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Genetic base of Indian potato selections as revealed by pedigree analysis

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Summary

Pedigree analysis of the 77 advanced Indian potato selections showed that their origin could be traced to only 49 ancestors out of which 29 were exotic, which accounted for 69.52% of the total genomic constitution and maximum contribution (40.65%) was by 10 ancestors from U.K. Breeders' tendency was to involve adapted advanced clones as immediate parents. Coefficient of relationship between pair of selections ranged from 0 to 0.68. The success of the parents used was not related to region-specific choice of parents. The findings are discussed in the context of "genetic uniformity" and the relevance of having separate breeding programmes for the three major areas of potato cultivation in India. Attempt has also been made to give some directions for choosing selections for use as parents and release as cultivars based on their coefficient of relationship so as to broaden the genetic base of the future potato cultivars.

Introduction

The "Irish famine" of mid 1840s caused by the killing of potato variety "Lumper" by the disease late blight (*Phytophthora infestans*), is a widely cited example of the devastating effect of growing large areas under a single variety (Bourke, 1991). Despite the wealth of genetic resources available for potato breeding, only a few species have been included in the genetic improvement programmes; mainly to introgress resistance genes into the tetraploid gene pool of North America and Europe (Ross, 1986; Plaisted & Hoopes, 1989; Ortiz, 2001; Gopal et al., 2003). Breeding gains have been reported both for table and processing attributes in tetraploid cultivated potato (Ortiz, 2001). Long-day adapted material like Neotuberosum has been developed from the short-day adapted *S. tuberosum* ssp. *andigena* (Glendinning, 1979). Several reports, however, showed that in many crops, the genetic improvement for yield generally was accompanied by a loss in genetic diversity among the cultivars released (Committee on Genetic Vulnerability of Major Crops, 1972; Walsh, 1981). Potato cultivars have also been reported to possess a narrow genetic base (Simmonds, 1962; Gopal, 1999).

Potato is not native to India. Spaniards or Portuguese introduced it to this country from Europe in the beginning of 17th century (Pushkarnath, 1976). Thus, initially potato from Europe was grown in India. But this introduction being adapted to long days of Europe was not suitable to Indian conditions and this led to the initiation of potato breeding programmes in India in 1935 (Kishore, 1974), wherein introduced strains and parental lines, referred as "exotic" were used as parents. There were, however, also some introductions or clones whose identity could not be ascertained. These were perhaps some very old unknown European cultivars or their natural variants selected for adaptability to Indian conditions. These were termed as "indigenous" (Pal & Pushkarnath, 1951).

In India, almost 90% of potato area is in plains where this crop is grown under short days of winter. There are three major Indian potato breeding programmes aimed at developing potato cultivars suitable for north-western plains, central plains and north-eastern plains, respectively. Till now 35 potato varieties have been released for various regions of the country (Gopal & Kumar, 2002), out of which 16 are presently in cultivation (CPRI, 2003). Though detailed pedigrees for most of these cultivars are not available (Gopal & Gaur, 1997), repeated use of a few genotypes as immediate parents indicated their narrow genetic base (Gopal et al., 2004).

At present a number of improved selections from various potato breeding programmes are under the multilocation trials conducted by All India Coordinated Potato Improvement Project (AICPIP). Some of these can be the future cultivars. Unlike already released varieties, the pedigrees of the advanced selections are better known. In the present study we analysed the pedigrees of 77 selections introduced into AICPIP since1990 from three major potato breeding programmes, with the following objectives:

1. To know the ancestors of the current selections and the extent of their use,
2. To determine the relative genetic contributions of various ancestors, and
3. To determine the pedigree relationships among the various selections.

The findings are discussed in the context of “genetic uniformity” and the relevance of having separate breeding programmes for the three major areas of potato cultivation in India. Finally, attempt is made to give some directions for choosing selections for use as parents and release as cultivars.

Materials and methods

Seventy seven potato selections (all of hybrid origin) introduced into AICPIP since 1990 from three major potato breeding programmes of India were used for the study (Figure 2). Thirty-nine of these were developed for north-western plains (NW), 25 for central plains (CP) and 13 for north-eastern plains (NE). Pedigrees of these selections were obtained from the records available with the breeders of the respective zones. For most of the selections, pedigrees were available for up to four ancestral generations, the range, however, was between 2–5 generations.

Number of times (frequency) an ancestor appeared in the pedigrees of various selections were counted. Relative genetic contribution (RGC) of different ancestors to a given selection was computed by partitioning the genetic constitution of a selection into theoretical percentage attributable to different ancestors assuming that every time a cross is made each parent transmits 50% of its genes to the progeny with equal probability. RGC estimates, therefore, are not real nuclear compositions but merely statistical representations. The cumulative genetic contribution of an ancestor was computed by summing its RGC to all selections, separately for each zone. Percent frequency of appearance in the pedigrees and cumulative genetic contribution of an ancestor combined over three zones were also estimated.

The pedigree information was also used to calculate the “Coefficient of relationship” (r_{xy}) for all pair-wise combinations of the 77 selections, using the computer software (developed by the second author using Fortran) which assumes that the original ancestors of a selection are unrelated ($r_{xy} = 0$) except where these proved to be related based on the pedigrees of other selections included in the present study. Coefficient of relationship (Falconer & Mackay, 1996) represents the genetic similarity and are calculated as follows

$$r_{xy} = \frac{2f_{xy}}{\sqrt{(1+F_x)(1+F_y)}}$$

where f_{xy} is a coefficient of coancestry, and F_x and F_y are inbreeding coefficients of X and Y, respectively. By definition, with itself a selection will have $r_{xy} = 1.0$, full sib selections (assuming that two parents have contrasting genotypes) have $r_{xy} = 0.5$, and selections without known common parentage have $r_{xy} = 0$. The pair-wise similarity matrix so obtained was used for grouping the selections using computer software NTSYS-pc2.20 (Excter, Setauket, NY, U.S.A.), wherein modules ‘Simqual’, ‘Sahn’ and ‘Tree’ were used for converting the qualitative data into similarity percent, clustering and graphical representation, respectively. This resulted in the placement of all the selections into a hierarchical dendrogram in which successive groups and selections within a group were joined based on their coefficients of relationship.

Results

Examination of the pedigrees of the 77 selections showed that their origin could be traced to only 49 ancestors, 29 of which were of exotic source and 20 indigenous (Table 1). Among the exotic ancestors, 10 were from U.K. and remaining 19 came from other 8 countries. Exotic ancestors accounted for 69.53% of

Table 1. Origin of various ancestors, their frequency of appearance in pedigrees and cumulative genetic contribution to 77 Indian potato selections

		Zone-wise[a]						Over zones	
		Frequency of presence in pedigrees			Cummulative genetic contribution			Percent frequency of presence in pedigrees	Percent cumulative genetic contribution
Origin	Germplasm	NW	CP	NE	NW	CP	NE		
Australia	Adina	0	5	0	0.00	0.31	0.00	1.14	0.44
Czechoslovakia	Krirrinee	5	0	0	2.50	0.00	0.00	1.14	3.56
	Serkov	0	5	0	0.00	0.31	0.00	1.14	0.44
Germany	Spatz	1	0	0	0.50	0.00	0.00	0.23	0.71
	Spika	4	8	3	1.00	1.38	0.63	3.41	4.27
Japan	Ekishirazu	2	9	1	0.03	0.31	0.06	2.73	0.58
Mexico	AGB 69-1	1	0	0	0.50	0.00	0.00	0.23	0.71
Netherlands	Dekama	0	4	0	0.00	1.00	0.00	0.91	1.42
	Dore	0	1	0	0.00	0.25	0.00	0.23	0.35
	Gineke	1	3	4	0.13	0.16	0.81	1.82	1.56
Peru	CIP379420.1	0	1	0	0.00	0.50	0.00	0.23	0.71
	CIP383300.21	0	1	0	0.00	0.50	0.00	0.23	0.71
	CIP702101	0	1	0	0.00	0.50	0.00	0.23	0.71
	CIP800955	0	0	1	0.00	0.00	0.50	0.23	0.71
U.K.	134-D	4	8	1	0.31	0.50	0.13	2.95	1.33
	692-D	0	1	0	0.00	0.13	0.00	0.23	0.18
	2814 (a) 1	48	33	7	7.63	2.73	0.81	20.00	15.92
	3069 (d) 4	48	33	7	7.63	2.73	0.81	20.00	15.92
	3070 (d) 4	0	1	0	0.00	0.13	0.00	0.23	0.18
	CP1207	0	6	0	0.00	1.50	0.00	1.36	2.14
	Craigs Defiance	4	1	0	1.00	0.25	0.00	1.14	1.78
	Croft	3	0	0	1.50	0.00	0.00	0.68	2.14
	Dr. Mc Intosh	0	1	0	0.00	0.50	0.00	0.23	0.71
	Sd 4485	0	0	1	0.00	0.00	0.25	0.23	0.35
U.S.A.	AG14 (×37)	10	2	2	2.75	0.38	0.25	3.18	4.81
	B3309-8	3	0	0	1.50	0.00	0.00	0.68	2.14
	Katahdin	2	8	1	0.03	0.25	0.63	2.50	1.29
	Kennebec	10	14	5	1.00	0.70	0.31	6.59	2.87
	PI161695.1	2	2	1	0.25	0.25	0.13	1.14	0.89
Total (Exotic)		148	148	34	28.26	15.27	20.59	75.01	69.53
India	A- 2235	0	1	0	0.00	0.50	0.00	0.23	0.71
	A-2708	9	0	0	2.25	0.00	0.00	2.04	3.21
	AB-286	0	2	0	0.00	1.00	0.00	0.46	1.42
	Darjeeling Red Round	2	6	7	0.13	0.42	0.59	3.41	1.62
	EB/C 879	0	0	1	0.00	0.00	0.25	0.23	0.35
	EM/H 1601	4	5	0	0.63	1.00	0.00	2.04	2.31
	EX/A 680-16	1	1	3	0.25	0.50	0.75	1.14	2.14
	JEX/A 9	0	0	2	0.00	0.00	1.00	0.46	1.42
	JEX/A 1984	0	2	0	0.00	0.50	0.00	0.46	0.71
	JEX/B 687	4	1	0	1.00	0.25	0.00	1.14	1.78

(*Continued on next page*)

Table 1. (*Continued*)

		Zone-wise[a]						Over zones	
		Frequency of presence in pedigrees			Cummulative genetic contribution			Percent frequency of presence in pedigrees	Percent cumulative genetic contribution
Origin	Germplasm	NW	CP	NE	NW	CP	NE		
	JLR/A 148	7	0	0	0.88	0.00	0.00	1.59	1.25
	K-10	0	2	2	0.00	0.50	0.50	0.91	1.42
	K-58	0	1	2	0.00	0.25	0.50	0.68	1.07
	Kufri Kuber	0	0	3	0.00	0.00	1.00	0.68	1.42
	ON 1645	0	1	0	0.88	0.50	0.00	0.23	0.71
	ON 2090	10	14	5	1.00	0.70	0.00	6.59	2.87
	PH 53-104	0	3	0	0.00	0.75	0.00	0.68	1.07
	PH/C 303	0	3	0	0.00	0.75	0.00	0.68	1.07
	PS 4904	0	0	5	0.00	0.00	2.25	1.14	3.21
	SLB/U 125	0	1	0	0.00	0.50	0.00	0.23	0.71
Total (Indigenous)		37	43	30	7.02	8.12	6.84	25.02	30.47

[a] NW: North-western plains; CP: Central plains; NE: North-eastern plains.

the total genetic contribution and appeared as many as 75% of the total times various ancestors were used in the development of 77 selections. Indigenous ancestors thus accounted for only 30.47% of the total genetic contribution.

The most frequent ancestors in the pedigrees of various selections were 2814 (a) 1 and 3069 (d) 4, each appearing as many as 88 times i.e. 20% of the total times various ancestors were used (Table 1). As expected, these two ancestors also had the maximum cumulative genetic contribution each accounting for 15.92% of the total genomic constitution of 77 selections. These two ancestors from U.K. along with another 8 from this country contributed 40.65% of the total genomic composition (Figure 1). U.S.A. was the next most important country for Indian potato breeding programmes contributing 12% of the total genomic constitution.

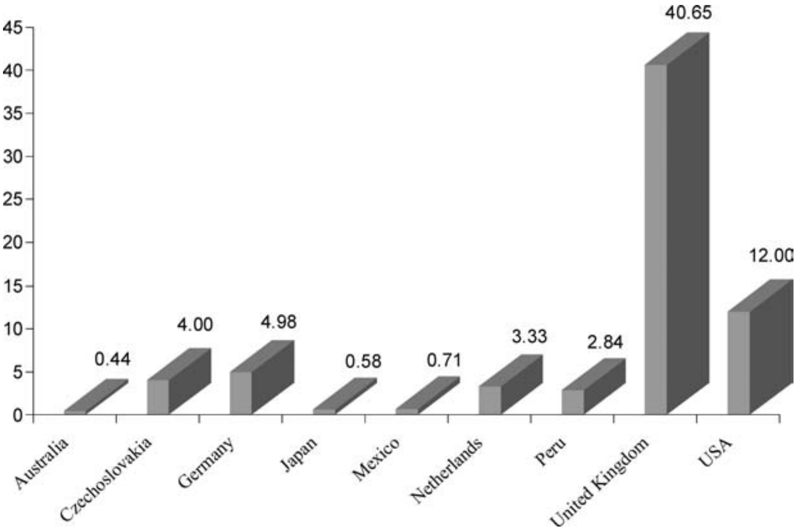

Figure 1. Percent cumulative relative genetic contribution of germplasm from various countries to the total genome of 77 Indian potato selections.

Zone-wise appearance of various ancestors (Table 1) again showed that ancestors 2814 (a) 1 and 3069 (d) 4 were the most frequent in all the three zones. Their maximum frequency of appearance (25.95% times) was in the selections from north-western zones followed by central plains (17.28% times) and the least (10.94% times) in north-eastern plains (Table 1). Thirteen ancestors were common to the pedigrees of selections from all the three zones and18 to the pedigrees of selections from any two zones. As many as 31 ancestors were present in the pedigrees of selections from only one of the three zones, but their frequency of use was much lower (range 0.5 to 7.8%) as compared to (range 0.3 to 25.9% times) those which were used in all the three zones. Fifteen ancestors appeared only once (Table 1).

Coefficient of relationship (r_{xy}) ranged from 0.00 to 0.68 (Figure 2), with many accessions closely related to one another ($r_{xy} \geq 0.50$). Grouping based on coefficient of relationship showed that selections from different regions were interspersed on the dendrogram (Figure 2), though intra-region grouping was also apparent. Coefficient of relationship (r_{xy}) among some inter-region selections was higher as compared to that of selections from the same region. For example, nine selections from North-western plains namely JX123, JX161, JX214, JX216, JX 234, JX249, JX 254, JX371 and JX576 which were full sibs ($r_{xy} = 0.50$) and hence grouped to-gather on the dendrogram, were closer ($r_{xy} = 0.32$) to 83P142, a selection from north-eastern plains than ($r_{xy} = 0.06$) from JV62 and JV67 selections from north-western plains. On the other hand a selection 83P12 from north-eastern plains was closer to JV62 and JV67 (selections from north-western plains) than from 92P27, a selection from its own region. Similarly a selection MS84-140 from central plains was grouped together with two selections (83P108 and 83P121) from eastern plains and the three were full-sibs ($r_{xy} = 0.50$). Many more such cases with inter-region distances lower than that of intra-region distances, as evident from Figure 2, showed that selections originating from different regions had some common ancestors.

Discussion

Estimates of the genetic divergence between pairs of parents elucidate the genetic base of the cultivars/lines under study and help in formulating the breeding programmes, besides giving an insight into the breeding process followed in the past. Genetic divergence can be calculated from pedigree, phenotypic, biochemical or molecular information. However, the best source of information for measuring genetic divergence is uncertain; usually different estimates are not related (Lefort-Bunson et al., 1986; Damerval et al., 1987; Loiselle et al., 1991). Unlike morphological, biochemical and molecular information, pedigree data do not require the observations to be recorded on the plant material and is not influenced by environment or the technique used. Further, isozyme or DNA markers may represent only a small portion of the genotype (Cox et al., 1986) and thus do not adequately reflect the genetic diversity among genotypes. Pedigree analysis thus is a useful method for determining the genetic relationships and inbreeding level of tetraploid potato cultivars (Mendoza & Haynes, 1974; Glendinning, 1997).

Results of the present study showed that more than 2/3 of the genetic contribution was from exotic ancestors indicating that the exotic germplasm continue to be of much importance to Indian potato breeding programmes even after more than 400 years of introduction of potato into India. This scenario is expected to continue, as there is little indigenous variability in potato (Gopal & Gaur, 1997). The appearance of only 49 ancestors in the pedigree of 77 selections was due to the fact that breeders limited their choice of immediate parents to advanced Indian hybrids or cultivars due to their improved agronomic features, which actually had been evolved from a few and mostly exotic ancestors. This thus led to the observed high contribution of exotic germplasm to the Indian selections. Ancestors 2814 (a) 1 and 3069 (d) 4, the two immediate parents of the most popular and widely adapted Indian cultivar Kufri Jyoti had the maximum genetic contribution because Kufri Jyoti had been the most frequent choice of the breeders and was present in the pedigrees of 68 selections out of the 77 included in this study. Ancestors 2814 (a) 1 and 3069 (d) 4 being from U.K., thus also resulted in the maximum genetic contribution (more than 40%) of this country to the Indian potato selections. Predominance of the use of germplasm from U.K. and U.S.A. was mainly because in the early years of Indian potato breeding programmes maximum introductions were from these two countries, respectively (Kishore, 1974). All this thus reflects the narrow genetic base of the 77 selections, which was also evident from the high coefficient of relationship (($r_p \geq 0.50$) among many selections. Although it was assumed that the original sources of germplasm were unrelated, many have virtually no documentation and could actually be related. For example, many indigenous ancestors namely A 2235, A

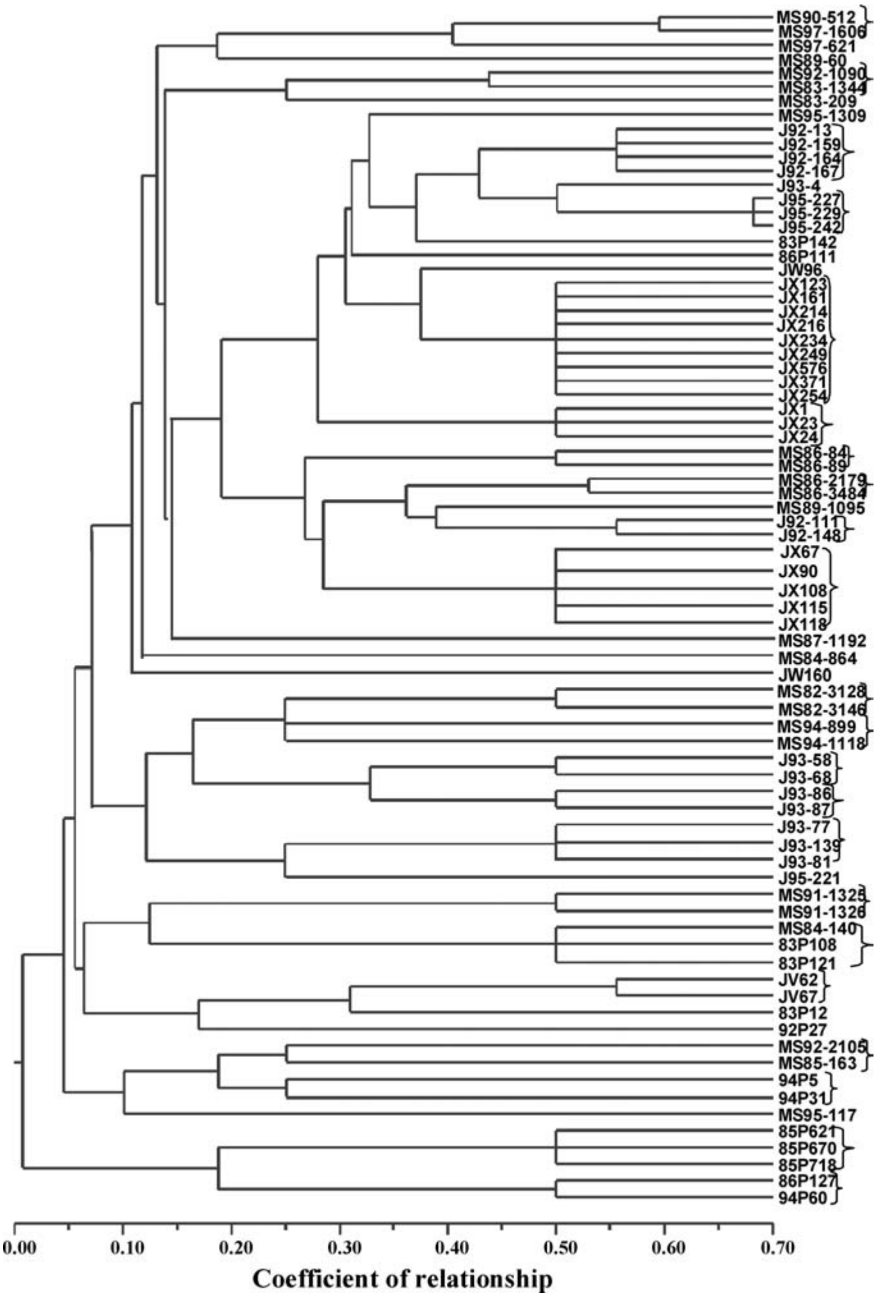

Figure 2. Dendrogram based on coefficient of relationship among 77 Indian potato selections belonging to different breeding zones. Central plains: selections with prefix 'MS', north-western plains: selections with prefix 'J', and north-eastern plains: selections beginning with a numeral.

2708, AB-286, EB/C 879, EM/H 1601, JLR/A148, K-10, K-58, ON 1645 and ON2090 are expected to have some parents common in their pedigrees because these are selections from early years of potato breeding when a few genotypes like Phulwa, Kufri Safed and Kufri Red, which were themselves closely related, were used as parents (Kishore, 1974). Ancestors having the same prefix like A2235 and A2708; K-10 and K-58; and ON1645 and ON2090 may even be full-sibs. If it is so, the genetic base of the current selections may be even narrower than that of revealed by the present analysis. It is, perhaps due to repeated use of few ancestors that the selection response has declined in the potato breeding programmes of India. At present though 16 potato varieties are under seed production programme in India, more than 37% of the breeder seed produced is only of the three potato varieties viz., Kufri Chandramukhi, Kufri Jyoti and Kufri Sindhuri (CPRI, 2003), which were released way back in 1968. Continuing popularity of these varieties indicates that varieties released thereafter were not substantially superior to old ones; rather some new varieties were reported to have poor keeping and cooking quality (Gopal & Kang, 1988).

A similar scenario had also been reported for North American potato varieties (Mendoza & Haynes, 1974). As is India, in North America too potato was introduced from Europe, by Scotch-Irish immigrants in 1719, and the imported germplasm had played a prominent role in potato variety development (Hougas, 1956). Plaisted & Hoopes (1989) reported the repeated appearance of a few ancestors in the pedigrees of American varieties and a clone "Rough Purple Chili" was found in the pedigrees of almost all modern American varieties leading to their narrow genetic base. European potato varieties too have been reported to have a narrow genetic base (Hawkes, 1979; Ross, 1986).

Region-wise frequency of use of different ancestors (Table 1) showed that 31 ancestors were used only in any one of the three zones indicating that breeders from different regions did prefer different parents. But their too low frequency of appearance showed that these were not of much success as compared to those which were common to all regions. Grouping of selections based on coefficient of relationship (Figure 2) too showed that region specific choice of parents (ancestors) was shadowed by the too frequent use of non-region specific (common) parents. As a result distances among selections from different regions were not necessarily lower than those of among intra-region selections. Selection MS84-140 from central plains and selections 83-P-108 and 83-P-121 from north-eastern plains were full sibs (Figure 2). Many selections from different regions were half-sibs. These results thus suggest that present approach of having separate hybridization programmes for the three regions perhaps is not essential. Rather a common hybridization programme for all regions followed by region-specific evaluation and selection of superior clones from the progenies so evaluated would be more appropriate. This will help in using more number of parents and evaluating more number of crosses at all the locations. This approach combined with progeny selection (Gopal, 1997) besides improving the efficiency of breeding would also help in broadening the genetic base of the potato selections.

There are practical examples of cases where a single cross produces several new varieties while in most cases most crosses do not produce even a single variety. In the present study too, a single cross (JE 812 × Kufri Jyoti) resulted in 9 selections namely JX 123, JX161, JX 214, JX 216, JX 234, JX 249, JX 254, JX 371 and JX 576 (Figure 2). This further highlights the importance of going in for progeny test to identify promising crosses so that bigger populations of these could be raised for practicing individual clone selection. The present results showed that pedigree information of the already selected advanced hybrids/clones could also be used to identify promising crosses. Yet, performance of the selected clones would be the most critical criteria for their release.

Although genetic uniformity in crops does not necessarily lead to immediate epidemics, it is desirable to have more diverse genetic background in currently grown cultivars (Chang, 1984). Resistance genes derived from different sources introgressed into recommended cultivars would provide better protection against the unexpected outbreaks of pests. Coefficient of relationship (Figure 2) can be used for selecting diverse genotypes for use as parents in future breeding programmes. For example, selections MS90-512 and MS97-1606 had maximum possible divergence ($r_{xy} = 0$) from selections 85P621, 85P67, 85P718, 86P127 and 94P60. Inter-mating such distantly related selections (e.g. MS90-512 × 94P60) may lead to highly heterozygous populations for practicing selection of superior clones. Heterozygosity in potato is known to be essential to realize heterosis for economic characters like tuber yield (Cubillos & Plaisted, 1976; Sanford & Hanneman, 1982; Gopal et al., 2000). Selection of genetically diverse parents based on pedigree information in order to obtain transgressive segregates has been found to be effective in oats (Rodgers et al., 1983; Cowen & Frey, 1987; Souza & Sorells, 1991), soyabean (Cox et al., 1985), cotton (Marani & Avieli, 1973), alfalfa (Sriwatanaponge & Wilsie, 1968), rapeseed (Lefort-Bunson et al., 1986), maize (Paterniani & Lonnquist, 1963) and wheat (Fonesca & Patternson, 1968). In potato, Gopal & Minocha (1997) reported that genetic divergence of parents based on morphological characters could be used to predict the progeny performance. Loiselle et al. (1991) reported that inbreeding coefficient was related to performance for tuber yield, total tuber number and specific combining ability effects in some potato progenies. The potential of pedigree analysis *vis-à-vis* biochemical or molecular diversity in selection of parents to predict progeny performance needs to be further investigated in potato. Molecular markers can be very useful in identification of diversity for important genes governing resistance to diseases and pests (Barone, 2004).

Although potato breeders desire to increase genetic diversity among new cultivars, at the same time they want to maintain the complex of desired agronomic and quality traits present in existing popular cultivars. Developing such a combination can be difficult as the introgression of new genetic material is expected to disturb genetic complexes responsible for desired traits. The use of crosses among divergent selections, as exemplified above could be a means to achieve both ends to a certain limit, as all selections of the present study had been advanced to multilocation trails after these were found to possess desired agronomic characters. Hybridization among diverse current elite selections would at least assure no further loss in the existing genetic diversity.

Similarly, if more than one of the current selections were to be released as varieties, it would be advisable to recommend those promising selections, which are more divergent from each other. For example if two selections are to be released for central plains from those used in this study, these should not be MS90-512 and MS97-1606 as these are closely related ($r_{xy} = 0.58$) to each other. Rather choice should be any one of these, and one from MS92-2105 and MS85-163 (provided these are otherwise acceptable), as coefficient of relationship between them is only 0.06. Cultivars relationships based on pedigree analysis have been shown to be useful in identifying diverse genotypes in other crops also including oat (Cowen & Frey, 1987), soybean (Delannay et al., 1983), peanut (Knauft & Gorbet, 1989), wheat (Murphy et al., 1986) and rice (Lin, 1991; Shivkumar et al., 1998).

In conclusion, current selections in Indian potato breeding programmes have a narrow genetic base owning to the tendency to concentrate on mating between adapted advanced clones that carry specific gene complexes necessary in successful varieties. These adaptive gene complexes have originated mainly from a few exotic clones/cultivars predominantly from U.K.. The genetic diversity among the current selections as revealed by their pedigree analysis can be used to mate diverse clones for broadening the genetic base of the future selections as well to conserve the adaptive gene complexes. The potential to broaden the genetic base of Indian potato cultivars and also to realize heterosis for tuber yield and its components (Gopal et al., 2000) is immense considering that only 49 ancestors appeared in the pedigrees of 77 selections, whereas Indian germplasm collection has more than 1000 elite parental lines/cultivars and more than 800 andigena clones from 30 countries (Gopal and Gaur, 1997).

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References

Barone, A., 2004. Molecular marker-assisted selection for potato breeding. Am J Potato Res 81: 111–117.

Bourke, A., 1991. Potato blight in Europe in 1845. The scientific controversy. In: J.A Lucas, R.C. Shattock, D. Shaw & L.R. Cooke (Eds.). Phytophthora. pp. 12–24. Cambridge University Press, Cambridge, U.K.

Chang, T.T., 1984. Conservation of rice genetic resources: Luxury or necessity? Science 224: 251–256.

Committee on Genetic Vulnerability of Major Crops. 1972. Genetic vulnerability of major crops. Natl Acad Sci, Washington, D.C.

Cowen, N.M. & K.J. Frey, 1987. Relationships between genealogical distance and breeding behaviour in oats (*Avena sativa* L.). Euphytica 36: 413–424.

Cox, T.S., Y.T. Kiang, M.B. Gorman & D.M. Rodgers, 1985. Relationships between coefficient of relationship and genetic similarity indices in the soybean. Crop Sci 25: 529–532.

Cox, T.S., J.P. Murphy & D.M. Rodgers, 1986. Changes in genetic diversity in the red winter wheat regions of the United States. Proc Natl Acad Sci U.S.A. 83: 5583–5586.

CPRI, 2003. Annual Report, Central Potato Research Institute, Shimla. pp. 97.

Cubillos, A.G. & R.L. Plaisted, 1976. Heterosis for yield in hybrids between *S. tuberosum* ssp. *tuberosum* and *tuberosum* ssp. *andigena*. Am Potato J 53: 143–150.

Damerval, C., Y. Hebert & D. de Vienne, 1987. Is the polymorphism of protein amounts related to phenotypic variability? A comparison of two-dimensional electrophoresis data with morphological traits in maize. Theor Appl Genet 74: 194–202.

Delannay, X., D.M. Rodgers & R.G. Palmer, 1983. Relative genetic contributions among ancestral lines to North American soyabean cultivars. Crop Sci 23: 944–949.

Falconer, D.S. & T.F.C. Mackay, 1996. *Introduction to Quantitative Genetics* 4th edn., pp. 153, Longman, Essex, U.K.

Fonesca, S. & F.L. Patterson, 1968. Hybrid vigor in a seven parent diallel cross in common winter wheat. Crop Sci 8: 85–88.

Glendinning, D.R., 1979. Enriching the potato gene pool using primitive cultivars. In: van A.M. Harten and A.C. Zeven (Eds.). Broadening the Genetic Base of Crops, pp. 39–45. Pudoc, Wageningen, The Netherlands.

Glendinning, D.R., 1997. Estimating of inbreeding in potato pedigrees. Potato Res. 40: 277–284.

Gopal, J. & G.S. Kang, 1988. Three new potato varieties for the plains. Ind Farm 38: 3–4.

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

Gopal, J. & P.C. Gaur, 1997. Potato genetic resources in India. Ind J Plant Genet Resour 10: 205–215.

Gopal, J. & J.L. Minocha, 1997. Genetic divergence for cross prediction in potato. Euphytica 97: 269–275.

Gopal, J., 1999. In vitro versus in vivo genetic divergence in potato. Theor Appl Genet 98: 299–304.

Gopal, J., G.S. Chahal & J.L. Minocha, 2000. Progeny mean, heterosis and heterobeltiosis in *Solanum tuberosum* × *tuberosum* and *S. tuberosum* × *andigena* families under a sort day sub-tropic environment. Potato Res 43: 61–70.

Gopal, J. & V. Kumar, 2002. Potato gene bank: Its role in developing improved cultivars. Ind Hort 47: 34–36.

Gopal, J., V. Kumar & S.K. Sandhu, 2003. Biosystematics and genetic resources of potato. In: S.M. Paul Khurana, J.S. Minhas & S.K. Pandey (Eds.) The Potato: Production and Utilization in Sub-Tropics, pp. 31–47. Mehta Publishers, New Delhi, India.

Gopal, J., S.K. Pandey & S.M. Paul Khurana, 2004. Utilization of germplasm in the development of Indian potato varieties. Ind J Plant Genet Resour (communicated).

Hawkes, J.G., 1979. Genetic poverty of the potato in Europe. In: Proc Conf Broadening Genetic Base of Crops (1978). pp. 19–27. Wageningen, The Netherlands.

Hougas, R.W., 1956. Foreign potatoes, their introduction and importance. Am Potato J 33: 190–198.

Kishore, H., 1974. The present status and approaches to the potato breeding in India. J Ind Potato Assoc 1: 11–18.

Knauft, D.A. & D.W. Gorbet, 1989. Genetic diversity among peanut cultivars. Crop Sci 29: 1417–1422.

Lefort-Bunson, M., Y. Dattée & B. Guillot-Lemoine, 1986. Heterosis and genetic distance in rapeseed (*Brassica napus* L.): Use of kinship coefficient. Genome 29: 11–18.

Lin, M.S., 1991. Genetic base of japonica rice varieties released in Taiwan. Euphytica 56: 43–46.

Loiselle, F., G.C.C. Tai & B.R. Christie, 1991. Pedigree, agronomic and molecular divergence of parents in relation to progeny performance in potato. Potato Res 34: 305–316.

Marani, A. & E. Avieli, 1973. Heterosis during the early phases of growth in intraspecific and interspecific crosses of cotton. Crop Sci 13: 15–18.

Mendoza, H.A. & F.L. Haynes, 1974. Genetic relationship among potato cultivars grown in the United States. Hort Sci 9: 328–330.

Murphy, J.P., T.S. Cox & D.M. Rodgers, 1986. Cluster analysis of red winter wheat cultivars based upon coefficients of parentage. Crop Sci 26: 672–676.

Ortiz, R., 2001. The state of the use of potato genetic diversity. In: H.D. Cooper, C. Spillane & T. Hodgkin (Eds.), Broadening the Genetic Base of Crop Production, pp. 181–200. FAO, IPGRI, CABI Publishing, CAB International, Wallingford, U.K.

Pal, B.P. & Pushkarnath,1951. Indian potato varieties. ICAR, Misc. Bull. 62: 63.

Paterniani, R. & J.H. Lonnquist, 1963. Heterosis in interracial crosses of corn (*Zea mays* L.). Crop Sci 2: 504–507.

Plaisted, R.L. & R.W. Hoopes, 1989. The past record and future prospects for the use of exotic potato germplasm. Am Potato J 66: 603–627.

Pushkarnath, 1976. Potato in sub-tropics. Orient Longman, New Delhi.

Rodgers, D.M., J.P. Murphy & K.J. Frey, 1983. Impact of plant breeding on the grain yield and genetic diversity of spring oats. Crop Sci 23: 737–740.

Ross, H., 1986. Potato breeding – Problems and perspectives. Adv in Plant Breed 13: 132.

Sanford, J.C. & R.E. Hanneman Jr., 1982. A possible heterotic threshold in the potato and its implications for breeding. Theor Appl Genet 70: 306–308.

Shivkumar, L., V. Subba Rao, T. Ram, N.D. Majumder, G. Padmavathi, U. Prasada Rao & K. Krishnaiah. 1998. Genetic base and coefficient of relationship of rice (*Oryza sativa*) varieties released in Kerala. Ind J Agri Sci 68: 1–6.

Simmonds, N.W., 1962. Variability in crop plants, its use and conservation. Biol Rev 37: 422–465.

Souza, E. & M.E. Sorells. 1991. Prediction of progeny variation in oat from parental relationships. Theor Appl Genet 82: 233–241.

Sriwantanapongse, S. & C.P. Wilsie, 1968. Intra- and intervariety crosses of *Medicago sativa* L. and *Medicago talcata* L. Crop Sci 8: 465–466.

Walsh, J., 1981. Genetic vulnerability down on the farm. Science 214: 161–164.