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RAPD and pedigree-based genetic diversity estimates in cultivated diploid potato hybrids

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Abstract In this study, RAPD and pedigree data were used to investigate the genetic relationships in a group of 45 diploid hybrid potato clones used in the breeding and genetics program of the Agriculture and Agri-Food Canada Potato Research Centre in Fredericton, New Brunswick, and used for the potato after-cooking darkness program at the Nova Scotia Agricultural College. These hybrids were derived from crossing primitive cultivated South American diploid species such as *Solanum phureja* or *Solanum stenotomum* and wild diploid species such as *Solanum chacoense* and other wild Argentine species with haploids of *Solanum tuberosum*. These hybrids have subsequently undergone up to 30 years of breeding and selection, for adaptation to local growing and storage conditions, processing traits and pest resistances. The objectives of this study were to estimate the level of genetic similarity (GS) among these sets of clones and to investigate the correlation between RAPD-based GS and *f*, based on pedigree information. Genetic similarity coefficients varied from 0.29 to 0.90 with a mean of 0.65 when based on the RAPD data, whereas the coefficient of parentage varied from zero to 0.75 with a mean of 0.11. The degree of relationship between the similarity matrices based on RAPD and pedigree was measured by comparing the similarity matrices with the normalized Mantel test. A low positive correlation ($R = 0.104$, $p = 0.999$) between the two matrices was observed. Cluster analysis using GS divided the clones into many subgroups that did not correspond well with the grouping based on pedigree. The level of genetic variation present in this set of potato clones is very high. Rigorous selection pressure aimed at different breeding purposes may result in the genetic differentiation of the clones from the same origin.

Keywords Potato · RAPD diversity · Coefficient of parentage · *S. phureja* · *S. stenotomum* · *S. chacoense*

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Introduction

The cultivated potato, *Solanum tuberosum* L., is one of the four most-valuable crops worldwide. Potato is exceeded only by wheat, rice and maize in world production for human consumption (Ross 1986). Potato tubers give an exceptionally high yield per acre, many times that of any grain crop (Burton 1969), and are used in a wide variety of table, processed, livestock feed and industrial uses (Feustel 1987; Talburt 1987).

Most potatoes now grown in North America are derived from cultivars introduced centuries ago from South America into Europe. These early introductions probably represented only a minute sample of the genetic variability available at or near the center of origin. As a result of this narrow genetic base, it has become increasingly difficult to develop new cultivars that are clearly superior to the old established ones. Potato breeders around the world are now convinced that improving the yield and quality of potatoes requires a broader foundation of genetic resources. Fortunately the building blocks for a broader base are available. The wild and cultivated potato species in Central and South America offer wide genetic diversity. In addition to contributing to building a broader genetic base, many accessions have valuable resistances to diseases, pests and stresses (Bamberg et al. 1994). The majorities of these species are diploid ($2n = 2x = 24$) and can readily be crossed with haploids of *S. tuberosum*. In addition to their use in breeding, the diploids can also be used in genetic

studies because their disomic inheritance pattern greatly facilitates genetic analysis. Several primitive cultivated diploid species (such as *Solanum phureja* and *Solanum stenotomum*) as well as wild diploid species (such as *Solanum chacoense* Bitt. and other wild Argentine species) have been incorporated into adapted breeding clones at the Potato Breeding Program at Fredericton.

A successful breeding program depends on the knowledge and understanding of the genetic diversity of the available germplasm. The information about genetic relationships among these diploid clones has important implications for breeding programs. Several methods have been used to assess the diversity of plant-breeding materials. Coefficient of parentage (*f*) (Kempthorne 1957) is an important method to estimate the genetic diversity based on pedigree (Cox et al. 1985a; Vello et al. 1988; Melchinger et al. 1991; Lima et al. 2002). It indirectly measures the genetic diversity among cultivars by estimating, from pedigree records, the probability that alleles, in a locus, are identical by descent. However, assumptions made when calculating *f* regarding the relatedness of ancestors, selection pressure and genetic drift are generally not met.

DNA markers are most suitable for genetic-diversity estimates (Plaschke et al. 1995; Kim and Ward 1997; Davila et al. 1998); however, the extent of their usefulness may depend on the nature of the marker, the number of markers involved, genome coverage and the population under investigation. Random-amplified polymorphic DNA (RAPD) analysis (Williams et al. 1990) is based on the amplification of DNA fragments with the polymerase chain reaction (PCR) starting from primers with arbitrary sequences. This technique is considerably faster and simpler than some other molecular techniques. RAPD markers have the potential to measure variation with good coverage of the entire genome. These markers have been used to examine both interspecific and intraspecific variation in a number of plant species and have been confirmed as efficient tools for estimating genetic variation among genotypes of any organism (Brummer et al. 1995; Sun et al. 1997; Bai et al. 1998; Fu et al. 2002). In tuber-bearing *Solanum* species, RAPD markers have been shown to be sufficiently sensitive to selected somatic hybrids (Baird et al. 1992), to detect genetic variation among androgenic monoploids (Singsit and Ozias-Akins 1993) and wild potato populations of the USA (del Rio et al. 2001), and to characterize the genetic composition of anther-derived plants of a diploid potato clone (Veilleux et al. 1995). RAPD markers have also been used successfully to detect segregation in F2 populations of potato (Hosaka and Hanneman 1994).

The objective of the present study was to estimate the genetic diversity among 45 cultivated diploid hybrids using RAPD and coefficients of parentage methods. Such information is useful in guiding the potato after-cooking darkening program and other potato breeding programs.

Materials and methods

The plant materials used in this study consisted of 45 diploid hybrid clones, which were selected based on tuber quality for the potato after-cooking darkness research, and were derived by crossing primitive cultivated South American diploid species such as *S. phureja* Juz. & Buk. or *S. stenotomum* and wild species with haploids of *S. tuberosum*. These hybrids have subsequently undergone up to 30 years of breeding and selection for adaptation to local growing and storage conditions, processing traits and pest resistances at the Potato Research Center, Fredericton.

DNA isolation

Leaf tissue samples were collected from these clones, frozen in liquid nitrogen and kept at –80 °C. DNA was extracted according to the method described by Junghans and Metzlaff (1990).

RAPD analysis

Amplification reactions were performed based on the standard protocol of Williams et al. (1990) with some modifications. PCR reaction mixtures of 20 µl contained 20 ng of template DNA, 0.2 mM of each deoxynucleotide (dATP, dCTP, dGTP and dTTP), 2.5 mM of $MgCl_2$, 1.0 U of *Taq* polymerase (Rose company, Canada) and 15 pmol of a single 10-mer primer purchased from University of British-Columbia (British-Columbia, Canada). Amplification was performed in a DNA Thermo-cycler (Perkin Elmer). The PCR program consisted of 30 cycles of denaturation at 94 °C for 1 min, annealing at 36 °C for 1 min and extension at 72 °C for 2 min. The final cycle had a 3-min extension step at 72 °C. The PCR fragments were electrophoresed through 1.2% agarose gels, stained with 0.5 g/ml of ethidium bromide and visualised with ultraviolet light.

RAPD data analysis

In this work each band was considered to be a single locus. Data were scored as 1 for the presence and 0 for the absence of a DNA band of each genotype. Data matrices were entered into the NTSYS program (Rohlf 1993). The data were analyzed using the Qualitative routine to generate Jaccard's similarity coefficient (1908): $Gsij = a/(a+b+c)$, where *Gsij* is the measurement of the genetic similarity between individuals *i* and *j*, *a* is the number of polymorphic bands present in both individuals, *b* is the number of bands present in *i* and absent in *j*, and *c* is the number of bands present in *j* and absent in *i*. Similarity coefficients were used to construct a dendrogram using the UPGMA (unweighted pair group method with arithmetic average) and the SHAN (sequential, hierarchical and nested clustering) routine in the NTSYS program. The principal coordinate analysis (PCA) was conducted with the same program using the DCENTER and EIGEN procedures. This multivariate approach was chosen to complement the cluster analysis information, because cluster analysis is more sensitive to closely related individuals, whereas PCA is more informative regarding distances among major groups (Hauser and Crovello 1982).

Coefficient of parentage

The calculation of the coefficient of parentage (*f*) between two genotypes, as defined by Kempthorne (1957), is carried out between genotypes and corresponds to the probability that alleles in a locus are identical by descent to alleles at the same locus in another cultivar. Pair-wise *f* values were used to generate a coefficient matrix. Clustering of the clones was performed as in the previous section "RAPD data analysis".

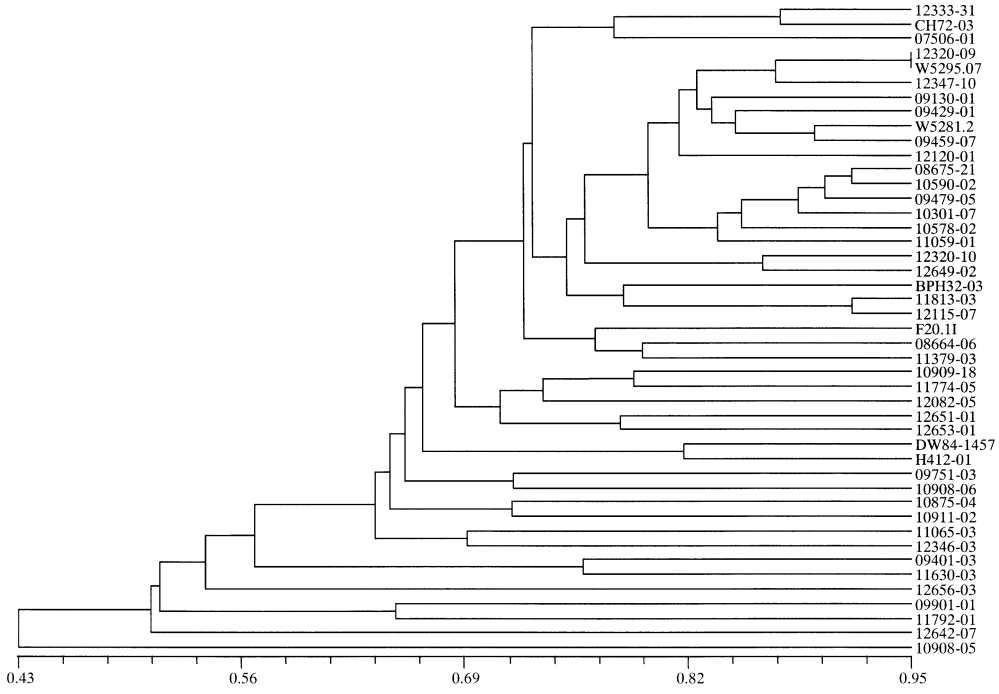

Fig. 1 UPGMA dendrogram showing genetic relationships among the 45 potato genotypes used in this study. The dendrogram was constructed based on genetic similarity calculated according to Jaccard's coefficient

Matrix comparison

The RAPD-based Jaccard's similarity matrix and the pedigree-based coefficient of parentage matrix were compared by the MAXCOMP routine of NTSYS-pc. The normalized Mantel statistic Z (Mantel 1967) was used to determine the level of association between the two matrices. The COPH subroutine of NTSYS-pc was employed to determine the cophenetic correlation coefficient between the similarity matrix and the similarity cluster for the two RAPDs and the pedigree data sets.

Results

RAPD analysis

A total of 60 RAPD primers from UBC (University of British Columbia, Vancouver, BC, Canada) were screened with four (DW84-1457, 12320-09, 11774-05 and 12649-02) random potato clones and 15 primers, which resulted in very clear RAPD patterns. These primers were selected to amplify fragments from the DNA templates of 45 genotypes. The reproducibility was considered as an important criterion for primer selection. Reproducibility is an intrinsic property of a particular primer sequence and, hence, can only be addressed experimentally. A total of 64 bands were scored with these 15 primers, of which 60 bands (94%) were polymorphic. An average of 4.3 RAPD markers per primer were scored, with the largest number (seven) obtained for UBC104, and the lowest number (two) obtained for the UBC103, 110 and 114 primers. None of the RAPD markers was specific to a genotype.

The pair-wise genetic similarity matrix was calculated on the basis of Jaccard's algorithm for RAPD data (data not shown). Genetic similarity coefficients varied from 0.29 in a pair of clones (09401-03 and 12642-07) to 0.90 in a pair of clones, (09479-05 and 10578-02), with a mean of 0.65.

The clustering of RAPD-based genetic similarity values using the UPGMA method resulted in the dendrogram shown in Fig. 1. In this dendrogram no group stood out in any special way, thus allowing all the clones to be in one main cluster, divided into subgroups, which presents some degree of similarity. The clone 10908-05 was the most diverse one among these 45 clones. Associations among the 45 genotypes were also examined with principal coordinate analysis (PCA). The results of PCA are shown in Fig. 2. The principal coordinates 1 and 2 encompassed only 12% and 10% of the total variation, respectively. In general, the results of PCA corresponded well to those from the cluster analysis obtained through UPGMA.

Pedigree analysis

The coefficient of parentage was calculated based on available information and varied from 0 to 0.75, with a mean of 0.11. Cluster analysis using UPGMA based on the coefficient of parentage is shown in Fig. 3. The dendrogram clearly separated the 45 clones into four different groups. Group I contains four clones. Group II comprised five clones. Group III contains only one clone, DW84-1457. Group IV contains 35 clones, which are divided into several subgroups.

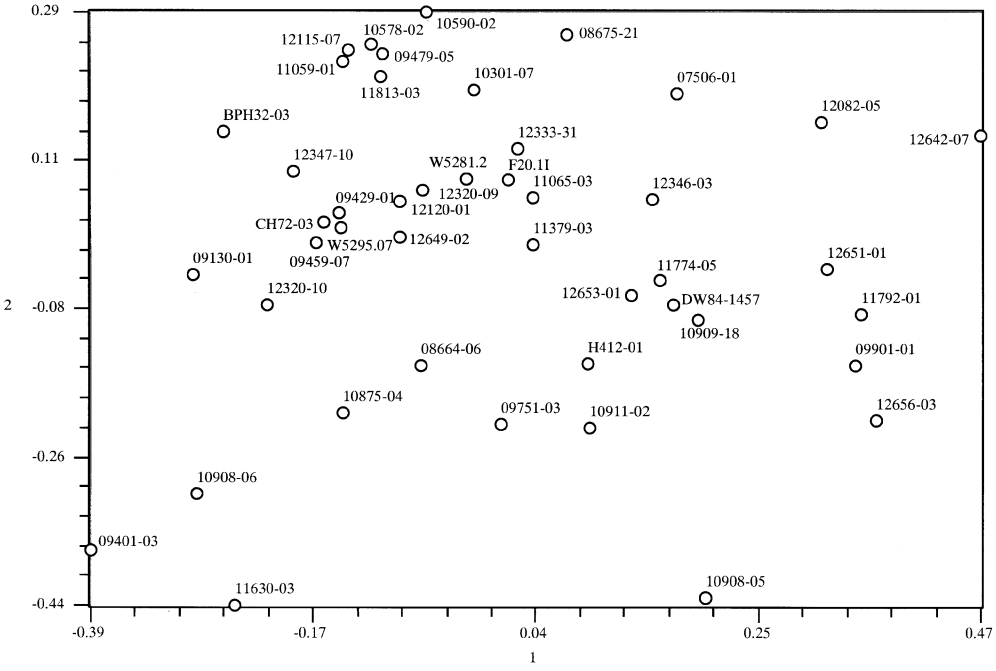

Fig. 2 Associations between 45 genotypes on the basis of the first two principal coordinates (PC1, PC2) obtained from a principal coordinate analysis of Jaccard similarity coefficients based on RAPD data

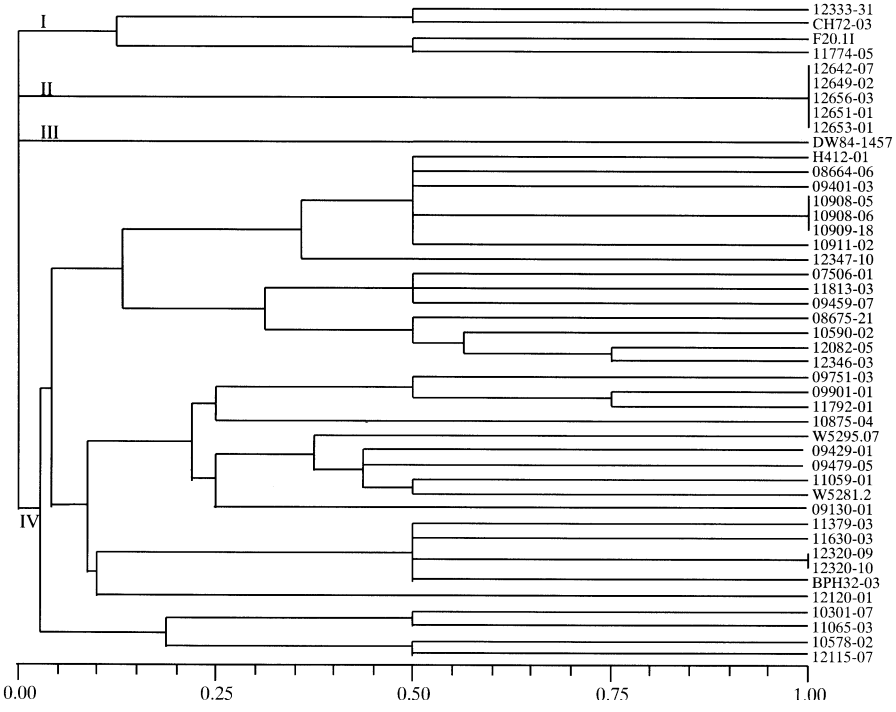

Fig. 3 UPGMA dendrogram showing genetic relationships among the 45 potato clones used in this study. The dendrogram was constructed using the matrix of coefficients of parentage

Matrix comparison and the Mantel test

The degree of relationship between the similarity matrices based on both RAPD and pedigree was measured by comparing the similarity matrices with the normalized Mantel test. A low positive correlation (R = 0.104, p = 0.999) between the two matrices was observed. The goodness of fit, determined by the correlation between the cophenetic matrix and similarity matrix, as described, between the pedigree dendrogram and the coefficient of parentage matrix was 0.99, and between the RAPD dendrogram and the similarity matrix was 0.87.

Discussion

The 94% level of polymorphism found among the 45 clones in the present study was higher than the RAPD polymorphism reported in previous studies on cultivated potato (Milbourne et al. 1997; McGregor et al. 2000). A

comparative assessment of DNA fingerprinting techniques (RAPD, ISSR, AFLP and SSR) in 39 tetraploid potato germplasms found that the frequency of polymorphic fragments ranged from 73.7% for RAPD to 98.4% for AFLP (McGregor et al. 2000). The level of RAPD polymorphism among 16 cultivars from a primarily northwestern European cultivated potato gene pool was 65.8% (Milbourne et al. 1997). The differences between studies in the levels of polymorphism that were detected can probably be attributed to differences in the materials and the numbers of materials chosen for the studies.

The molecular analysis reported here was aimed at the assessment of the genetic diversity of the 45 diploid potato clones. The genetic similarities calculated for all pairwise comparisons among the 45 clones, which ranged from 0.29 to 0.90 for RAPD data, showed that there is a higher level of genetic diversity among the clones in this study. In comparison, a study of 28 European and Argentinian cultivated potatoes for three inter-simple sequence repeats found that similarities between the cultivars ranged from 0.275 to 0.930 (Bornet et al. 2002). Microsatellite analysis of 18 tetraploid potato cultivars revealed that the similarity value was from 0.44 to 0.81 (Provan et al. 1996). RAPD analysis of 128 *S. phureja* accessions resulted in a similarity value ranging from 0.65 to 1.0 (Ghislain et al. 1999). Previous comparisons of marker systems with common genetic materials have shown that the level of polymorphism revealed by microsatellites was higher than by RAPD in potato (Milbourne et al. 1997; McGregor et al. 2000). The level of RAPD polymorphism detected in the present study is similar to the level of microsatellite polymorphism in previous studies, reflecting that the genetic diversity among this set of potato clones was very high. The high diversity among this set of potato clones may be the result of the broadening of the genetic base by the use of primitive cultivated, as well as wild diploid, species.

Clustering of these 45 potato clones based on RAPD data was different from that based on the coefficient of parentage. The low correlation coefficient (R = 0.104) was found between matrices based on RAPD genetic diversity estimates, and the coefficient of parentage is much lower than the value (r = 0.61) observed between RAPD-based GS and f estimates in barley by Tinker et al. (1993). Graner et al. (1994) compared RFLP-based GS with the coefficient of parentage-estimates generated for a set of 48 barley cultivars, finding a low correlation for the winter type (r = 0.21) and a moderate one for the spring type (r = 0.42). Evaluating the correlation between isozyme-based GS and f estimates for wheat cultivars, Cox et al. (1985b) obtained a value of r = 0.27. Lima et al. (2002) compared AFLP-based GS with f for a set of 79 sugarcane cultivars, and observed a value of r = 0.42. A similar value (r = 0.45) was found in Canadian durum wheat (Soleimani et al. 2002) comparing estimates of AFLP and kinship coefficient. Plaschke et al. (1995) found a value of r = 0.55 between GS based on microsatellites and f. The incongruities may be the result of one or more of several factors outlined in Mumm and Dudley (1994). DNA markers, when identical in size, may represent alleles that are only *identical in state* or *alike in state* (for definitions, see Falconer 1981), and may not always be *identical by descent*. In addition, pedigree data can be subjective, and does not account for the effects of selection, mutation and inadequate simplification in the underlying model that assumes equal parental contributions (Souza and Sorrells 1989; Cox and Murphy 1990; Tinker et al. 1993). These estimates may be biased due to selection pressure, unequal parental contribution and the relatedness of ancestors without a known pedigree. DNA markers may be affected by selection, drift and mutation. Finally, incongruities can result from the clustering process whenever clusters are non-overlapping. Because of the latter, a clone that is related to two other clones from separate clusters will only be grouped with the one to which it is most closely related.

The high RAPD – based genetic similarity (0.90) detected between clones 09479-05 and 10590-02 was not expected, as the pedigree information shows a very distant relationship. However, clones 09479-05 and 10590-02 might in some way be related to each other via the cultivar Katahdin which appears in the pedigree of 09479-05, and may possibly also be in the pedigree of 10590-02 (although this cannot be verified). Pairs of clones such as 12651-01 and 12653-01, and 12333-31 and CH72-03, that were closely related in the pedigree-based dendrogram (Fig. 3) were also related in the RAPD-based dendrogram (Fig. 1). On the other hand, 10908-05, 10908-06 and 10909-18 derived from the same cross combinations, clustered together in the pedigree-based dendrogram (Fig. 3) but was widely spread in the RAPD-based dendrogram (Fig. 1). The two clones, 12320-09 and 12320-10, originated from the same cross, but were not clustered together by RAPD analysis. These differences may be due to the selection for different breeding purposes, which are unaccounted for by pedigree analysis but detected at the DNA level. The original hybrids were derived from crossing primitive cultivated South American diploid species such as *S. phureja* or *S. stenotomum*, as well as several wild species such as *S. chacoense* and other wild Argentine species with haploids of *S. tuberosum*. They were then selected for their adaptation to Canadian growing conditions, including tuberization under long days and long dormancy. In addition to these two traits, the hybrids have been subjected to selection for acceptable tuber shape, tuber size, shallow eyes, chip quality, resistance to various diseases as well as 2n pollen formation for up to 30 or more years. For example, the three sibling clones, 10908-05, 10908-06 and 10909-18, differ from each other on the degree of after-cooking darkness (unpublished data). Selection probably accounts for the genetic differences among these full sibs.

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