



Research Article

Heterosis and combining ability for tuber dry matter and yield in potato (*Solanum tuberosum* L.) over two clonal generations under short-day subtropical conditions

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Abstract :

The potato processing industry requires cultivars with high tuber dry matter and acceptable colour of processed products. Hence an attempt was made to find out the extent of heterosis, type and nature of gene action and the suitable parents for tuber dry matter, yield, tuber number and average tuber weight. Fourteen parents and their 40 progenies from factorial (10 × 4) mating design were evaluated for two clonal generations. Data were recorded and subjected to heterosis and combining ability analyses. In general, progenies were better than mid parent value for number of tubers, lower for average tuber weight and as good as for yield and dry matter. Mean squares due to various sources including interactions with generations were significant for all the characters. Both additive and non-additive gene actions were equally important for various characters. Specific combining ability effects of crosses were related to general combining ability effects of the parents involved. Use of at least one parent with good general combining ability resulted in high-performing heterotic progenies for various characters. Superior parents and hybrids for yield and dry matter were also identified.

Key words:

Potato, clonal generations, dry matter, yield, combining ability, heterosis

Introduction

Potato (*Solanum tuberosum* L.) processing is fast emerging as an important industry in India, partly due to increasing urbanization and changing food habits and partly due to entering of multinationals like Frito-Lay, McCain, etc. following the economic liberalization (Gaur *et al.*, 1999). This requires development of high yielding processing varieties with high dry matter which may be processed to give desirable quantity of quality processed products. Potato is a highly heterozygous crop where intra- and inter-locus interactions are important for yield potential in a genotype (Mendoza and Hynes, 1974). Increase in heterozygosity results in increased heterosis (Cubillos and Plaisted, 1976; Glendinning, 1969; Gopal, 1997; Gopal and Minocha, 1998). For realizing the maximum heterosis, it is important to identify desirable parents while formulating a crossing plan. The breeding value of a potato genotype cannot be predicted from its phenotypic performance; hence the knowledge of its combining

ability is very important (Bradshaw and Mackay, 1994; Kang and Birhman 1993).

Combining ability analysis provides not only an assessment of parents' gametic input, but also helps to interpret the genetic basis of quantitative traits such as dry matter, yield and yield associated traits (Mendoza and Hynes, 1974). The literature on combining ability in potato is not extensive (Bradshaw and Mackay, 1994). For tuber dry matter, one of the most important processing quality traits, only few studies have been reported (Tai, 1976; Killick, 1977; Veilleux and Lauer, 1981; Maris, 1989; Neela *et al.*, 1991; Kang and Birhman, 1993; Gaur *et al.*, 1983, 1985 and 1993). However, almost all the studies on combining ability in potato have been confined to a single clonal generation (Bradshaw and Mackay, 1994), while variations among generations in potato clones and progenies are well documented (Anderson and Howard, 1981; Brown *et al.*, 1987; Gopal, 1997; Gopal *et al.*, 1992). To get an unbiased estimate of heterosis and combining ability effects, the present study was conducted over two clonal generations.

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Further, Potato breeders have a strong tendency to use commercial varieties and advanced breeding lines only as parents (Hawkes, 1990). In such situation the knowledge on combining ability of these varieties and breeding lines through progeny test can help identify valuable parents and crosses before the build up of a larger population based on selected crosses. Hence, in the present study few processing commercial varieties and advanced generation clones selected for processing purpose have been included to study their progeny. The main aim of the present experiment was to study the behaviour of 14 parents representing released processing cultivars and advanced generation clones in a line \times tester (10×4) cross over two clonal generations, viz. first clonal generation (FCG) and second clonal generations (SCG) in potato for four important traits related to processing breeding, viz., tuber dry matter, yield, number of tubers and average tuber weight.

Material and Methods

Plant material

Fourteen potato genotypes belonging to *Solanum tuberosum* subsp. *tuberosum* were selected for the present study and they were: Kufri Chipsona-1, Kufri Chipsona-2, Kufri Jyoti, MP/90-94, MP/91-35, MP/91-51, MP/91-65, MP/91-76, MP/91-86, MP/92-30, MP/92-136, MP/92-139, MP/92-154 and QB/A-120. Kufri Chipsona-1 and Kufri Chipsona-2 are the first two indigenous processing cultivars released in India (Gaur *et al.*, 1999). Kufri Jyoti is a well-adapted cultivar released in 1968 and being cultivated in a wide range of agro-climatic zones ranging from plains to high hills in India. Even though this cultivar was released for table purposes it is also being used as a processing variety by the processing industries. Remaining 11 genotypes represented the advanced generation clones. Most of these genotypes have one or more of the following characters i.e. high dry matter (>20%), acceptable chip colour, good tuber shape and size, resistance to late blight and good yield.

Hybridization programme

These selected genotypes were grown and crossed during summer at the Central Potato Research Stations, Kufri (32° N, 77° E, 2500 m above sea level) in a 10×4 factorial mating design (line \times tester pattern, Kempthorne, 1957). Based on high pollen fertility MP/91-35, MP/90-94, Chipsona-1 and Chipsona-2 were used as male parents and Kufri Jyoti, MP/92-30, MP/91-51, MP/91-65, MP/91-76, MP/91-86, MP/92-136, MP/92-139, MP/92-154 and QB/a-9-120 as female parents. At maturity the hybrid berries were harvested and seeds were extracted.

Evaluation of progenies

The 40 progenies thus generated were evaluated in an experimental field at the Central Potato Research Institute Campus, Modipuram (29° N, 76° E, 222 m above sea level) during autumn (October-February) for three successive generations, i.e. seedling generation (SG), first clonal generation (FCG) and second clonal generation (SCG). In the SG, there were three replications with each progeny represented by 90 randomly selected seedling (30 seedlings per replication). At harvest three well-developed tubers per seedlings from each of 60 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 applied to form material for SCG in which every progeny was represented by 60 genotypes and three replications. Along with hybrid progenies all the 14 parents were also included in all the experiments. All experiments were conducted in a completely randomized block design in 3 m rows of 15 tubers each at recommended inter- and intra-row distance of 20 cm \times 60 cm, respectively. The crop was harvested at maturity (110 days after planting). Standard manurial and cultural practices were followed to raise a healthy crop. Data were recorded on plot basis in all replications for 40 progeny in SG, FCG and SCG for the four characters, viz. tuber yield (g/plant), tuber number/plant, average tuber weight (g) and tuber dry matter (%).

Observation of data

Data were recorded on single plant basis in all replications for all the 40 progenies and 14 parents in three generations for four characters, viz. tuber yield (g), tuber number per plant, average tuber weight (g) and tuber dry matter (%). Per cent tuber dry matter was estimated from freshly harvested tubers i.e. each one tuber per plant was sampled; equal portion of each tuber was mixed, oven dried and % dry matter was estimated by (fresh weight – dry weight) \times 100.

Statistical analyses

Comparison of seedling (true seed crop) families with the tuber crop of the parent is not justified. Hence the heterosis over mid-parent was calculated only over first and second clonal generations using the following formula:

Heterosis (%) = $(F_1 - MP) / MP \times 100$, where, F_1 is the mean value of hybrid progeny. MP is the average value of two parental clones.

Simple correlation coefficients (r) were calculated between parents and progenies using computer software MSTAT-C (Michigan State University, USA). Heritability (narrow sense) was computed as follow:



Heritability (%) = $100 \sigma^2A / (\sigma^2A + \sigma^2D + \sigma^2e)$. where, σ^2A , σ^2D , σ^2e are additive, dominance and error variances, respectively. Combining ability analysis was carried out, and general and specific combining ability effects (gca and sca) were estimated using the computer software SPAR1 (IASRI, New Delhi). A fixed effect model was used for the test of significance at $P \leq 0.05$.

Results and Discussion

Analysis of variance of parents and hybrids

The analyses of variance pooled over two clonal generations showed that the performance of various characters varied over generations (Table 1). FCG and SCG were genetically alike, and hence the variations over generations in the present study could only be due to the difference in environments over years. Gopal and Minocha (1998) also observed similar variations. Mean square due to female parents was significant for tuber yield, tuber number and average tuber weight and mean squares due to male parents was significant for average tuber weight indicating the presence of considerable variability among the parents. Mean square due to hybrids (female x male) was highly significant for all the characters. Differences between females, males and female *versus* males were also significant for most of the characters. Mean squares due to various interactions with generations were significant for most of the characters, reflecting thereby the need of conducting such studies over generations. Mean squares due to parents *versus* hybrids were significant for tuber number and average tuber weight, indicating the presence of heterosis for these characters.

Heterosis (%) over mid-parent

Both positive as well as negative heterosis was observed. The majority of the populations showed significant heterosis for most of the characters and the magnitude varied within as well as between the characters (Table 2). The negative heterosis is not always a disadvantage, e.g. negative heterosis for date of emergence is favourable (Maris, 1989). The heterotic effect was generally high for number of tubers, while it was low for tuber dry matter. Almost all the populations had higher significant positive heterosis for tuber number and negative heterosis for average tuber weight. Negative correlation between these two characters were already reported (Maris, 1989). The average heterosis for tuber yield, number of tubers, average tuber weight and dry matter was -2.89, 27.50, -23.50, and 0.57%, respectively. Negative heterotic effect for tuber yield and other characters are rather common for within subsp. *tuberosum* crosses (Tarn and Tai, 1977).

The maximum heterosis (up to 68.5%) was observed for number of tubers per plant being significantly positive in 31 crosses followed by dry matter in 12 crosses (Table 2). This indicated the presence of higher variability for tuber number and dry matter in the progeny than in the parents. This might be because a progeny was represented by a segregating population from the cross between highly heterozygous parents, whereas a parent was represented by a homogenous clonal population. For tuber yield, only 14 crosses showed positive but non-significant heterosis. Almost all the crosses involving Kufri Jyoti and MP/91-76 as one of the parents had positive heterosis for tuber yield and tuber number but negative heterosis for average tuber weight. The positive heterotic effect for tuber yield can probably be attributed to the positive heterotic effect for number of tubers of the population concerned. For tuber number all the hybrids in a population had positive heterosis; on the other hand for average tuber weight they showed negative heterosis except in the cross QB/A-9-120 x Kufri Chipsoan-1 (Table 2). This was expected as the number of tubers per plant was negatively correlated with average tuber weight (Gopal, 1997).

In general, for all the characters, except for number of tubers per plant, most of the hybrids showed negative heterosis. It indicated that the parents used in this study were of narrow genetic base. This was because most of them were derived from a common pedigree (Table 4) and were selected as parents by giving major emphasis on processing traits like dry matter and chip colour. This may perhaps be the main reason for poor heterosis for tuber yield also. It appears that the effect of the advanced generation clones on the genotypic variation of hybrids is generally not high, which does not mean that no different alleles from advanced generation selections may be introduced. It is rather obvious, however, that several identical alleles occur in both hybrids so that the number of different alleles introduced in one population is limited. Pandey and Gupta (1995) reported low genetic diversity in the advanced germplasm collection developed from the same parentage or those involving one common parent. Hence the available heterozygosity for yield in the present experimental material might be low. Potato being a tetraploid crop, a close correlation between heterozygosity and yield was explained through over dominance (Mendoza and Haynes, 1974). Armoros and Mendoza (1979) worked with population with different levels of heterozygosity and found high heterotic levels with most heterozygous material. Most of the crosses involving the released cultivar Kufri Jyoti as female parent showed positive heterosis for yield, tuber number and tuber dry matter. Heterosis for tuber yield, tuber number and



tuber dry matter was positive in most of the crosses involving Kufri chipsona-1 as the male parent.

The range of heterosis for dry matter was from -12.84 to 9.62% with a mean of 0.57%, and 12 populations had significantly positive heterosis. Maris (1989) reported heterosis for specific gravity from -6 to 13% with a mean of 2.02% from crosses between *tuberosum* and *andigena* clones in second clonal generation. The low mean heterosis in our study may probably be due to already higher dry matter in the parents and the narrow variability. Like yield, dry matter may not be improved beyond certain limit (> 30%). Except the cultivar Kufri Jyoti, all the parents used in the study were having higher (> 22%) dry matter (data not presented). Strong negative correlation between tuber dry matter and tuber yield has also been reported (Maris, 1989). In the present study, the significant heterotic crosses (higher heterosis over the better parent also) for tuber dry matter, viz. MP/92-139 × Kufri Chipsoa-1, MP/91-86 × Kufri Chipsoa-1, MP/92-139 × Kufri Chipsoa-2, MP92-136 × Kufri Chipsoa-1, and MP/91-65 × MP/91-35 had negative heterosis for tuber yield. It indicated that these crosses might mostly give good clones with higher dry matter and low yield. Similarly, the best heterotic cross (even over their better parent) for tuber yield, viz. MP/91-65 × Kufri Chipsoa-2 and MP/91-76 × Kufri Chipsoa-1 had higher significant negative heterosis for dry matter. Selecting good clones with higher yield but low dry matter may mostly be possible. Hence, an approach for developing processing varieties should aim at high dry matter (>22%) with moderate to good yield potential. Further, all the above mentioned crosses showed over dominance for either dry matter or yield as explained by Mendoza and Hynes (1974) and Armoros and Mendoza (1979) since all these crosses showed heterosis over their better parent for either of these two characters or both. In contrast, few authors reported positive correlation between yield and dry matter. In such a situation, the breeder has a choice to select genotypes with desirable dry matter and yield. Moreover, the selection for one character may automatically improve the other trait. By identifying such crosses/parents, one could get better processing varieties through proper clonal selection. In the present study, interestingly three hybrids populations, viz. K. Jyoti × Kufri Chipsona-1, MP/91-65 × Kufri Chipsona-1, and QB/A-9-120 × Kufri Chipsona-1 had positive heterosis for tuber yield and dry matter. Hence simultaneous clonal selection for both dry matter and yield may be possible from these crosses. All these hybrid populations except MP/91-65 × Kufri Chipsona-1 had higher mean and significant sca effect for both the characters. Hence these are

viable crosses for developing varieties for processing.

It is interesting to note that most of the crosses involving Kufri Chipsona-1 as male parent performed well either for dry matter or yield. Kufri Chipsona-1 had significant GCA effects (Table 4) for dry matter and average tuber weight (both are important in processing point of view), besides good SCA effects for all the characters in most of the crosses in which it was as one of the parents (Table 1). Another interesting observation was when Kufri Chipsona-1 was crossed with advanced generation clones selected from same parent (Table 4), viz. MP/91-51, MP/91-65, MP/91-76 and MP/91-86, the heterosis for yield and dry matter varied much i.e. one cross (MP/91-86 × Kufri Chipsona-1) had positive heterosis for dry matter and negative for yield; second one (MP/91-65 × Kufri Chipsona-1) had positive heterosis for both dry matter and yield, whereas the third one (3MP/91-51 × Kufri Chipsona-1) had negative heterosis for both. It might perhaps be due to the higher or lower heterozygosity between alleles at different loci for these two traits. Hence, using advanced generation clones as one of the parents in potato breeding, particularly for development of processing varieties is advisable. However, the other parent may be a well-adopted cultivar or diverse identified good general combining germplasm line. Bradshaw and Mackay (1994) also emphasized that as the new improved cultivars would be produced by pair-crosses of improved parental clones, the long-term success of a potato breeding programme will be determined by the overall efficiency of germplasm enhancement by recurrent selection, i.e. by increasing the frequency of desirable genes in the population as a whole, so that future pair-crosses have a greater likelihood of producing yet higher frequencies of desirable combinations. However, Akeley and Stevenson (1944) found that the specific gravity (dry matter) of progeny from crosses involving two high specific gravity parents was higher than the specific gravity of progeny from crosses in which only one parent was high in specific gravity.

Analysis of variance of combining ability

All the characters were affected over generations. Interactions due to females × generation, male × generations and females × males × generation were also significant (Table 1) for tuber yield and dry matter as observed by Gaur *et al.*, (1993). Male × generation interaction was significant for all the four characters. However, female × generation and female × male × generation interactions were non significant for number of tubers and average tuber weight. Tai (1976) also observed non significant interaction of general combining ability and specific combining



ability with years. Mean square due to female \times male was significant for all the characters. Similarly mean square due to female was significant for all the characters except for dry matter; and due to male for average tuber weight and dry matter. Hence the performance of most of the characters in the progeny would be affected by the choice of females, males and/or their specific combinations.

Estimates of variance component

Both GCA and SCA variances were equally important for all the characters (Table 3). The idea of multi-allelic loci for polygenically inherited characters in the autotetraploid fits well in with the observation that both additive and non-additive gene effects were important for all characters studied, as appeared from significant GCA and SCA mean squares. Tai (1976), Bradshaw and Mackay (1994) and Pandey and Gupta (1997) also suggested that both GCA and SCA contributed to the genetic variation observed in a population. Similar results were obtained by Gaur *et al.* (1993) for these characters except for tuber dry matter, where only non additive type of gene action was important. However, Gaur *et al.* (1985) reported non additive type of gene action for tuber yield and dry matter and additive gene action for average tuber weight and tuber number. As observed in the present study, nearly equal proportion of GCA and SCA variances for dry matter have been reported by several workers (Killick, 1977; Gaur *et al.*, 1983; Plaisted *et al.*, 1962; Sanford, 1979). The low proportion of GCA in the populations studied by other workers could be due to reduced variance among parents resulting from several generations of recurrent selection cycles and/or informal previous selection which narrowed the genetic base of the tested genotypes (Plaisted *et al.*, 1962; Pandey and Gupta, 1997).

Maris (1989) reported more GCA than SCA for these four characters. Thomson *et al.* (1983) observed only non-additive variance for yield, but additive variance estimates were relatively high for tuber number and size. Thomson and Mendoza (1984) found relatively high additive variances for yield as well as for tuber number and size. It is apparent that the answer to the question whether GCA or SCA is the most important in the same quantitatively inherited characters was not always the same. This may depend on kind of material, experimental design and/or environmental conditions and selection protocols. The σ^2 sca \times generation and σ^2 gca (both female and male) \times generation interaction effects were lower than the corresponding σ^2 sca and σ^2 gca, respectively (Table 3). This indicated that both σ^2 sca and σ^2 gca were less influenced by generations (environment). In contrast, Gopal and Minocha (1998) observed more

influence of generations on σ^2 sca than σ^2 gca for most of the characters.

General combining ability effects

MP/92-136 was the best general combiner for most of the characters including tuber yield, number of tubers per plant and dry matter (Table 4). It has EX/A-680-16, a *andigena* clone, as a female parent and QB/B-92-4, a high dry matter advanced breeding clone, as a male parent in its pedigree (Table 4). EX/A-680-16 reported to have a good general combining ability for yield and its related characters (Gopal and Minocha, 1998 and Gaur *et al.*, 1983, 1985). It means that majority of genes for yield and related characters from EX/A-680-16 and genes responsible for tuber dry matter from the male parent QB/B-92-4 might have probably introgressed into the clonal selection MP/92-136. That is why MP/92-136 had best GCA effects not only for dry matter, but also for yield and its related characters. The marked difference in the breeding behaviour of QB/A-120, as compared to Kufri Chipsona-1 for tuber dry matter, could be explained in terms of their origin (Table 3). Kufri Chipsona-1, which produced high dry matter, was selected from a high dry matter parental cross. By contrast QB/A-120 with low gca effects was a selection from a cross (EX/A-680-16 \times Kufri Jyoti) having low dry matter parents. Similarly the contrast between MP/92-136 and MP/92-154 for tuber yield (Table 3) also could be explained in terms of their origin. The former was developed from a cross between *andigena* \times *tuberosum* parents, while, the later was developed between *andigena* \times *andigena* parents. It is known that *andigena* \times *tuberosum* crosses produces high yielding progenies than *andigena* \times *andigena* and *tuberosum* \times *tuberosum* crosses (Gopal 2002). It does appear from the results that the differences in gca effects of QB/A-120 and Kufri Chipsona-1 for dry matter and MP/92-136 and MP/92-154 for tuber yield were due to the dissimilarity of the parents from which they were developed.

MP/91-65 and MP/91-35 were other two good general combiners for yield. Kufri Jyoti, QB/A-9-120 and Kufri Chipsoan-1 were good general combiners for average tuber weight and Kufri Chipsoan-1 for average tuber weight and dry matter. These genotypes should be used as parents in potato breeding programme for processing. Gopal and Minocha (1998) and Gaur *et al.* (1993) also reported some advanced hybrids as good combiners for yield and average tuber weight. Only for yield there was a fairly close relationship between the means of parents and the GCA effects (Table 5), and negative relationship for other characters. It indicated that the selection of parents only based on its *per se* performance might not be effective and parents could



be selected only based on test cross in line x tester or any other design. However, Maris (1989) observed high correlation between GCA and mean performance of the parents for these characters. It might be due to the fact that they used mostly diverse *andigena* and *tuberosum* parents in their study.

Specific combining ability effects

High heritabilities based on population means, as was the case in this study, provide the possibility for an efficient selection of parents for the characters involved, i.e. the selection of parent with the best GCA. They also enable an efficient selection to be made among populations. Generally, heritabilities based on population means are considerably greater than those based on individual seedling. This was observed by Tai and Young (1984). They, however, also found that the advantage of higher heritabilities based on population mean was more than undone by the lower variation among population means so that the response to individual clone selection was still higher than that due to population selection for the character studied.

The crosses with significant positive SCAs for tuber yield, tuber number, average tuber weight and dry matter were 6, 6, 5 and 5, respectively. Crosses with high positive SCAs for tuber yield also had higher SCAs for tuber number and/or average tuber weight. The top six crosses with positive SCA effects for tuber yield were MP/92-154 x Kufri Chipsona-1, MP/91-65 x Kufri Chipsona-2, MP/91-86 x Kufri Chipsona-2, MP/92-30 x MP/90-94, MP/92-139 x MP/91-35 and MP/91-51 x Kufri Chipsona-2. Likewise for tuber dry matter these were MP/91-76 x MP/91-35, Kufri Jyoti x MP/90-94, MP/92-139 x Kufri Chipsona-2, MP/91-65 x MP/91-35, QB/A-9-120 x Kufri Chipsona-1 and MP/92-139 x Kufri Chipsona-1.

None of the crosses had significant SCA effects for both tuber yield and dry matter. However, significant sca effects for yield and positive sca effects for dry matter were present in the cross MP/92-154 x Kufri Chipsona-1, and vice versa in Kufri Jyoti x MP/90-94, MP/92-139 x Kufri Chipsona-2 and QB/A-9-120 x Kufri Chipsona-1. There was an association between GCA of parents and SCA of the crosses. Hence, selection of parents on the basis of GCA and SCA effects will improve the tuber dry matter, yield and its component. The sca effect of yield and average tuber weight appeared to be positively correlated which confirmed the observations of Gaur *et al.* (1983). For all the characters there was a high correlation ($r = >0.60$) between SCA and heterosis (except for tuber number) and very high correlation ($r = > 0.80$) between SCA and crosses *per se* (Table 5). Hence the selection of best hybrid based on mean

performance may be practiced for these traits in the present material which in turn indirectly give the good specific combiners also.

Progeny mean vs. combining ability vs. heterosis

The best cross MP/92-136 x MP/91-35 had both the parents with high general combining ability. The top six crosses with high progeny mean for tuber yield, involved either both or at least one good general combiner. Performance of crosses involving parents with low GCAs was, in general, poor. Thus, for high performance, a cross must have at least one parent with high GCA. For tuber yield, most of the top performing crosses had higher sca effects and positive heterosis. Gopal and Minocha (1998) also reported high heterotic values for high yielding crosses. For tuber dry matter also most of the top performing crosses had at least one good general combiner and also had higher sca effect and significant positive heterosis.

The yield is negatively correlated with tuber dry matter (Keijzer-Van Der Stoel *et al.*, 1991). The present study also confirms this finding as all the top performing hybrids for yield had low dry matter and *vice versa*. However, the cross QB/A-9-120 x Kufri Chipsona-1 had higher yield, tuber dry matter and average tuber weight with higher sca effects. Hence this cross may give better segregants with high yield and dry matter with sizable tuber for processing. For tuber number and average tuber weight also similar pattern like yield and dry matter was observed.

References

- Akeley R.V. and F.J. Stevenson. 1944. The inheritance of dry-matter content in potatoes. *Am. Potato J.*, 21: 83-89.
- Anderson J.A.O. and H.W. Howard. 1981. Effectiveness of selection in early stage of potato breeding. *Potato Research*, 24: 289-299.
- Armoros W.R. and H.A. Mendoza 1979. Relationship between heterozygosity and yield in autotetraploid potatoes. *American Potato J.* 56: 455.
- Bradshaw J. E. and G.R. Mackay. 1994. Breeding strategies for clonally propagated potatoes, pp. 467-497. - In: BRADSHAW J. E., and G.R. MACKAY (eds.) *Potato Genetics*. CAB International, Wallingford, U.K.
- Brown J., P.D. S. Caligari and G.R. Mackay. 1987. The repeatability of progeny means in the early generation of a potato breeding programme. *Ann. Appl. Biol.*, 110: 365-370.
- Cubillos A.G. and R.L. Plaisted. 1976. Heterosis for yield in hybrids between *S. tuberosum* ssp. *tuberosum* and *S. tuberosum* ssp. *andigena*. *Am. Potato J.*, 53: 145-150.
- Gaur P.C., J. Gopal and M.S. Rana. 1983. Combining ability for yield, its components and tuber dry matter in potato. *Indian J. Agric. Sci.*, 53: 876-879.



- Gaur P.C., J. Gopal and M.S. Rana. 1985. Combining ability performance of recently developed potato hybrids. *J. Indian Potato Asso.*, 12: 195-198.
- Gaur P.C., S.K. Pandey and S.V. Singh. 1993. Combining ability study in the development of potato hybrids suitable for processing. *J. Indian Potato Asso.*, 20: 144-149.
- Gaur P.C., S.K. Pandey, S.V. Singh and Dinesh Kumar. 1999. Indian potato varieties for processing. *Tech. Bull. No. 50*, Central Potato Research Institute, Shimla, India 5p.
- Glendinning D.R. 1969. The performance of progenies obtained by crossing group *Andigena* and *Tuberosum* of *Solanum tuberosum*. *Eur. Potato J.* 12: 13-19.
- Gopal J. J.L. Minocha. 1998. Heterosis and combining ability analysis in potato over two clonal generations. *J. Indian Potato Assoc.*, 25: 8-15.
- Gopal J. 1997. Progeny selection for agronomic characters in early generation of a potato breeding programme. *Theor. Appl. Genet.*, 95 : 307-11.
- Gopal J. 2002. Nature of gene action in *tuberosum x tuberosum* and *tuberosum x andigena* families in potato. *Bangladesh J. Agril. Res.*, 27: 543-551.
- Gopal J., P.C. Gaur. and M.S. Rana. 1992. Early generation selection for agronomic characters in a potato breeding programme. *Theor. Appl. Genet.*, 84: 709-713.
- Hawkes J.G. 1990. The potato-evolution, biodiversity and genetic resources. Belhaven Press, London.
- Kang G.S. and R.K. Bihman. 1993. Potato Breeding for Plains, pp.51-84. In: Chadha, K.L. and J.S. Grewal (eds.) *Advances in Horticulture* Vol. 7-Potato. Malhotra Publishing House, New Delhi-110 064, India.
- Keijer-Van Der Stoel M.C., M.W. Pegels-van-Deelen and A.E.F. Neela. 1991. An analysis of breeding value of diploid potato clones comparing 2x-2x and 4x-2x crosses. *Euphytica*.52: 131-136.
- Killick R.J. 1977. Genetic analysis of several traits in potato by means of a diallel cross. *Ann. Appl. Biology*, 86: 279-89.
- 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.
- Mendoza H A and Haynes F L. 1974. Genetic basis of heterosis for yield in the autotetraploid potato. *Theoretical Applied Genetics* 45 : 21-5.
- Neela A.E.F., H.J. Nab and K.M. Louwes. 1991. Identification of superior parents in a potato breeding programme. *Theoretical and Applied Genetics*, 82:264-272.
- Pandey S.K. and P. K. Gupta. 1997. Genetic divergence and combining ability studies on true potato seed (TPS) in potato (*solanum tuberosum* L.). *J. Indian Potato Assoc.*24: 1-16.
- Pandey S.K., P.K. Gupta. 1995. Genetic divergence in some Indian and exotic varieties and advanced potato hybrids. I. *Indian Potato Assoc.*, 22:38-45.
- Plaisted R. L., L.L. Sanford., W.T. Federer, A.E. Kehr, A.E., Peterson L.C. 1962 - Specific and general combining ability for yield in potatoes. *Amer. Potato J.*, 39: 185-197.
- Sanford L.L. 1979. Effect of random mating on yield and specific gravity in *Solanum tuberosum* populations. *Amer. Potato J.*, 56: 597-607.
- Tarn T.R. and G.C.C. Tai. 1977. Heterosis and variation of yield components in F₁ hybrids between group *Tuberosum* and group *Andigena* potatoes. *Crop Sci.* 17: 517-521.
- Tai, G.C.C. 1976. Estimation of general and specific combining abilities in potatoes. *Canadian Journal of Genetics and Cytology*, 18:385-394.
- Tai G. C. C. and D. A. Young. 1984. Early generation selection for important agronomic characteristics in a potato breeding population. *American Journal of Potato Research* 61 (7) 419-434.
- Thomson P G, H.A. Mendoza and R.L. Plaisted. 1983. Estimation of genetic parameters for characters related to potato propagation by true potato seed (TPS) in an *andigena* population. *American Potato Journal* 60 : 393-401.
- Thompson P.G. and H.A. Mendoza. 1984. Genetic variance estimates in a heterogeneous potato population propagated from true seed. (TPS). *Am Potato J* 61 : 697—702
- Veilleux R. E. and F. I. Lauer. 1981. Breeding behaviour of yield components and hallow heart in tetraploid-diploid vs. conventionally derived potato hybrids. *Euphytica*. 30: 547-561.



Table 1. Analysis of variance for combining ability

Source	Df	Tuber yield	Tuber number	Average tuber weight	Dry matter
Generations (G)	1	73571**	272**	3684**	205**
Females (F)	9	11373**	9.8**	120**	2.2
Males (M)	3	4305	4.7	108**	8.2
F x M	27	6887**	10.1**	96.7**	5.6**
F x G	9	4025**	4.5	44.9	5.6**
M x G	3	8596**	10.3**	77.8*	7.8**
(F x M) x G	27	5649*	4.4	48.6	3.8*
Error	156	3456	5.79	48.6	2.2

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

**Table 2. Heterosis (%) of progeny means over their mid parents and specific combining ability effects of crosses over first and second clonal generations in potato**

Cross\$	Heterosis over mid parent (%)				SCA effects			
	Tuber yield	Tuber number	Average tuber weight	Dry matter	Tuber yield	Tuber number	Average tuber weight	Dry matter
F1 x M1	-3.78	-77.00	-23.92**	-12.84**	-46.11	0.15	-4.47*	-0.95
F1 x M2	7.76	-75.63	-15.10**	-2.60**	24.42	0.51	-0.68	1.35*
F1 x M3	4.61	-76.40	-14.20**	-5.24**	-0.14	0.43	-0.91	0.43
F1 x M4	12.74	-79.73	-7.19**	-7.70**	21.83	-1.09	6.06**	-0.83
F2 x M1	4.31	26.21**	-22.45**	-2.50**	20.21	0.01	0.59	0.86
F2 x M2	5.18	13.41	-9.25**	-8.14**	38.49*	-1.36	6.27**	-0.69
F2 x M3	-6.43	19.18*	-24.40**	-3.63**	-27.15	-0.33	-1.25	0.11
F2 x M4	-4.30	36.44**	-27.94**	-2.41*	-31.55	1.68**	-5.62*	-0.28
F3 x M1	-6.31	28.43**	-28.07**	-6.43**	14.07	-3.35	0.98	0.03
F3 x M2	-13.92	44.81**	-37.52**	-6.06**	-15.90	1.52*	-4.33*	-0.10
F3 x M3	-15.88	21.91**	-30.72**	-3.64**	-34.51	-0.60	-1.15	0.22
F3 x M4	-0.83	21.46**	-14.68**	-2.40*	36.35*	-0.57	4.50*	-0.15
F4 x M1	-3.86	18.08*	-20.28**	4.11**	-27.84	-2.32**	3.92	1.10*
F4 x M2	-5.88	55.83**	-32.75**	-0.84	-24.19	1.52*	-3.10	-0.27
F4 x M3	9.86	37.28**	-20.89**	-3.82**	48.17*	0.04	2.55	-1.19*
F4 x M4	4.30	44.05**	-27.01**	5.96**	3.86	0.76	-3.37	0.33
F5 x M1	2.29	29.83**	-21.27**	8.06**	-6.58	-0.16	0.04	1.93**
F5 x M2	3.70	36.98**	-23.33**	-0.36	14.45	0.69	-1.37	-0.22
F5 x M3	-0.93	23.64**	-19.81**	2.40*	-17.23	-0.36	-0.31	0.16
F5 x M4	7.86	24.65**	-9.41**	-3.51**	9.37	-0.17	1.63	-1.88*
F6 x M1	-6.79	20.82**	-27.22**	-0.52	-2.28	-0.20	0.77	0.10
F6 x M2	-5.93	24.25**	-27.48**	2.33*	16.49	0.22	0.33	0.54
F6 x M3	1.01	31.02**	-27.23**	-2.40*	43.98*	1.35	-0.06	-0.82
F6 x M4	-16.30	5.43	-23.57**	4.94**	-58.19**	-1.37	-1.04	0.18
F7 x M1	2.71	17.99*	-14.59**	-1.82	26.96	-0.52	3.85	-0.32
F7 x M2	-6.61	19.86*	-19.77**	1.13	-10.85	-0.26	0.78	0.13
F7 x M3	-6.28	23.59**	-25.27**	2.10*	-16.86	0.57	-2.33	0.10
F7 x M4	-0.23	19.79*	-19.11**	5.21**	0.75	0.20	-2.30	0.10
F8 x M1	-0.61	66.65**	-38.83**	-7.36**	37.27*	1.28	-0.36	-1.78**
F8 x M2	-11.76	32.88**	-32.24**	-0.44	-10.44	-1.78*	3.58	-0.42
F8 x M3	-4.00	30.80**	-28.20**	8.16**	24.19	-1.60*	5.43*	1.31*
F8 x M4	-15.36	68.55**	-48.09**	9.62**	-51.01**	2.10**	-8.65**	0.90
F9 x M1	-8.86	64.75**	-44.86**	-3.45**	0.65	2.40**	-4.98*	0.15
F9 x M2	-17.10	29.25**	-36.24**	-5.16**	-27.25	-0.99	-0.32	-0.48
F9 x M3	-16.34	26.26**	-34.38**	-3.09**	-30.55	-0.92	0.18	-0.26
F9 x M4	4.24	29.82**	-18.74**	-3.41**	57.15**	-0.49	5.12	0.59
F10 x M1	-4.67	10.01	-15.28**	7.29**	-16.34	-0.29	-0.33	-1.12*
F10 x M2	-5.25	11.82	-15.76**	0.80	-5.20	-0.08	-1.17	0.13
F10 x M3	-0.67	21.26**	-16.10**	0.42	10.12	1.41*	-2.17	-0.05
F10 x M4	2.63	-0.65	3.03	7.56**	11.43	-1.05	3.67	1.04*

*,** Significant at P<0.05, 0.01, respectively; \$ Parent's names are given in Table 4.

**Table 3. Estimates of variance components pooled over first and second clonal generations**

Estimate	Tuber yield	Tuber number	Average tuber weight	Dry matter
σ^2_{gca} (females)	254.6	-0.02	1.13	-0.21
σ^2_{gca} (males)	-92.2	-0.19	-0.29	0.09
σ^2_{gca} (Pooled)	412.9	1.90	16.04	0.59
σ^2_{sca}	427.0	1.62	16.26	0.60
σ^2_{gca} (females) x generations	-135.3	0.01	-0.31	0.15
σ^2_{gca} (males) x generations	98.26	0.19	0.97	-0.10
σ^2_{sca} (pooled) x generations	397.76	0.51	-0.02	0.19
$\sigma^2_{gca}/\sigma^2_{gca} + \sigma^2_{sca}$	0.49	0.54	0.50	0.49

Table 4. General combining ability of parents pooled over first and second clonal generations

Code No.	Name	Pedigree	Tuber yield (g/plant)	Tuber number /plant	Average tuber weight (g)	Dry matter (%)
F1	Kufri Jyoti	3069 d (4) x 2814 a (1)	-4.73	-1.22**	3.52**	-0.24
F2	MP/92-30	CP 2370 x CP 2334	-14.63	0.17	-1.48	-0.48**
F3	MP/91-51	CP 2370 x PH/E-1545	19.07*	0.29	0.86	0.11
F4	MP/91-65	CP 2370 x PH/E-1545	17.56	0.22	1.35	-0.06
F5	MP/91-76	CP 2370 x PH/E-1545	4.31	0.00	0.22	0.18
F6	MP/91-86	CP 2370 x PH/E-1545	-12.09	0.50	-0.84	0.27
F7	MP/92-136	EX/A-680-16 x QB/B-92-4	29.18**	0.76*	-0.25	0.22
F8	MP/92-139	QB/B-92-4 x CP 2334	2.54	0.78*	-1.21	0.33*
F9	MP/92-154	JEX/8-2950 x EX/A-680-16	-44.99**	0.23	-4.50**	0.16
F10	QB/a-9-120	EX/A-680-16 x K. Jyoti	3.32	0.73*	2.33	-0.49**
M1	MP/91-35	CP 2334 x QB/B-92-4	12.62*	-0.12	0.99	-0.43**
M2	MP/90-94	CP 2417 x MS/78-79	-4.45	0.36*	-1.03	-0.18
M3	Kufri Chipsona-2	CP 2346 x QB/B-92-4	-5.24	0.04	-1.28	0.25
M4	Kufri Chipsona-1	CP 2416 x MS/78-79	-2.93	-0.29*	1.31*	0.36*
	SE (Females)		9.13	0.31	1.16	0.20
	SE (Males)		4.42	0.14	0.67	0.12

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

Table 5. Heritability, correlation between GCA and mean of parents, correlation between SCA and per se of hybrid population and correlation between SCA and mid parent heterosis of hybrids for various processing characters over two clonal generations in potato

	Heritability	Correlation between		
		GCA and mean of parents	SCA and per se of hybrid population	SCA and mid parent heterosis of hybrids
Tuber yield	0.89	0.45	0.0717**	0.79**
Tuber number	0.90	-0.64**	0.08	0.85**
Average tuber weight	0.89	-0.21	0.53**	0.81**
Dry matter	0.85	-0.16	0.67**	0.88**