Genetic Control of Seven Enzyme Systems in *Ipomoea* Species

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Abstract. Genetic control of seven enzymes in *Ipomoea trifida* (H.B.K.) G. Don. (diploid, tetraploid, and hexaploid populations) and *I. batatas* (L.) Lam. was studied by starch gel electrophoresis. Inter- and intraspecific polymorphisms were detected for all enzymes in the populations analyzed, except catalase (CAT, EC 1.11.1.6). Phosphoglucosmutase (PGM; EC 2.7.5.1), phosphoglucose isomerase (PGI; EC 5.3.1.9), glutamate oxaloacetate transaminase (GOT; EC 2.6.1.1), menadione reductase (MNR; EC 1.6.99.2), shikimate dehydrogenase (SAD; EC 1.1.1.25), and malate dehydrogenase (MDH; EC 1.1.1.37) collectively were encoded by a minimum of 13 genetic loci resulting in 24 allozymes. Results from the diploid *I. trifida* were used to infer the genetic basis of these enzymes in the polyploid species. All polyploid populations shared almost the same number of allozymes with diploid *I. trifida*. PGM and PGI showed evidence of duplicated genes in the polyploid series. A unique allele for MNR was detected only in polyploid series.

Sweetpotato germplasm exhibits great genetic variability in many characters; however, wild species have attracted attention of plant breeders because of lack of demonstrated variability in some important traits sweetpotato. Wild species may be the only source of variability for these specific traits for cultivar improvement (Iwanaga, 1988). Much effort has been made to characterize the wild germplasm related to sweetpotato, but morphological and cytogenetic studies have failed to establish the relationships between species related to *I. batatas*. Isozyme analysis could be used to clarify those relationships. In contrast to many morphological traits, the phenotypic expression of isozymes is often under relatively simple genetic control. Generally, isozymic alleles are codominantly expressed, so heterozygotes may often be unambiguously distinguished from homozygotes. Pleiotropic, epistatic, and genotype-by-environment effects are often minimal (Smith, 1989).

Ipomoea trifida is the species purported to be most closely related to sweetpotato. It exists in nature mainly as a diploid, but plants purported to be tetraploids and hexaploids have also been collected. *Ipomoea trifida* has been shown to possess traits that are needed in commercial sweetpotato (Iwanaga, 1988) and are of interest to breeders. However, the relationship between the two taxa is unclear. The objectives of this study were therefore to :1) characterize populations of *I. trifida* of ploidy levels 2x, 4x, and 6x and of *I. batatas* (6x) using isozyme polymorphism; 2) test the genetic basis for the expression of these isozymes; and 3) provide information that might help clarify the relationship between these two species.

Materials and Methods

Plant material. Young leaf tissue of *I. trifida* and *I. batatas* of diverse origin was used in all tests (Table 1). All plant material originated from botanical seed. *Ipomoea trifida* and *I. batatas* are self-sterile so all seeds result from outcrossing.

About 1500 plants were surveyed during the course of this study, including backcross (BC) and F₂ progenies of diploid populations. Original populations and crosses were maintained

under controlled conditions (Southeastern Plant Environment Laboratories) under a short day light regimen of 9 h with a photosynthetic photon flux of photosynthetically active radiation (PAR) of 735 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and photomorphogenic radiation of 10.3 $\text{W}\cdot\text{m}^{-2}$ for fluorescent and incandescent lights. The chamber was at 26C during the light period and at 22C during the dark time.

Twenty-five plants from each of the eight populations, except for the hexaploid population of *I. trifida* (WT 63-70) for which only 15 plants were available, were electrophoresed to ascertain the level of heterogeneity within each accession. Variation was observed between and among populations. Inter- and intra-population crosses were attempted to produce heterozygous individuals. About 750 hand pollinations per population were accomplished in the mornings between 8 to 10 AM. Mature seeds were collected and stored at room temperature. Just before planting, seeds were scarified for 20 min with concentrated H₂SO₄. Twelve to 50 seeds from each cross were used for inheritance studies. A total of 69 of 91 crosses were successful. Polyploid populations showed a high level of incompatibility within and among taxa (inter- and intraspecific). No seeds were obtained from tetraploid or hexaploid populations despite $\approx$ 6000 pollinations.

Electrophoretic assays. Starch gel electrophoresis was performed on crude protein extracts of leaf tissue of 1-month-old seedlings. Extraction procedures, electrophoretic conditions, and staining protocols are described by Reyes (1991).

Genetic model. Allozyme loci were postulated based on the phenotypic variation patterns and segregation ratios obtained in numerous controlled crosses. When an enzyme system was controlled by multiple loci, each locus was identified by assigning to it an abbreviation of the name given by the International Union of Biochemistry and a numerical code. The locus most anodal to the origin was designated as "1," the next "2," etc (for example, *Pgi-1* and *Got-3*). Electrophoretic bands were denoted by their mobility to one commonly occurring band, which was arbitrarily assigned the relative mobility of 1.0. At each locus the fastest migrating (most anodal) allozyme had the alphabetical code "a." Other allozymes at that locus were as-

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Abbreviations: CAT, catalase; EST, esterase; GOT, glutamate oxaloacetate transaminase; MDH, malate dehydrogenase; MNR, menadione reductase; PGI, phosphoglucose isomerase; PGM, phosphoglucosmutase; SAD, shikimate dehydrogenase.

Table 1. Populations of *I. trifida* and *I. batatas* included in isozyme analysis.

Taxonomic species	Accession (no.)	Source	Ploidy	Plants per population
<i>I. trifida</i>	87-6	CIP ^z	2n = 30	25
	87-10	CIP	2n = 30	25
	86-1	Indonesia ^y	2n = 30	25
	WT 1-36	Mexico ^y	2n = 30	25
	WT 37-62	Mexico ^y	2n = 60	25
	WT 63-70	Mexico ^y	2n = 90	15
<i>I. batatas</i>	W-99	USDA ^x	2n = 90	25
	W-109	USDA	2n = 90	25

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signed codes in alphabetical order relative to their position of migration in the starch gel. Number of phenotypes was determined for each enzyme in every level of ploidy.

Data analysis. Genetic interpretations of allozyme loci were based on phenotypic variation patterns within and among populations. Segregation ratios obtained in numerous controlled crosses among the diploid populations were tested by χ^2 goodness of fit to expected Mendelian ratios. The results obtained from diploid species were used to infer the genetic basis of these enzymes not only at the diploid level but also in polyploid series.

Results

In a preliminary experiment, 20 enzymes were assayed. Seven presented clear consistent isozyme bands: CAT, GOT, MDH, MNR, PGI, PGM, and SAD. All subsequent studies were focused on these enzymes systems. Other enzymes, besides the seven mentioned above, did provide banded phenotypes but were not clear enough for scoring. Five more presented no acceptable level of resolution.

A graphic summary of all observed isozyme zymograms for the systems resolved are presented in Figs. 1 and 2. Differences in phenotypes within and among levels of ploidy were detected. Thirteen loci specifying 25 alleles were identified. An average

of 1.9 alleles per locus was calculated including the monomorphic ones. Polymorphism was detected for seven isozymes with a mean of 2.7 alleles per locus. Table 2 shows the number of alleles per locus by ploidy level for both polymorphic and monomorphic loci.

Monomorphic enzymes. Very good resolution was obtained for CAT in all populations. A similar pattern was shown for diploid and polyploid populations; however, no polymorphism was detected (Fig. 2).

Polymorphic enzymes. Genetic interpretation of alleles detected for polymorphic enzymes are presented graphically in Fig. 1 (PGI, PGM, MNR, and SAD) and Fig. 2 (GOT, MDH, and EST). Mendelian segregation was confirmed from the crosses performed within and among diploid populations. All isozymes followed Mendelian inheritance patterns except at the *Mdh-2* locus (probabilities associated with χ^2 not shown).

GOT. Three zones of activity were detected in GOT zymograms. The zone close to the anode, GOT-1, presented three alleles among populations. *Got-1a* corresponded to the most anodal migrating allozyme. *Got-1b* and *Got-1c* refer to slower migrating alleles. GOT-2, the intermediate locus, presented variation for *Got-2a* and *Got-2b* in the eight populations assayed (Fig. 2). The most cathodal area of activity, GOT-3, presented no variation with the lowest intensity in staining.

GOT is known to be a dimeric protein (Crawford and Wilson 1979; Suiter, 1988). Interlocus dimerization between the gene products of GOT-1, GOT-2, and GOT-3 was absent. Gene segregation data for *Got-1* and *Got-2* conformed to expected Mendelian ratios. Such a segregation pattern was consistent with the interpretation that these isozymes are specified by single genes (*Got-1* and *Got-2*). A three-banded pattern was seen in the hybrid progeny of crosses between plants carrying electrophoretically variant GOT-1 and GOT-2 isoenzymes, confirming the interpretation of the dimeric nature of this enzyme (Table 3).

MDH. MDH patterns were complex. Three zones of act MDH-1, MDH-2, and MDH-3, were detected in the starch MDH-1 was invariant in all individuals electrophoresed, with a constant double-pattern banding (Rf 1.0 and 0.91, respectively). No segregation was obtained when crosses were made using heterozygous plants (two bands). We considered this second band to be an artifact, perhaps due to post-translation modifi-

Fig. 1. Graphic representation and genetic interpretation of alleles detected for PGI, PGM, MNR, and SAD enzyme systems in *Ipomoea* species. All enzymes migrated anodally. The last column in each enzyme represents a heterozygous individual.

Fig. 2. Graphic representation and genetic interpretation of alleles detected in GOT, MDH, EST, and CAT enzyme systems in *Ipomoea* species. Enzymes migrated anodally. Dashed lines (EST) represent missing bands. Heterozygous phenotypes are represented in the last column for each enzyme.

Table 2. Number of alleles among levels of ploidy for *I. trifida* and *I. batatas* species for seven enzymes.

Locus	Total no. of alleles observed	No. of alleles observed				No. of shared alleles
		2x ^z	4x ^z	6x ^z	SP ^y	
<i>Cat-1</i>	1	1	1	1	1	1
<i>Got-1</i>	3	3	3	2	2	2
<i>Got-2</i>	2	2	1	1	2	1
<i>Got-3</i>	1	1	1	1	1	1
<i>Mdh-1</i>	1	1	1	1	1	1
<i>Mdh-2</i>	3	3	3	3	3	3
<i>Mdh-3</i>	1	1	1	1	1	1
<i>Mnr-1</i>	2	1	2	2	2	1
<i>Pgi-1</i>	1	1	1	1	1	1
<i>Pgi-2</i>	4	4	4	4	4	4
<i>Pgm-1</i>	1	1	1	1	1	1
<i>Pgm-2</i>	3	3	3	2	2	2
<i>Sad-1</i>	2	2	2	2	2	2
Total	25	24	24	22	23	21

^zPolyploid series of *I. trifida*.

^ySweetpotato (6x).

cation. A similar pattern was observed in *Prunus* (Byrne and Littleton, 1988). Band intensity in the last anodal region was also invariant. It was designated MDH-3 (Rf. 0.14).

The intermediate zone of activity for MDH consisted of one strong band, similar to that in MDH-1, always present in every individual scored (Rf. 0.71). This band shares some variants that were named *a* and *c*. The strong band was identified as predominant allele *b* (Fig. 2). Progenies from crosses among diploid individuals had confusing banding patterns, with one of these crosses not following Mendelian ratios (Table 3). The results gave no indication of the subunit structure of this enzyme in *Ipomoea* spp. MDH has been reported as a dimeric enzyme in many species. It has been shown to be encoded by three or four loci with subcellular activity (Chaparro et al., 1989; Gottlieb, 1982a).

MNR. Zymograms for MNR enzyme revealed only one zone of activity. Locus *Mnr-1* revealed polymorphism among polyploid populations. An invariant band was always observed in

diploid populations. In polyploids, three phenotypes, identified as MNR-1aa, MNR-1ab, and MNR-1bb were observed. Because of the great difficulty of obtaining seeds from crosses among polyploid populations, no segregation patterns were obtained to test the hypothesis of a monomeric enzyme. The monomeric nature of MNR-1 isoenzyme has been reported in other plant species such as potato (*Solanum tuberosum*) (Douches and Quiros, 1988) and maize (*Zea mays* L.) (Wendel et al., 1988).

PGI. Five electrophoretic phenotypes of PGI were present in the populations of *Ipomoea*. All individuals had one common area, designated PGI-1, with the same or a closely similar electrophoretic mobility in the most anodal position. Very close to this region appeared the PGI-2 isozymic area, which behaved as a dimer controlled by gene locus *Pgi-2*. This gene presented four variant alleles (a,b,c,d) among populations. The Indonesian population carries the fourth allele (d) at the *Pgi-2* locus. A minimum of three alleles was present in each population. The most common alleles were *Pgi-2b* and *Pgi-2c*.

Segregation data for PGI-2 supported monogenic inheritance (Table 3). A three-banded pattern for heterozygous individuals was detected when homozygous parents were crossed, which is consistent with the assumption of a dimeric structure for this enzyme.

PGI showed two or four bands spaced 0.5 cm apart in the region of PGI-2. The most anodal variant seemed to be very close or comigrating with the monomorphic variant of *Pgi-1*.

The *Pgi-2* locus displayed up to five bands in the phenotypes of a few individuals in the polyploid series, corresponding to banding positions of alleles detected in diploid species and their heterodimers. This pattern suggested that all observed alleles in the diploid populations were expressed in polyploid species. Similar results have been reported in polyploid series of other species (Cai and Chinnappa, 1989; Vorsa et al., 1988). Crosses among these individuals were unsuccessful and no segregation data were available.

Two isozymes are usually reported for PGI in diploid plant species, one specific to the plastid and the other cytosolic (Bayer and Crawford, 1986; Gottlieb, 1982a). No intergenic bands were present for this enzyme in the populations analyzed. PGI-1 and PGI-2 seem to be controlled by nuclear genes *Pgi-1* and *Pgi-2*,

Table 3. Representative progenies illustrating the genetic control of eight isozymic loci in diploid species of *I. trifida*.

Locus	Cross	Plants (no.)	Expected ratio	Observed ratio	X ²	df
<i>Got-1</i>	bc x bc	12	1:2:1	2:8:2	1.32	2
	aa x ac	10	1:1	4:6	0.40	1
	ab x aa	12	1:1	5:6	0.16	1
	ab x bb	17	1:1	9:8	0.06	1
	aa x bb	13	---	100% ab	---	---
	aa x cc	12	---	100% ac	---	---
<i>Got-2</i>	bb x cc	9	---	100% bc	---	---
	ab x aa	15	1:1	8:7	0.06	1
	ab x bb	17	1:1	9:8	0.06	1
<i>Mdh-2</i>	aa x bb	8	---	100% ab	---	---
	ab x bc	24	1:1:1:1	14:0:0:10	25.26**	3
	bc x bb	21	1:1	11:10	0.05	1
<i>Mnr-1</i>	ab x bb	22	1:1	10:12	0.18	1
	bb x bb	19	---	100% bb	---	---
<i>Cat-1</i>	aa x aa	12	---	100% aa	---	---
<i>Pgi-2</i>	bc x ac	24	1:1:1:1	4:7:8:4	2.16	3
	ab x cd	22	1:1:1:1	6:5:5:5	0.18	3
	ab x bc	40	1:1:1:1	7:9:8:16	5.00	3
	bc x bc	43	1:2:1	10:21:12	0.21	2
	aa x bc	16	1:1	9:7	0.25	1
	bc x cc	12	1:1	8:3	2.16	1
	cc x cd	18	1:1	9:9	0.00	1
	aa x bb	12	---	100% ab	---	---
	bb x cc	12	---	100% bc	---	---
	ac x ab	21	1:1:1:1	6:6:5:4	0.52	3
<i>Pgm-2</i>	ab x bc	27	1:1:1:1	10:5:7:5	2.47	3
	ac x bc	32	1:1:1:1	5:10:8:9	1.75	3
	ac x ac	20	1:2:1	6:10:4	0.40	2
	ab x ab	24	1:2:1	5:11:8	1.66	2
	aa x bc	22	1:1	9:13	0.73	1
	ab x bb	10	1:1	7:3	1.60	1
	aa x bb	6	---	100% ab	---	---
	aa x cc	15	---	100% ac	---	---
<i>Sad-1</i>	ab x ab	21	1:2:1	6:11:4	0.43	2
	ab x bb	18	1:1	8:10	0.22	1
	aa x bb	18	---	100% ab	---	---
	aa x aa	18	---	100% aa	---	---

**Significance level at 1% for deviation from expected ratio.

respectively. This result is concordant with previous findings in other crops (Schnarrenberger and Oeser, 1974; Schnarrenberger et al., 1975; Tanksley and Rick, 1980). PGI-2 was the most polymorphic isozyme studied. An average of 3.5 alleles per population was calculated, corresponding to 25% of the total polymorphism observed in *I. trifida* (polyploid series) and *I. batatas*.

PGM. Two zones of activity were detected in all plants studied. The fast migrating zone, PGM-1, was invariant for two strongly staining bands in diploid, tetraploid, and hexaploid accessions. We believe this reflects the presence of duplicated loci, similar to that found in *Layia* by Warnick and Gottlieb (1985), *Gossypium* (Suiter, 1988), and *Lotus* (Raelson and Grant, 1989).

The more cathodal locus, in the area of PGM-2, exhibited three variant alleles among diploid and polyploid populations. Heterozygous individuals displayed two bands of activity for the locus *Pgm-2*. Segregation data from backcrosses and crosses between heterozygous parents suggested that PGM-1 and PGM-2 were the products of two different single genes (Table 3).

Three banding patterns for the *Pgm-2* locus were observed among hexaploid populations, perhaps corresponding to three

different alleles. Differences in staining intensity also were detected. These two observations were interpreted as a gene dosage effect, with individuals having all copies of alleles and all of them being expressed. Failure to obtain seeds from polyploid populations precluded further testing of this hypothesis. Similar results were reported for other polyploid species (Ness et al., 1989; Soltis and Rieseberg, 1986).

SAD. Single banded patterns of enzymes of SAD have been reported in a variety of plants (Gastony and Gottlieb, 1985; Millar, 1985). Double-banded allozymes of SAD have also been reported in several plant taxa (Harry, 1986; Tanksley, 1984). The gels stained for SAD enzyme in this study exhibited a single zone of activity. Crosses among homozygous individuals bearing *a* and *b* variants produced heterozygous progeny expressing parental bands. These observations suggest that a single locus governs SAD in the *Ipomoeas* studied. Segregation ratios in progenies of available crosses were consistent with the interpretation that this is specified by a single gene, *Sad-1*, that codes for a functional monomeric protein (Table 3).

Esterase (EST; EC 3.1.1.1) At least three zones of activity were seen after electrophoresis of the enzyme; however, no clear phenotypes were established for this enzyme, probably due

to the low penetrance of the bands in these areas. The electrophoretic variants were not genetically interpretable.

To acquire additional information for EST enzymes, a procedure used for maize was attempted (Stuber et al., 1988). Locus *Est-8* is evident in gels stained for GOT when β -naphthylacetate is added to the GOT staining solution. Two areas of activity were stained in the GOT gels. EST-1 localized in the most anodal region (Rf. 1.2) and EST-3 (Rf. 0.68) shared the staining area of GOT-2. Each locus showed a single banding pattern with no segregation. No information about the structure of the protein was possible (Fig. 2).

Polyploid series. All diploid populations were monomorphic for the same alleles at seven of 13 genes examined: *Pgm-1*, *Pgi-1*, *Got-3*, *Cat-1*, *Mdh-1*, *Mdh-3*, and *Mnr-1*. The population from Indonesia (86-1) was the most distinct as it showed two different alleles in addition to the previous detected in *Pgi-2* and *Got-1*. The *I. trifida* polyploid series (4x and 6x) was monomorphic for the same set of isozymes except for the *Mnr-1* gene, with all individuals from all populations possessing enzyme bands with identical mobility.

The polyploid series of *I. trifida* as well as *I. batatas* displayed a banding pattern identical to the respective diploid relative for GOT, SAD, MNR, and MDH enzymes. One and two bands were observed for monomeric enzymes in homozygous and hybrid individuals, respectively. In the case of dimeric enzymes, one and three bands were detected in tetraploid and hexaploid plants, respectively.

Polyploid *I. trifida* (4x and 6x) shared 24 and 23 alleles, respectively, of 25 present among populations. A high degree of similarity between *I. batatas* and *I. trifida* was also observed with 24 alleles common among these taxa (Table 2).

Discussion

All populations studied exhibited genetic similarity. The three cytotypes appear to possess the same enzyme bands at all monomorphic loci and possess very similar arrays of allozymes at all polymorphic loci (Table 2).

Electrophoretic data on 13 enzyme loci from eight populations of *I. trifida* and *I. batatas* showed that six loci (*Pgi-1*, *Pgm-1*, *Got-3*, *Cat-1*, *Mdh-1*, and *Mdh-3*) were invariant for all populations. *Mnr-1* varied among but not within level of ploidy, and the other six (*Pgm-2*, *Pgi-2*, *Got-1*, *Got-2*, *Sad-1*, and *Mdh-2*) showed intra- and interspecific variation. For loci that were invariant within the diploids, the polyploid series uniformly expressed the same alleles as were fixed in the diploids. However, the loci that were variable in the diploids were also variable in tetraploid and hexaploid populations. This pattern of variation in the polyploids for loci that are also variable in their diploid progenitors is almost certainly a result of repeated allopolyploidizations involving diploid pairs of different genotypes (Werth et al., 1985).

Electrophoretic banding pattern of *I. trifida* and *I. batatas* leaf extracts exhibited the presence of duplicate genes for PGM-1. The multiple isozyme bands observed for PGI-2 in polyploid series are probably the result of an ancient polyploid event. The patterns of variation for these enzymes are suggestive of the kind of enzyme variation found in polyploid series (Gottlieb, 1982b); but, many other enzyme systems studied displayed typical diploid isozyme patterns.

Heterozygous polyploid phenotypes were in most cases two-banded for monomeric proteins (SAD) and three banded for dimeric proteins (PGI, GOT, and MDH). This behavior among

polyploid series has been reported for allopolyploid species (Werth et al., 1985). However, no segregation patterns were obtained from polyploid plants to confirm this observation. The differences in electrophoretic staining intensities between ploidies in these enzymes suggest that subunit interactions for these enzymes are additive and presumably result from the equal expression of genes coding for different allelic forms. Actual protein levels may be regulated, however, so that only the diploid level is maintained in the cell (Danzmann and Bogart, 1982).

The presence of two invariant bands in PGM-1 isozyme for individuals electrophoresed among different levels of ploidy was interpreted as possible evidence for fixed heterozygosity in these populations. Fixed heterozygosity has been pointed out as evidence of an allopolyploid event in several species (Roose and Gottlieb, 1976). According to Gottlieb (1981), the presence of a fixed heterozygous phenotype in a polyploid is a direct consequence of its mode of origin either from chromosome doubling in a single individual or fertilization involving unreduced gametes. Unreduced pollen in tetraploid *Ipomoea* species has been observed (Jones, 1990). This observation supports the idea of unreduced gametes as a natural mechanism for raising 4x to 6x following pollination of 2x ovules with unreduced pollen (4x).

Crawford (1985) stressed the value of isozyme data for documenting the origin of hybrid plants. He stated that the most desirable situation is that the two taxa under consideration each be monomorphic for mutually exclusive alleles at some locus and that both of these alleles be found within populations of the derived species. One of the criteria in this analysis is based on that concept. We found that MNR-1a was monomorphic in all populations of *I. trifida* and also in the polyploid series. However, a new variant, MNR-1b, observed only in polyploids, was detected. This difference could be due to the accumulation of a new allele in the polyploid cytotypes from another species closely related to sweetpotato.

The presence of heterozygous individuals exhibiting asymmetrical banding intensities in PGM-2 and PGI-2 was interpreted as a gene duplication among polyploid series. The existence of asymmetrical banding intensities may be due to different dosages of alleles in the same locus. During the scoring of hexaploid populations, a few individuals showed multiple alleles at the monomeric *Pgm-2* locus. This observation suggested gene duplication in *I. batatas* due to the presence of at least two species very similar in constitution; however, other possible mechanisms, such as fixed mutations, could also explain these results.

The apparent diploid patterns of many of the enzymes resolved in this study, and the polyploid patterns of some of them, may be explained by polyploidization followed by the loss of duplicate gene expression (Allendorf, 1979; Haufler and Sweeney, 1989). Similar events have been proposed for the allotetraploid AD genome of *Gossypium* (Suiter, 1988).

The electrophoretic results of this study give some support to the previous hypothesis that *I. trifida* may be one of the ancestors of *I. batatas* (Austin, 1988). The data were consistent with the cytogenetic evidence in this regard. Polyploid series exhibit a high degree of homology, but differ by small structural changes (B1 and B2 genomes) in *I. batatas* (Shiotani, 1988). The data support the hypothesis that a possible segmental allopolyploidy mechanism may be present in this polyploid series with parents phylogenetically close and with *I. trifida* being the prime candidate. However, other species cannot be ruled out without further analyses.

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