**	0.50**	0.34**
Tuber number	0.37**	0.44**	0.36**
Average tuber weight	0.26*	0.49**	0.21*
General impression	0.60**	0.62**	0.53**
Plant vigour	0.57**	0.65**	0.51**
Tuber colour	0.81**	0.52**	0.49**
Tuber shape	0.69**	0.53**	0.50**
Uniformity in tuber colour	0.92**	0.73**	0.69**
Uniformity in tuber shape	0.51**	0.13	0.14
Uniformity in tuber weight	0.55**	0.27*	0.26**

*, ** Significant at $P < 0.05$, 0.01, respectively

the target values (Table 4) were mostly significant. Like correlation coefficients for progeny means, here also correlations between two immediate generations were, in general, higher than between two distant generations.

Correlations for observed proportions (i.e. Obs-SG vs. Obs-FCG; Obs-FCG vs. Obs-SCG; Obs-SG vs. Obs-SCG) were, in general, of low magnitudes for all the characters (Table 4). The only correlation worth consideration was for general impression, where the observed proportions in SG were moderately correlated ($r = 0.61$) with that of FCG. Correlation coefficients for predicted versus observed proportions (i.e. Pre-SG vs. Obs-FCG; Pre-FCG vs. Obs-SCG; Pre-SG vs. Obs-SCG) were also of low magnitudes for various characters. The highest correlation was $r = 0.50$ for general impression between predicted proportions in SG and observed proportions in FCG.

Discussion

The objective of the present study was to discover whether the superior progenies selected in seedling generation will remain superior in clonal generations. In order to be able to apply the results generally, we studied a large population consisting of 90 progenies of diverse genetic constitutions involving Tuberosum × Tuberosum and Tuberosum × Andigena crosses as well as selfs. In potato breeding programme for short days, as in India, both Tuberosum and Andigena parents are used, as they have similar tuberisation behaviour under these conditions. It is not so in long days where Andigena does not tuberise well. Andigena, however, is generally used as the male parent because Tuberosum × Andigena crosses are known to result in more productive progenies with more desirable tuber characters than Andigena × Tuberosum crosses (Hoopes et al. 1980; Sanford and Hanneman 1982; Maris 1989). Although 'selfs' are not typical progenies used for cultivar breeding, they have been exploited in some studies. For example, cv Kufri Safed was a clonal

Table 4 Correlation coefficients between generations for predicted and observed proportions of clones exceeding the target value, based on 90 progenies (*Pre* predicted proportion, *Obs* observed proportion, *SG* seedling generation, *FCG* first clonal generation, *SCG* second clonal generation)

Character	Obs-SG vs. Obs-FCG	Obs-FCG vs. Obs-SCG	Obs-SG vs. Obs-SCG	Pre-SG vs. Obs-FCG	Pre-FCG vs. Obs-SCG	Pre-SG vs. Obs-SCG
Tuber yield	0.42**	0.39**	0.20	0.45*	0.33**	0.27*
Tuber number	0.29**	0.43**	0.34**	0.28**	0.44**	0.28**
Average tuber weight	0.19	0.28**	0.03	0.24**	0.27**	0.07
General impression	0.61**	0.48**	0.31**	0.50**	0.42**	0.29**

*, ** Significant at $P < 0.05$, 0.01, respectively

selection from the self progeny of an old variety Phulwa of ssp. *andigena* (Misra et al. 1984). In the present study, data were initially analysed in two sets, i.e. with and without selfs, but the results were similar in both cases. This may be because clonal generations were reproduced vegetatively. Consequently, we presented results based on combined populations of crosses and selfs.

The increase in mean tuber yield as the generations advanced was mainly due to an increase in average tuber weight as no notable change occurred in tuber number per plant. Tubers were longer in SCG than in earlier generations, probably due to the better expression of tuber shape with increase in tuber size in SCG. Due to the improvement in these traits, general impression, which took in account all visual characters at harvest, also improved. More vigorous growth in clonal generations than in seedling generation indicated that raising the crop from tuber seeds is better than raising it from true potato seeds, with respect to plant vigour.

The negligible change in the magnitudes of CV over the generations for various characters was as expected, because over generations the population was represented by a random sample of genotypes for the same 90 progenies. Whatsoever change has occurred in the CV may be due to environment and/or genotype × environment interaction.

Repeatabilities of progeny means

The magnitudes of the correlation coefficients between generations for progeny means (Table 3) indicated that in early generations moderately effective selection based on progeny means could be conducted for most of the characters, with the highest efficiency for uniformity in tuber colour. General impression could also be selected for with moderately reasonable accuracy. However, the magnitudes of the correlation coefficients in the present study were somewhat lower than those reported by Brown et al. (1987a) and higher than those reported by Maris (1988). The correlations between SG and FCG as observed in this study were higher than that reported by Neele et al. (1991a), whereas those between FCG and SCG were more or less of similar magnitudes in the two studies. The higher correlations between SG and FCG as observed in the present study may be because seedlings were raised in the field rather than in pots as done by Maris (1988) and Neele et al. (1991a). The raising of seedlings in the field results in a fuller expression of the characters. However, Brown et al. (1987a) had raised the seedlings in pots, yet they got quite high correlation coefficients. However, their study was based on only 8 progenies in contrast to 90 progenies used in the present study. Therefore, it does, appears that the raising of seedlings in the field rather than in pots would be better for progeny selection.

From a practical point of view, correlations between SG versus SCG are more important than those between SG versus FCG or FCG versus SCG. Because, if SG versus SCG correlations are strong, high selection pressure can be applied in the SG itself to eliminate the unproductive crosses early. In the present study, these correlation coefficients were of low to moderate magnitudes, indicating that high selection pressure in SG would be detrimental. The magnitudes of the correlation coefficients between FCG and SCG suggest that high selection pressure should also be avoided in FCG.

Gopal et al. (1992) studied the repeatabilities of individual genotypes' performance in early generations under conditions similar to those of the present study, i.e. short days. A comparison of the repeatabilities of progeny means in the present study with that of repeatabilities of individual genotypes (Gopal et al. 1992) showed that the correlation coefficients of seedling generation with clonal generations were higher for progeny means than those for individual genotypes for characters like tuber yield and tuber number; for average tuber weight these were more or less of similar magnitudes. Correlation coefficients between clonal generations in the two studies were not much different. Brown et al. (1987a) reported that progeny means have higher repeatabilities than individual clones in the early generations for character breeder's preference score (general impression). They, however, did not compare the repeatibilities on this pattern for other characters. It appears that, in general, for seedling versus clonal generations, the repeatability of the progeny mean is better than that of individual genotypes' performance.

Univariate cross prediction

The results of univariate cross prediction may be affected by the target values set for calculating the predicted and observed proportions exceeding the target. In the present study, instead of selecting these targets arbitrarily, we used the mean (rounded to nearest integer) of the best performing progeny in a generation as it can be considered a reasonably high value for selection purposes.

Though correlation coefficients for predicted and observed proportions of clones exceeding the target value in different generations were calculated in all of the possible combinations, breeders would be mainly interested in knowing whether the proportion of clones expected to transgress a particular target value in later generations can be predicted from the observed or predicted proportions transgressing the target value in an earlier generation. Therefore, only relevant correlation coefficients were presented (Table 4).

Caligari and Brown (1986), on the basis of 8 progenies, reported that predicted and observed proportions of clones exceeding a target value had high repeatabilities over generations as well as under different environments. They had recommended this as a good method of cross prediction after testing it over 52 crosses (Brown et al. 1988). However, our results indicated that though predicted as well as observed proportions were repeatable over generations, yet these had only a low to moderate efficiency in cross prediction (Table 4). Brown et al. (1988) had reported that predictions based on the expected proportion of clones that would transgress a given target value was better than the prediction based on the observed frequency of desirable clones in a progeny sample. However, in the present study, there did not appear to be much difference in the effectiveness of these two types of proportions with regard to effectiveness of prediction.

General

Higher correlations between two immediate generations than between two distant ones may be due to the type and size of seed used for raising the successive generations. This type of effect called 'carry over' effect has also been reported in earlier studies (Brown et al. 1987b; Gopal et al. 1992).

A comparison of repeatabilities of progeny means (Table 3) to that of repeatabilities of proportions (Table 4) showed that progeny means were better than the proportions for cross prediction. These findings agree with those of Brown et al. (1988) who reported that for character breeder's preference score (general impression) cross prediction based simply on the mean performance provided better estimates of a progeny's performance in later generations than those based on expected or observed proportions.

The moderate efficiency of selection for progeny means for most of the characters, as observed in the present study, can be exploited for making initial choices in identifying the crosses which have a high probability of producing clones with desirable phenotypes. Those progenies which have a low probability can be discarded in seedling generation. This can be adopted in practical potato breeding programmes: a large number (may be hundreds) of crosses may be evaluated in seedling generation by raising as few as 50–60 genotypes per cross. Negative selection (rejection of a poor phenotype) may be practiced for the characters under evaluation and a larger population of the selected crosses can be raised to practice within-progeny individual clonal selection. The procedures suggested by Gopal et al. (1992, 1994) and Gopal and Minocha (1997) may be considered while practising individual clonal selection. This idea of reducing the number of crosses to be evaluated in later generations has also been strongly recommended by Simmonds (1996) who, based on the magnitudes of between- and within-family variations, reported that discrimination between family means must be very much more efficient than discrimination between individuals within a family. There is and has been for a long time a general awareness that outstanding new cultivars nearly always emerge from exceptionally good parental combinations. The procedure suggested here should thus be economically as well as practically more viable.

Acknowledgements I am thankful to Dr. J. L. Minocha for kind guidance and Dr. P. C. Gaur for clarifying certain points.

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