Theor Appl Genet (1998) 96 : 287–293 © Springer-Verlag 1998

J. Gopal

Identification of superior parents and crosses in potato breeding programmes

Received: 23 April 1997 / Accepted: 6 August 1997

Abstract The effectiveness of parent per se performance and their self values in the selection of superior parents and crosses in potato breeding programmes was studied by evaluating progenies of 72 crosses from 18 × 4 (female × male) matings, parents and their selfs for ten agronomically important characters for three successive generations. Simple correlation coefficients were computed between parent per se performance versus general combining ability effects, female per se performance versus progeny means of females, female self values versus progeny means of females, mid-parent values versus progeny means of crosses and mid-self values versus progeny means of crosses. The magnitude of the significant correlation coefficients showed that progeny means of crosses could be moderately predicted by the mid-self values for plant vigour and general impression in clonal generations. Similarly, the progeny means of females in clonal generations could be predicted by their per se performance for general impression. Female self values in the second clonal generation were moderately associated with progeny means of females in that generation for general impression and plant vigour. Parent per se performance and mid-parent values were, in general, ineffective in predicting the general combining ability and the progeny means of the crosses, respectively. The poor predictive powers of parent per se performance and mid-parent values are discussed in relation to the relative importance of specific and general combining ability effects.

Key words Potato breeding · Cross prediction · Parent per se performance · Mid-self values · *Solanum tuberosum*

Introduction

The choice of parents and crosses for breeding programmes constantly puzzles plant breeders. Methods such as diallel crosses (Griffing 1956) and North-Carolina design II (Comstock and Robinson 1952), which are useful for identifying superior parents and cross combinations, are rarely used in practical potato breeding programmes, being labour intensive, time consuming and tedious. The problem of sterility makes the task of obtaining the required cross combinations difficult (Plaisted et al. 1962; Plaisted and Peterson 1963; Killick and Malcolmson 1973; Killick 1977; Gopal 1994, 1996). The highly heterozygous and tetraploid status of *Solanum tuberosum* further complicates the application of various biometrical models. Progeny means though reliable in identifying superior cross combinations (Brown et al. 1988; Gopal 1997) requires the evaluation of a large (may be hundreds) number of crosses to identify a few promising ones. Thus, simple and reliable methods are required to identify the superior parents and cross combinations.

If phenotypic performance of the parents had a strong relationship with their general combining ability and progeny means of the crosses, the selection of parents would be straightforward. Maris (1989) reported that parent per se performance was a good indicator of general combining ability of the parents and that mid-parent values can be used to identify crosses with high progeny means for various agronomically important characters. However, Brown and Caligari (1989) and Neele et al. (1991) were not able to accurately predict progeny performance by the

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Communicated by H. C. Becker

J. Gopal (✉)
Division of Genetics and Plant Breeding, Central Potato Research Institute, Shimla 171 001, HP, India
Fax: 0177-224460
E-mail: cpri@x400.nicgw.nic.in

mid-parent values, and results varied with the character and the duration (period from planting to haulms cutting) of the crop.

Mid-self values (in analogy to mid-parent values) measured as mean performance of the self progenies of parents involved in a cross could be another method of cross prediction. This method has the advantage over the combining ability methods that it requires only one offspring population per evaluated parent. By evaluating self progenies of *n* parents, breeders could predict the value of $n(n-1)$ cross combinations. However, this can be used only for self-fertile parents. Brown and Caligari (1989) reported that mid-self values were more effective than mid-parent values in cross prediction for tuber yield and its components. However, Neele et al. (1991) concluded that there was little or no advantage in using mid-self values over mid-parent values as cross predictors.

The available reports thus show that no definite conclusion could be drawn about the effectiveness of parent per se performance and mid-self values in identifying superior parents and crosses in potato breeding. All these studies were confined to potato crops grown under long days (as in temperate regions) and seedlings raised in glasshouses. The present study reports the effectiveness of parent per se performance and self values in the selection of superior parents and crosses in potato breeding for crops grown under short days (as in sub-tropical regions) where seedlings were raised in the field.

Materials and methods

Twenty-two potato genotypes representing advance generation selections, germplasm accessions and exotic and Indian varieties generally used as parents were 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'), belong 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 seasons (May–August) of 1992 at the Central Potato Research Station, Kufri (32°N, 77°E, 2500 m above sea level) in an 18 × 4 (females × males) factorial 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 females, 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 during the autumns (October–January) of 1993–1996 (31°N, 75°E, 230 m above sea level) for three successive generations, i.e. seedling generation (SG), first clonal generation (FCG) and second clonal generation (SCG). In the SG, there were two replications each with 60 randomly selected seedlings per progeny. At harvest, 3 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 the FCG. The same procedure was adopted to assemble material for the SCG in which each progeny was represented by 40 genotypes and six replications. Parents were also evaluated along with the crosses in the clonal generations during the autumns of 1994–1995 and 1995–1996 using 15 tubers per parent per replication. All experiments were carried out in a completely randomised block design in short rows of 5 tubers each at recommended intra- and inter-row distances of 20 cm and 60 cm, respectively. The crop was harvested at maturity. Normal manuring and cultural schedules were followed.

Characters recorded

Data were recorded for ten characters (Table 1) on all the plants of all 90 progenies and 22 parents. Plant vigour was recorded at full growth (80 days after sowing) and all other characters at maturity (120 days after sowing). General impression was based on various tuber characters recorded at harvest, including tuber yield and its components.

Statistical analysis

Combining ability analysis according to the factorial mating design was conducted separately for each of the three generations using the statistical computer package SPAR 1 (IASRI, New Delhi). Parents

Table 1 Correlation coefficients between per se performance and general combining ability effects of parents in different generations based on 22 genotypes

Character	Seedling generation	First clonal generation	Second clonal generation
Tuber yield (g/plant)	− 0.11	0.01	0.39
Tuber number (per plant)	0.17	0.39	0.15
Average tuber weight (g)	− 0.24	0.57**	0.48*
General impression (score 1 = very high to 5 = very poor)	− 0.10	0.06	0.39
Plant vigour (score 1 = very high to 5 = very poor)	0.24	0.10	0.27
Tuber colour (score 1 = white to 5 = purple)	0.31	0.18	− 0.28
Tuber shape (score 1 = round to 4 = long-oblong)	0.48*	0.56**	0.49*
Uniformity in tuber colour (1 = high to 3 = low)	0.02	0.04	− 0.10
Uniformity in tuber shape (1 = high to 3 = low)	− 0.09	− 0.39	− 0.29
Uniformity in tuber weight (1 = high to 3 = low)	− 0.26	− 0.03	0.18

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

per se performance was measured as their average performance over 2 years, and progeny means of females were calculated as the average performance of the crosses involving the concerned female. Mid-parent and mid-self values for 56 combinations (14 × 4, excluding the 4 females which did not produce any self seed) were calculated as means of the pairs of concerned parents and their selfs, respectively. Simple correlation coefficients were computed between parent per se performance versus general combining ability, female per se performance versus progeny means of females, female self values versus progeny means of females, mid-parent values versus progeny means of crosses and mid-self values versus progeny means of crosses.

Results

The analysis of variance showed significant differences among the progenies (both crosses and selfs) and the parents for various characters in all generations. In a pooled analysis over generations, mean squares due to generations and various interactions with generations were also significant for all characters. The results of the combining ability analysis are not presented here, as these do not fall within the objectives of the present study. However, general combining ability effects (GCAs) of various characters were used in the following correlation analysis.

Parent per se performance versus general combining ability

Correlation coefficients between per se performance of the 22 parents and their estimated general combining ability effects varied in the different generations (Table 1), and except for a few exceptions, most of the correlations were non-significant. Per se performance had no relationship with the general combining ability effects in the SG for various characters except for tuber shape. In the clonal generations, general combining ability effects only for average tuber weight and tuber shape were positively and significantly associated with the corresponding per se performance of the parents. The magnitude of significant correlation coefficients varied between 0.48 and 0.57.

Female per se performance versus progeny means of females

Correlation coefficients for various characters in the different generations (Table 2) showed that most of them were non-significant. Significant correlations were observed only in the clonal generations. In the FCG relationships were significant for tuber number, average tuber weight, general impression and tuber shape. In the SCG there were significant correlations for tuber yield and general impression only. The magnitude of the significant correlations varied between 0.48 and 0.70.

Table 2 Correlation coefficients between female per se performance and progeny means of females based on 18 genotypes

Character	Seedling generation	First clonal generation	Second clonal generation
Tuber yield	0.07	0.30	0.64**
Tuber number	0.26	0.48*	0.29
Average tuber weight	− 0.21	0.70**	0.32
General impression	0.09	0.48*	0.66**
Plant vigour	− 0.27	0.06	0.20
Tuber colour	0.22	− 0.11	− 0.27
Tuber shape	0.47	0.58*	0.23
Uniformity in tuber colour	0.03	0.05	− 0.20
Uniformity in tuber shape	− 0.08	− 0.40	− 0.21
Uniformity in tuber weight	− 0.30	0.03	0.24

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

Female self values versus progeny means of females

Most of the correlation coefficients between female self values and progeny means of the females, within and between generations, were non-significant (Table 3). Significant correlations were observed for general impression (within SG and within SCG) and plant vigour (between FCG and SCG, within FCG and within SCG) only.

Mid-parent values versus progeny means of crosses

Most of the correlation coefficients between mid-parent values and progeny means of the crosses in different generations were non-significant and varied from generation to generation (Table 4). It was only for tuber shape that correlations were significant in all the generations. Associations for tuber yield were negative. However, all of the correlation coefficients were of low magnitude.

Mid-self values versus progeny means of crosses

Most of the correlation coefficients between mid-self values and progeny means of crosses, within as well as between generations, were significant except for tuber colour, tuber shape, uniformity in tuber shape and uniformity in tuber weight (Table 5). Correlation coefficients for various characters were, in general, positive, except for uniformity in tuber shape where most of the correlations were negative. All of the correlation coefficients were of low to moderate magnitude. Correlation coefficients between mid-self values in the SG versus progeny means of crosses in the clonal generations were, in general, of lower magnitude than the corresponding correlation coefficients between the clonal generations for various characters. The highest

Table 3 Correlation coefficients between female self values and progeny means of females based on 14 progenies (*SG* seedling generation · *FCG* first clonal generation · *SCG* second clonal generation)

Character	Female's self value	Progeny mean of female		
		SG	FCG	SCG
Tuber yield	SG	− 0.16	− 0.17	− 0.39
	FCG	–	0.14	0.08
	SCG	–	–	0.12
Tuber number	SG	0.29	0.35	0.39
	FCG	–	0.26	0.43
	SCG	–	–	0.09
Average tuber weight	SG	0.29	0.27	0.17
	FCG	–	0.33	0.28
	SCG	–	–	0.51
General impression	SG	0.73**	− 0.10	0.16
	FCG	–	− 0.08	0.18
	SCG	–	–	0.63*
Plant vigour	SG	− 0.06	− 0.23	0.31
	FCG	–	0.54*	0.65*
	SCG	–	–	0.58*
Tuber colour	SG	0.14	0.16	− 0.17
	FCG	–	0.08	− 0.18
	SCG	–	–	0.01
Tuber shape	SG	0.12	0.17	− 0.12
	FCG	–	0.49	0.09
	SCG	–	–	0.43
Uniformity in tuber colour	SG	− 0.02	− 0.33	0.52
	FCG	–	− 0.17	− 0.06
	SCG	–	–	0.08
Uniformity in tuber shape	SG	− 0.19	− 0.47	0.03
	FCG	–	− 0.14	0.01
	SCG	–	–	0.05
Uniformity in tuber weight	SG	0.33	0.39	− 0.05
	FCG	–	0.26	0.05
	SCG	–	–	− 0.35

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

Table 4 Correlation coefficients between mid-parent values and progeny means of crosses based on 56 progenies

Character	Seedling generation	First clonal generation	Second clonal generation
Tuber yield	− 0.31*	− 0.35**	− 0.13
Tuber number	− 0.29*	0.12	− 0.09
Average tuber weight	0.29*	0.34**	0.18
General impression	− 0.25	− 0.17	0.07
Plant vigour	0.01	0.02	− 0.03
Tuber colour	0.21	0.21	0.12
Tuber shape	0.42**	0.32*	0.35**
Uniformity in tuber colour	− 0.21	− 0.21	− 0.24
Uniformity in tuber shape	− 0.03	− 0.20	− 0.19
Uniformity in tuber weight	− 0.06	− 0.05	0.02

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

Table 5 Correlation coefficients between mid-self values and progeny means of crosses for various characters based on 56 progenies (*SG* seedling generation · *FCG* first clonal generation · *SCG* second clonal generation)

Character	Mid-self value	Progeny mean of cross		
		SG	FCG	SCG
Tuber yield	SG	0.37**	0.36**	0.26*
	FCG	–	0.47**	0.36**
	SCG	–	–	0.33*
Tuber number	SG	0.32**	0.26*	0.29*
	FCG	–	0.31*	0.35**
	SCG	–	–	0.36**
Average tuber weight	SG	0.31*	0.35**	0.13
	FCG	–	0.40**	0.36**
	SCG	–	–	0.43**
General impression	SG	0.31*	− 0.02	− 0.08
	FCG	–	0.60**	0.64**
	SCG	–	–	0.56**
Plant vigour	SG	− 0.14	0.24	0.38*
	FCG	–	0.53*	0.67**
	SCG	–	–	0.64**
Tuber colour	SG	0.15	0.13	0.14
	FCG	–	0.30*	0.14
	SCG	–	–	0.19
Tuber shape	SG	0.30*	0.17	0.08
	FCG	–	0.33*	0.21
	SCG	–	–	0.21
Uniformity in tuber colour	SG	0.27*	0.23	0.35**
	FCG	–	0.41**	0.40**
	SCG	–	–	0.43**
Uniformity in tuber shape	SG	− 0.22	− 0.32*	0.02
	FCG	–	− 0.25	− 0.25
	SCG	–	–	− 0.25
Uniformity in tuber weight	SG	0.17	0.18	0.16
	FCG	–	0.08	0.19
	SCG	–	–	− 0.13

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

correlation coefficient was between mid-self value in the FCG and progeny means of crosses in the SCG for plant vigour ($r = 0.67$) followed by general impression ($r = 0.64$).

Discussion

The population studied for three generations had the same genetic constitution as it was propagated vegetatively. Therefore, the generation-to-generation variations in various correlation coefficients (Tables 1–5) could be due to environment and/or genotype × environment interaction, and the type of the seed used. The SG was raised from true seeds, whereas the clonal generations were from tubers, and seed tubers were of a smaller size in the FCG than in the SCG. Due to significant progeny (both cross and self) × generation and combining ability (both general and specific) × generation interactions, the results were presented generation-wise. Correlations of progeny means of males with male per se performance and with male self values were not computed as only 4 males were used in the present study.

The various correlation coefficients were, in general, positive. Negative correlations for tuber yield, as observed between mid-parent values and progeny means of crosses (Table 4), may have occurred because 2 of the male parents, EX/A680-16 and EX/A723, were of *andigena* origin. These parents had poor yields, but due to the heterotic performance of *Tuberosum* × *Andigena* crosses (Howard 1963; Glendinning 1969; Tarn and Tai 1977; Gopal and Minocha 1997) their progenies had high yields (Gopal 1996). Negative associations between mid-self values and progeny means of crosses for uniformity in tuber shape (Table 5) may have occurred because very little segregation was observed for tuber shape in the self progenies in contrast to the variation present in the cross progenies.

Our findings (Tables 1, 4) that parent per se performance and mid-parent values were, in general, ineffective in predicting the general combining ability of parents and progeny means of crosses, respectively, do not agree with those of Maris (1989) who had obtained moderate to good correlations between these parameters for various characters. Our results, however, do agree with those of Brown and Caligari (1989) and Neele et al. (1991) who also found low correlations between mid-parent values and progeny means of crosses, particularly for crops harvested at full maturity.

Theoretically, where GCA is more important than SCA (specific combining ability), it should be possible to predict the general combining ability and progeny means by parent per se performance and the mid-parent values, respectively (Bradshaw and Mackay 1994). A combining ability study conducted with the present material had shown that for most of the characters, SCAs were more important than GCAs (Gopal 1996). Thus, the poor predictive powers of per se and mid-parent values were expected Maris (1989) found that GCAs were more important than SCAs for most of the agronomic characters, and he also observed good correlations between parent per se performance and GCA, and mid-parent values and progeny means of crosses. Such relationships have also been reported for late blight resistance (Stewart et al. 1992) and cyst nematodes resistance (Phillips et al. 1979).

The above generalisation, however, may not be always true. Maris (1989) reported that for haulms type, though SCA was more important than GCA, correlations between GCA and parental mean values were quite high ($r = 0.77$). In the present material also, GCA was more important than SCA for plant vigour in the FCG (Gopal 1996), yet the GCA of this character could not be predicted by parent per se performance (Table 1). On the other hand, SCA was more important than GCA for average tuber weight in the FCG, yet GCA could be predicted by parent per se performance. The reasons for these deviations could not be ascertained.

A comparison of correlation coefficients presented in Tables 2 and 3 shows that female per se performance and female self values in the second clonal generation were almost equally effective in predicting the progeny means of females for general impression. Female self values were, however, also effective in predicting the progeny means of females for plant vigour in the clonal generations. A similar comparison of the magnitude of correlation coefficients presented in Tables 4 and 5 shows that in contrast to mid-parent values, mid-self values were, in general, better for cross prediction. This may be because self/mid-self values reflect the potential of the parents based on the performance of new genotypic combinations produced after selfing, whereas, parent per se performance/mid-parent values are based on the phenotypic performance of the parents, which may or may not be reflected in their progeny. Further, parents were grown from normal size tubers, whereas self and cross progenies were raised from true seeds (botanical seeds) in the SG and seed tubers of smaller size in the clonal generations.

These results confirm the findings of Brown and Caligari (1989) who reported that mid-self values provide a more accurate estimation of prediction of progeny worth than mid-parent values. However, the correlations observed in the present study were lower than those reported by Brown and Caligari (1989) and Neele et al. (1991). Their studies were, however, based on fewer crosses: 14 in the case of Brown and Caligari (1989) and 20 in the case of Neele et al. (1991), in contrast to 56 crosses in the present study.

Though correlation coefficients between female self values and progeny means of crosses, and between mid-self values and progeny means of crosses, were calculated in all possible combinations, those between female self values/mid-self values in a later generation and progeny means of females/crosses in an early generation were not presented (Tables 3, 5), as these are of little practical significance. Rather, one may be more interested in correlations between self values/mid-self values based on an early generation and progeny mean of the females/crosses in the later generations. Later generations, being based on a higher number of replications, provide more reliable information about the worth of a cross than the early generations, and predictions based on mid-self values in an early generation will help in limiting the evaluation of self progenies to a few generations. So, if correlations between female self values/mid-self values in the SG versus progeny means of females/crosses in the SCG are strong, superior parental combinations can be identified by raising the self progenies of the parents for 1 generation i.e. the SG only. But in the present study these correlation coefficients were of low magnitude. In comparison, the correlation coefficients between females self values/mid-self values in the FCG versus progeny means of females/crosses in the SCG were higher for most of the characters (Tables 3, 5). This may be because the SG was raised from true seeds and the clonal generations from seed tubers. The magnitude of the within-generation correlation coefficients (Tables 3, 5 – diagonal values) showed that the predictive power of female self values/mid-self values within a generation were not much different from those between the generations for most of the characters.

The results show that among the various characters studied, general impression and plant vigour could be predicted more effectively. A comparison of the highest correlation coefficients for general impression between female per se performance and female progeny means ($r = 0.66$), between female self values and and female progeny means ($r = 0.63$) and between mid-self values and females progeny means ($r = 0.64$) shows that these are almost of the same magnitude. These correlations, though of moderate magnitude, were high enough to suggest that female per se performance/female self values/mid-self values can be used in cross prediction with a reasonable working accuracy. The other characters for which correlation coefficients were low may be automatically taken care of when selection would be directed for general impression, which is based on all the characters at harvest including tuber yield and its components.

The relative behaviour of *Tuberosum* × *Tuberosum* and *Tuberosum* × *Andigena* crosses with regard to prediction of progeny means of crosses by mid-parent and mid-self values, was studied by drawing two correlation plots (Figs. 1, 2). General impression, being based on all of the important characters at harvest and also being most responsive, was thought to be the appropriate one for the purpose. The correlation plot (Fig. 1) for mid-parent values versus progeny means of crosses (SCG) shows that the distribution pattern of correlation points for *Tuberosum* × *Tuberosum* crosses was distinctly different from that of the *Tuberosum* × *Andigena* crosses. This was so because the mid-parent values of the *Tuberosum* × *Andigena* crosses had a higher score (i.e. poor general impression) than that of the *Tuberosum* × *Tuberosum* crosses. However, the corresponding plot (Fig. 2) for mid-self values (SCG) versus progeny means of crosses (SCG) showed that the correlation points of the two types of crosses overlapped. This was because of the similar mid-self values for the two types of the crosses. Thus, in contrast to mid-parent values, predictions based on mid-self values have a more general application, being independent of the nature of the population (progenies) involved.

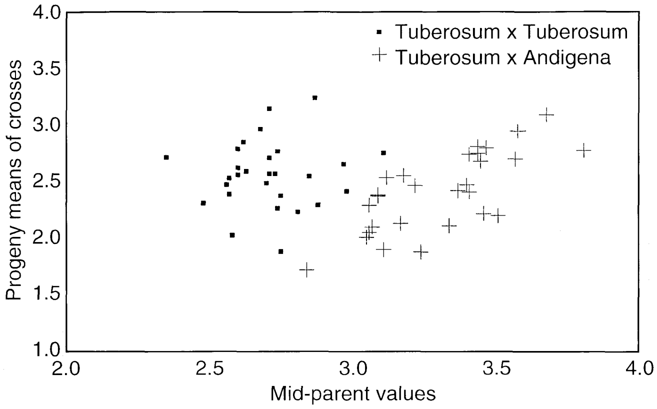

Fig. 1 Correlation plot for mid-parent values versus progeny means of crosses (SCG) for general impression

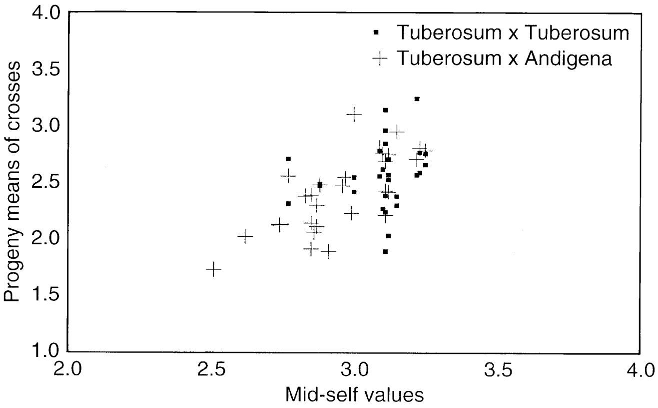

Fig. 2 Correlation plot for mid-self values (SCG) versus progeny means of crosses (SCG) for general impression

Conclusions

Parent per se performance and mid-parent values are ineffective for selecting superior parents and crosses in potato breeding programmes. However, female per se performance/female self values and mid-self values can be used to identify superior females and crosses, respectively, for general impression. For this, evaluation of self progenies should be based on clonal generations (the earliest being FCG).

Acknowledgments I thank Dr. J. L. Minocha for his kind guidance, and Dr. P. C. Gaur and Dr. S. K. Pandey for critical reading of the manuscript.

References

Bradshaw JE, Mackay GR (1994) Breeding strategies for clonally propagated potatoes. In: Bradshaw JE, Mackay GR (eds) Potato genetics. CAB International, Wallingford, UK, pp 467–497

Brown J, Caligari PDS (1989) Cross prediction in a potato breeding programme by evaluation of parental material. Theor Appl Genet 77 : 246–252

Brown J, Caligari PDS, Dale MFB, Swan GEL, Mackay GR (1988) The use of cross prediction methods in practical potato breeding programmes. Theor Appl Genet 76 : 33–38

Comstock RE, Robinson HF (1952) Estimation of average dominance of genes. In: Gowen JW (ed) Heterosis. Iowa State University Press, Des Moines, Iowa, pp 494–516

Glendinning DR (1969) The performance of progenies obtained by crossing groups Andigena and Tuberosum of *Solanum tuberosum*. Eur Potato J 12 : 13–19

Gopal J (1994) Flowering behaviour, male sterility and berry setting in tetraploid *Solanum tuberosum* germplasm. Euphytica 72 : 133–142

Gopal J (1996) In vitro selection, genetic divergence and cross prediction in potato. PhD thesis, Punjab Agricultural University, Ludhiana, Pb, India

Gopal J (1997) Progeny selection for agronomic characters in early generations of a potato breeding programme. Theor Appl Genet 95 : 307–311

Gopal J, Minocha JL (1997) Genetic divergence for cross prediction in potato. Euphytica 97 : 269–275

Griffing B (1956) Concept of general and specific combining ability in relation to a diallel crossing system. Aust J Biol Sci 9 : 463–493

Howard HW (1963) Some potato breeding problems. Report of the Plant Breeding Institute 1961–1962. Cambridge, UK, pp 5–21

Killick RJ (1977) Genetic analysis of several traits in potato by means of a diallel cross. Ann Appl Biol 86 : 279–289

Killick RJ, Malcolmson JK (1973) Inheritance in potatoes of field resistance to late blight (*Phytophthora infestans*) Physiol Plant Pathol 3 : 1221–1231

Maris B (1989) Analysis of an incomplete diallel cross among three ssp. *tuberosum* varieties and seven long day adapted ssp. *andigena* clones of the potato (*Solanum tuberosum* L.). Euphytica 41 : 163–182

Neele AEF, Nab HJ, Louwes KM (1991) Identification of superior parents in a potato breeding programme. Theor Appl Genet 82 : 264–272

Phillips MS, Wilson LA, Forrest JMS (1979) General and specific combining ability of potato parents for resistance to the white cyst nematodes (*Globodera pallida*) J Agric Sci UK 92 : 255–256

Plaisted RL, Peterson LC (1963) Two cycles of phenotypic recurrent selection for high specific gravity. Am Potato J 40 : 396–402

Plaisted RL, Sanford L, Federer WT, Kehr AE, Peterson LC (1962) Specific and general combining ability for yield in potatoes. Am Potato J 39 : 185–197

Stewart HE, Wastie RL, Bradshaw JE, Brown J (1992) Inheritance of resistance to late blight in foliage and tubers of progenies from parents differing in resistance. Potato Res 35 : 313–319

Tarn TR, Tai GCC (1977) Heterosis and variation of yield components in F1 hybrids between group Tuberosum and group Andigena potatoes. Crop Sci 17 : 517–521