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Isozyme and plastid DNA assessment of pedigrees of nineteenth century potato cultivars *

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Summary. Isozyme and ctDNA RFLP patterns were determined for ten historically important potato cultivars (*Solanum tuberosum* ssp. *tuberosum*) in order to relate and confirm their pedigrees. Isozyme polymorphism was detected at 11 of 13 loci examined, whereas only T-type cytoplasm, the predominant ctDNA of *S. tuberosum* ssp. *tuberosum*, was observed. Isozyme analysis indicated that potato cultivars previously presumed to be derived from open-pollinated berries of Garnet Chili and Early Rose were in fact the result of hybridizations. In addition, putative pedigrees of Irish Cobbler, White Rose, and Bliss Triumph were not supported. Garnet Chili, the first derivative of Rough Purple Chili, carries allozmyes at *Mdh-1* and *Pgm-2*, which supports the Chilean origin of Rough Purple Chili. The identical ctDNA pattern among the cultivars may indicate a common maternal lineage that traces through Garnet Chili to Rough Purple Chili. The allozyme frequencies estimated from these cultivars provide a base from which subsequent introductions of *Solanum* species into the ssp. *tuberosum* gene pool can be assessed.

Key words: *Solanum tuberosum* – Potato breeding – ctDNA

Introduction

The first significant achievements in potato breeding in the United States were made in the second half of the nineteenth century. The first advance was the release of the South American introduction, Rough Purple Chili, in 1851 (Goodrich 1863). The importance of this selection was not its widespread use in production, but as germplasm useful in breeding. Between 1956 and 1985, 126 U.S. cultivars could be traced to Rough Purple Chili (Plaisted and Hoopes 1989), as well as at least 300 European cultivars (Hawkes 1979).

Early derivatives of Rough Purple Chili include Garnet Chili, Early Rose, Prolific, Peerless, Burbank, Early Ohio, Beauty of Hebron, Bliss Triumph, and Irish Cobbler. Many of these cultivars had, or still have, significant roles in production or breeding efforts. These early cultivars were released primarily by private breeders and little consideration was given to maintaining or publishing cultivar pedigrees. Moreover, cross-pollination techniques were not widely practiced and many selections were made from seed obtained from open-pollinated berries (Stuart 1937). The putative relationships of these and other nineteenth century cultivars are indicated in Fig. 1. Maternal lineage is generally agreed upon (Salaman 1926; Clark et al. 1931; Folsom 1945; Hosaka and Hanneman 1988), but it has not been possible to determine the level of inbreeding incurred during the development of these cultivars.

With the advent of codominant molecular markers, such as isozymes and RFLPs (Olivier and Martinez-Zapater 1984; Hosaka 1986; Douches and Quiros 1988; Hosaka and Hanneman 1988), it is feasible to reassess the pedigrees of these early cultivars. In this paper we report the results of using such techniques to examine the lineage and isozyme diversity of ten historically important potato cultivars released in the nineteenth century. The findings provide useful information in devising breeding strategies using these germplasm.

Materials and methods

The ten potato cultivars (*Solanum tuberosum* ssp. *tuberosum*) were kindly provided by Drs. N. S. Wright (Agriculture Canada,

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Vancouver, BC) and J. Bamberg (USDA, IR-1, Sturgeon Bay/WI) (Table 1). These clones fit the early tuber descriptions and were thus assumed to be properly labelled (Stuart 1937).

ctDNA analysis

Potato ctDNA was isolated from 30 g of leaf tissue of a diploid potato line, 106-2-1 (*S. chacoense*, P. I. 230580), according to Hosaka (1986). To obtain total plant DNA 10 g of succulent leaf tissue was obtained from greenhouse-grown plants and ground in 30 ml of CTAB extraction buffer (0.1 *M* TRIS-HCl (pH 8.0), 1.4 *M* NaCl, 0.02 *M* EDTA, 2% hexadecyltrimethyl ammonium bromide, Sigma) (Guri and Sink 1988). Two mercaptoethanol (1% v/v) was added to the extraction buffer immediately prior to maceration. The macerated tissue was passed through four layers of cheesecloth, incubated at 60 °C for 1 h, and then extracted three times with an equal volume of 24:1 chloroform:isoamyl alcohol. Sodium acetate (3 *M*; 1/10 vol.) was added to the supernatant, and the DNA was then precipitated with isopropyl alcohol at −20 °C for 1–2 h. Following centrifugation (2,500 × *g*), the pellet was resuspended in 0.8 ml of TE buffer (10 m*M* TRIS, 1 m*M* EDTA). The DNA was then precipitated with 80 µl of 3 *M* sodium acetate and 2 ml of 95% ethanol. Following centrifugation (13,000 × *g*), the pellet was washed with 70% ethanol for 5 min. The air-dried pellet was resuspended in 500 µl of TE with RNase A (20 µg/ml.).

From each cultivar, 5 µg of total DNA was digested with EcoRI, HindIII, BamHI, and XbaI according to the supplier's instructions (Gibco, BRL), and fractionated on 0.9% agarose gels. The DNA was Southern transferred to Nylon membranes (Zetabind, Cuno). Potato ctDNA was ^{32}P-labelled by Nick-translation and hybridized to Southern blots overnight, then washed to high stringency according to the manufacturer. Blots were then exposed overnight to X-ray film (Kodak) with one intensifying screen (Dupont Cronex) at −80 °C.

Isozymes

Both leaf and tuber tissues were independently surveyed for a total of 12 enzyme systems which produce 15 consistently resolvable isozyme loci. Esterase (EST), peroxidase (PRX), alcohol dehydrogenase (ADH), glutamate oxaloacetate transaminase (GOT), phosphoglucomutase (PGM), and diaphorase (DIA) were resolved with a lithium-borate pH 8.3 buffer system (Stuber et al. 1988). Malate dehydrogenase (MDH), isocitrate dehydrogenase (IDH), shikimic acid dehydrogenase (SDH), phosphoglucose isomerase (PGI), 6-phosphogluconate dehydrogenase (6-PGDH), and acid phosphatase (APS) were examined by the histidine-citrate pH 5.7 buffer system (Stuber et al. 1988). Tissue processing, nomenclature, and allelic descriptions were followed as published for potato (Douches and Quiros 1988), while general techniques and staining protocols were those described by Quiros (1981) and Vallejos (1983), respectively. Each cultivar was examined four times through starch electrophoresis.

Results

ctDNA analysis

The potato ctDNA digestion patterns of the ten cultivars were identical within each of the four restriction digests. Restriction patterns with BamHI and HindIII (Fig. 2) were typical of the T-type potato cytoplasm, as published by Hosaka (1986), the predominant cytoplasm of *S. tuberosum* ssp. *tuberosum*.

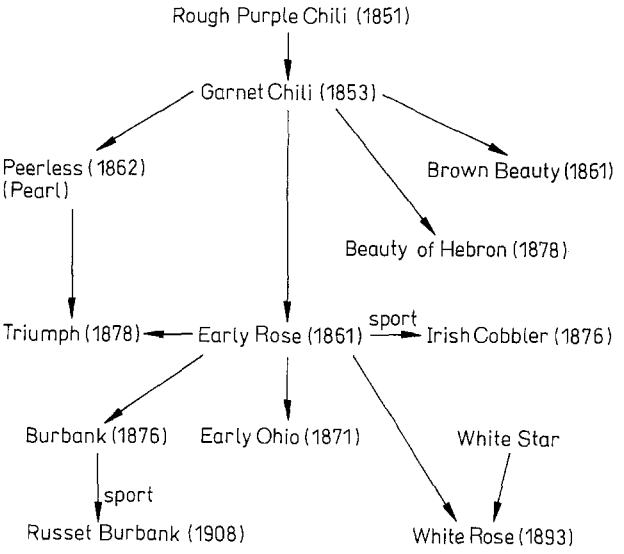

Fig. 1. Putative pedigrees of some important potato varieties (1850–1900) based upon Stuart (1937), Folsom (1945), and Plaisted and Hoopes (1989)

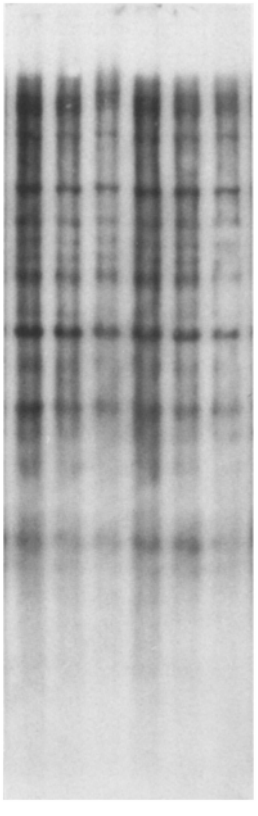

Fig. 2. Chloroplast DNA restriction patterns with BamHI show T-type cytoplasm in Rural New Yorker, Green Mountain, Burbank, Russet Burbank, Early Rose, and Irish Cobbler

Table 1. Isozyme genotypes of ten North America potato cultivars from the nineteenth century

Variety	Year released	Isozyme loci[a]												
		Mdh-1	*Mdh-2*	*6-Pgdh-3*	*Pgi-1*	*Pgm-1*	*Pgm-2*	*Got-1*	*Got-2*	*Dia-1*	*Prx-3*	*Aps-1*	*Adh-1*	*Idh-1*
Carnet Chili	1853	2224[b]	2222	1222	2222	1333	2223	3334	3555	1111	1122	1111	2222	1122
Beauty of Hebron	1878	1222	2222	2222	2222	1133	2223	3344	3555	1112	1122	1111	2222	1112
Irish Cobbler	1876	2233	2222	1122	2222	1133	2223	3334	3555	1112	1113	1114	2222	1122
Early Rose	1861	1222	2222	2222	2222	1133	2223	3334	3555	1112	1122	1111	2222	1112
Burbank	1876	1222	2222	1222	2222	1133	2222	3334	3555	1112	1112	1111	2222	1112
Early Ohio	1871	2233	2222	1222	2222	1333	2222	3344	3555	1111	1113	1111	2222	1122
Bliss Triumph	1878	1224	2222	1112	2222	1133	2222	3344	3555	1112	1113	1144	2222	1222
Green Mountain	1885	1122	2222	1222	2222	1333	2223	3334	3555	1111	1111	1114	2222	1112
Rural NY No. 2	1888	2222	2222	1222	2222	1333	2222	3344	3555	1112	1111	1111	2222	1111
White Rose	1893	1224	2222	1112	2222	1333	2222	3334	3555	1122	1111	1111	2223	1122
Allele total		4	1	2	1	2	2	2	2	2	3	2	2	2

[a] Nomenclature according to Douches and Quiros (1988) and Quiros and McHale (1985)
[b] Allelic designation of tetraploid locus: 2224 = *Mdh-1*^{2}*1*^{2}*1*^{2}*1*^{4}

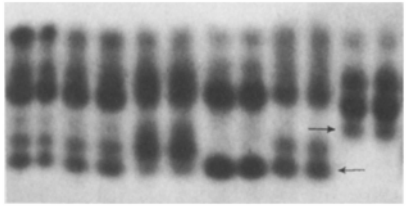

Fig. 3. Zymogram of 6-PGDH showing genotypes for *6-Pgdh-3* locus (*lower zone*). The *right-* and *left-handed arrows* point to the *6-Pgdh-3*^{1} (fast band) and *6-Pgdh-3*^{2} (slow band) homodimers, respectively. Each cultivar is run in pairs and allelic dosage is in parentheses. They are from *left* to *right* as follows: Russet Burbank (1222), Burbank (1222), Irish Cobbler (1122), Early Rose (2222), Early Ohio (1222), and a diploid (*S. phureja*) line, 84S10 (11)

Isozyme analysis

The electrophoretic patterns for 13 isozyme loci of the ten cultivars are summarized in Table 1. A total of 27 allozymes were identified. *Mdh-2* and *Pgi-1* are monomorphic, whereas *Adh-1* is heterozygous in only one of ten cultivars. *Prx-3* and *Mdh-1* are polymorphic for three and four allozymes, respectively. *Sdh-1* and *Est-c* were excluded from the analysis because their banding patterns were too complex to determine the isozyme locus genotype. Triallelic loci were only observed at *Mdh-1* in White Rose and Bliss Triumph. Irish Cobbler has the greatest number of heterozygous loci (10 of 13), while Rural New Yorker and Early Ohio had the least, with 5 of 13 and 6 of 13 heterozygous loci, respectively.

The first relationships examined were between Garnet Chili and its presumed offspring, Early Rose and Beauty of Hebron. Garnet Chili is homozygous for *Mdh-2, Pgi-1, Dia-1, Adh-1,* and *Aps-1* isozyme loci. Both Early Rose and Beauty of Hebron are simplex heterozygotes at *Dia-1*. The *Mdh-1*^{1} allozyme, absent in Garnet Chili, is present in Early Rose and Beauty of Hebron.

The next relationships we examined involved putative progeny of Early Rose: Burbank, Early Ohio, Bliss Triumph, and White Rose. Irish Cobbler, a putative sport of Early Rose, was also compared. Early Rose is homozygous for the *6-Pgdh-3*^{2}, *Aps-1*^{1}, and *Adh-1*^{2} allozymes. Burbank is heterozygous at the *6-Pgdh-3* locus (*6-Pgdh-3*^{1}*3*^{2}*3*^{2}*3*^{2}). Early Ohio also carries the *6-Pgdh-3*^{1} allozyme in a simplex state (Fig. 3), in addition to the *Mdh-1*^{3} allozyme, which is not observed in either Early Rose or Garnet Chili. Irish Cobbler is electrophoretically distinct from Early Rose. They are differentiated by 5 of 13 loci. Bliss Triumph carries three additional allozymes (*Mdh-1*^{4}, *6-Pgdh-3*^{1}, and *Aps-1*^{4}) compared to Early Rose; however, these allozymes are not unique to Bliss Triumph. The first two are also present in Garnet Chili. The heterozygous state at the *6-Pgdh-3* locus (*6-Pgdh-3*^{1}*3*^{1}*3*^{1}*3*^{2}) in Bliss Triumph indicates that Early Rose could not have been a direct parent in the pedigree. White Rose is distinct because it carries the *Adh-1*^{3} allozyme, which is absent in the other nine cultivars. White Rose also carries the *Mdh-1*^{4} and *6-Pgdh-3*^{1} allozymes, which are absent in Early Rose. Like Bliss Triumph, the heterozygous state of the *6-Pgdh-3* locus in White Rose excludes Early Rose from being a direct parent.

Discussion

Isozyme analysis provided an effective means to examine and resolve the pedigrees of early potato cultivars. Isozyme loci, as genetic markers, offer codominance, simple Mendelian inheritance, and absence of environmental and epistatic effects (Tanksley 1983). In contrast, morphological markers are unreliable in potato due to dominance effects, incomplete penetrance, and tetra-

somic segregation. Male sterility in one of the cultivars (i.e., Burbank) also precludes progeny testing. Isozyme analysis is also well suited to the potato since a high level of polymorphism exists within the cultivated (Martinez-Zapater and Olivier 1986; Douches and Ludlam 1990) and wild gene pools (Douches et al. 1989). Electrophoretic analysis herein offered 13 discreet loci, which we were able to utilize to examine qualitative and quantitative phylogenetic relationships in potato.

Allozyme diversity in S. tuberosum ssp. tuberosum prior to twentieth century

Potato breeding in the United States in the second half of the nineteenth century was essentially a private undertaking; thus, records were not maintained, became lost, or were not disclosed. Therefore, the exact pedigrees of old cultivars are frequently unknown. The American potato breeders of this period, with the exception of C. G. Pringle, did not use cross-pollination (Stuart 1937). Therefore, it is commonly accepted that open- or self-pollinated berries were the source of most of these cultivars. Garnet Chili, Early Rose, Beauty of Hebron, Early Ohio, and Burbank were developed in this manner.

Garnet Chili is a seedling descendent of Rough Purple Chili (Goodrich 1863), which has been particularly valuable as a parent in breeding. Early Rose, Beauty of Hebron, Peerless, and Brown Beauty all originated from open-pollination of Garnet Chili. Moreover, Plaisted and Hoopes (1989) were able to trace the pedigree records of almost all North American cultivars since 1956 to Garnet Chili. In particular, 11% of the commercially important cultivars introduced since 1932 are only two or three generations removed from Garnet Chili.

Because Garnet Chili is a prominent introduction of modern potato cultivars, it can be used as a reference point to examine subsequent introgression of germplasm in the modern cultivated potato. It has the T-type cytoplasm and a total of 21 allozymes distributed among 13 loci. Five of these loci are fixed for a specific allele. Assuming that the maternal lineage is correct, the question is whether these offspring, which were derived from open-pollinated berries, are from self or hybrid seed. If these offspring carry at least one allozyme that is absent in the parent, we can assume selfing did not occur.

Isozyme analysis shows that both Early Rose and Beauty of Hebron are of hybrid origin rather than selfing. As a result of hybridization, these two cultivars carry two allozymes that are absent in Garnet Chili. Burbank and Early Ohio are subsequent hybrid seedlings from Early Rose. Three additional allozymes are carried in Burbank and Early Ohio, while absent in Early Rose, and two of these are also absent in Garnet Chili. Therefore, open-pollination contributed four additional allozymes to the modern cultivated gene pool following the release of Garnet Chili.

Irish Cobbler, a putative sport of Early Rose, is quite distinct in its electrophoretic pattern from Early Rose. The two cultivars differ at 5 of 13 isozyme loci. Electrophoretic differences of this nature suggest that the presumed sport of Irish Cobbler is inaccurate (Douches and Ludlam 1990). Sports or line selections from a cultivar should maintain nearly identical electrophoretic patterns. Irish Cobbler was most likely a variant found among a seedlot of Early Rose (Clark and Lombard 1946); therefore, we conclude that its origin is unknown. Irish Cobbler carries four allozymes not found in Early Rose and it is the first post-1850 cultivar to carry the *Aps-1*^{4} allozyme.

Electrophoretic analysis indicated that the putative pedigrees of Bliss Triumph and White Rose (Fig. 1) are probably incorrect. Thus, it is questionable how direct their lineage traces back to Garnet Chili. These two cultivars carry four allozymes in addition to all those observed for Garnet Chili. It is noteworthy that these are the first two cultivars studied to have a triallelic state at an isozyme locus (*Mdh-1*). In addition, White Rose carries the *Adh-1*^{3} allozyme, which is a rare allele in the North American potato cultivars (Douches and Ludlam 1990).

The cultivar Green Mountain does not have a putative pedigree that traces directly to the cultivars we examined. The parents of Rural New Yorker were apparently never recorded. The allelic state at each locus does not discount the possibility that the pedigrees of these two cultivars could trace to Garnet Chili. However, the allozyme diversity observed in Green Mountain and Rural New Yorker does not provide any indication of unique germplasm introgression in their pedigrees.

Plaisted and Hoopes (1989) discussed the uncertainty of the Green Mountain pedigree. Questions arise as to

Table 2. Frequencies of most common alleles

Locus	Predominant allele	Allele frequency
Mdh-1	*Mdh-1*^{2}	0.65
Mdh-2	*Mdh-2*^{2}	1.00
6-Pgdh-3	*6-Pgdh-3*^{2}	0.68
Pgi-1	*Pgi-1*^{2}	1.00
Idh-1	*Idh-1*^{1}	0.63
Aps-1	*Aps-1*^{1}	0.88
Got-1	*Got-1*^{3}	0.65
Got-2	*Got-2*^{5}	0.75
Pgm-1	*Pgm-1*^{3}	0.65
Pgm-2	*Pgm-2*^{2}	0.88
Prx-3	*Prx-3*^{1}	0.78
Adh-1	*Adh-1*^{2}	0.97
Dia-1	*Dia-1*^{1}	0.80

the method of crossing and the origin of the putative parents; however, they proposed that 7/8 of the pedigree of Green Mountain likely traces back to Garnet Chili. Rural New Yorker, as assessed by Plaisted and Hoopes (1987), could have also descended from Garnet Chili. In spite of the close genetic relationship of Green Mountain and Rural New Yorker to Garnet Chili, they carry three allozymes not found in Garnet Chili.

In summary, the potato cultivars released after Garnet Chili carried six new allozymes, a 28% increase in variant allozymes. Heterozygous loci were detected at 11 of the 13 loci but, at each polymorphic locus, a predominant allele was observed (Table 2). These allozyme frequencies form a base from which we can detect subsequent allozyme introgression from other *Solanum* species in the twentieth century.

Relationships between North and South American cultivated tetraploid potatoes

Only the T-type cytoplasm ctDNA restriction pattern was found among the ten nineteenth century cultivars. This could be a result of a common maternal lineage through Garnet Chili or a common cytoplasm between Garnet Chili and all other pre-1850 potato cultivars. Hosaka and Hanneman (1988), based upon ctDNA determination, proposed that prior to the introduction of Rough Purple Chili and its derivatives, the European cultivars were bred from *S. tuberosum* ssp. *andigena* (A-type cytoplasm). If the pre-1850 North American cultivars were introduced from Europe, it is likely they also contained the A-type cytoplasm of spp. *andigena*. Since only the T-type cytoplasm was found in the ten post-1850 cultivars, these potato clones most likely have a maternal lineage that traces to Rough Purple Chili via Garnet Chili. This common cytoplasm represents a base from which we can examine subsequent ctDNA germplasm introduction over the past century.

Garnet Chili is only one generation removed from Rough Purple Chili and may reflect most of the allozymes present in the original introduction. Based upon ctDNA (Hosaka and Hanneman 1988) and factors conditioning cytoplasmic sterilities (Grun et al. 1977), Rough Purple Chili was selected from Chilean Tuberosum. Isozyme analysis lends support to this hypothesis. The cultivated potatoes of North America carry the *Pgm-2*^{3} and *Mdh-1*^{4} allozymes in frequencies of 0.17 and 0.16, respectively (Douches and Ludlam 1990). Garnet Chili also carries these two allozymes. Olivier and Martinez-Zapater (1984) observed that the *Pgm-2*^{3} allozyme was absent in 258 genotypes tested from Group Andigena, but that it segregates in progeny of three Chilean Tuberosum cultivars. Zimmerer and Douches (1990) observed allele frequencies of 0.03 and 0.015 for these allozymes in a sample of 30 Andean cultivars. In addition, Quiros et al. (1990) found the *Pgm-2*^{3} and *Mdh-1*^{4} allozymes in only 3 and 10 out of 260 Andean cultivars, respectively. Interestingly, no Andean cultivar simultaneously carried both allozymes. An electrophoretic survey of Chilean Tuberosum cultivars would provide data to assess their relationship to North American derivatives and also any changes that may have occurred in the development of the present *S. tuberosum* ssp. *tuberosum* gene pool.

Role of open-pollination in cultivar development

In the cultivated potato, about 80–85% of the seeds produced from open-pollination under field conditions is due to selfing (Anonymous 1987). Based upon historical records and this high degree of selfing in tetraploid potatoes, various authors (Salaman 1926; Jellis and Richardson 1987; Hosaka and Hanneman 1988; Plaisted and Hoopes 1989) have suggested that such inbreeding led to the development of Garnet Chili, Early Rose, Beauty of Hebron, Early Ohio, and Burbank. If this assumption is correct, a minimum inbreeding coefficient (F) estimate for Burbank and Early Ohio would be 0.42. Potato cultivar development over the past century, despite close genetic relationships of parents, has not incurred inbreeding to the same extent (Mendoza and Haynes 1974). Glendenning (1976) estimated that open-pollinated seed of tetraploid potatoes (Neotuberosum) may contain >80% selfed seed. However, he observed that hybrids tended to be more vigorous than selfs and, in mixed seedlots, there may be a tendency for the latter to be preferentially selected. Our isozyme analysis supports this observation. It indicated that Early Rose and Burbank, along with Beauty of Hebron and Early Ohio, are of hybrid origin. Since the past breeders' reports do not indicate which cultivars were present in their fields, we can only speculate on the origin of the male parents. Since Rough Purple Chili is no longer available, we were not able to test it relative to the origin of Garnet Chili. Therefore, we can conclude that, at most, only one generation of self-pollination may have contributed to the development of Early Rose, Beauty of Hebron, Early Ohio, and Burbank.

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