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Allozyme Variability and Pbylogenetic Relationships in the Cultivated Potato (*Solanum tuberosum)* and Related Species

By

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Abstract: Gene frequencies at 13 isozyme loci were determined in three South American taxa of cultivated potatoes [the diploid group (gp.) Stenotomum, the diploid subgroups (subgp.) Goniocalyx, and the tetraploid gp. Andigena of S. ***tuberosum],*** in the diploid weed species S. ***sparsipilum,*** and in most of the main cultivars now raised in the Northern Hemisphere (the tetraploid gp. Tuberosum of S. ***tuberosum).*** High levels of genetic variability (mean number of alleles per locus, percentage of polymorphic loci, and mean heterozygosity) were detected, being higher in tetraploid potatoes. An equilibrium among the evolutionary factors which increase genetic variability and artificial selection for maximum yield would explain the high uniformity of heterozygosity values we observed in both Andigena (0.36 ± 0.02) and Tuberosum (0.38 ± 0.01) cultivars. -The low value of genetic distance (D = 0.044) between Stenotomum and Goniocalyx does not support the status of species for S. *goniocalyx.* – In most isozyme loci, the electromorphs of gp. Andigena were a combination of those found in both gp. Stenotomum and S. ***sparsipilum,*** suggesting an amphidiploid origin of gp. Andigena from that two diploid taxa. The presence in Andigena of unique electromorphs, which were lacking in both gp. Stenotomum and S. ***sparsipilum,*** suggests that other diploid species could be also implied in the origin of tetraploid Andean potatoes. Furthermore, since Andigena were more related to Stenotomum (D = 0.052) than to S. ***sparsipilum*** (D = 0.241), the autopolyploidization of Stenotomum individuals and the subsequent hybridization with gp. Andigena may also have occurred. Thus, our study suggests a multiple origin (amphidiploidy, autoploidy, and hybridization at tetraploid level) of gp. Andigena. – Most of the electromorphs of gp. Tuberosum were also found in gp. Andigena; both the direct derivation of that group from the Andean tetraploid potatoes and the repeated introgression provided by breeding programmes could explain this result. However, the allele c of Pgm-B, present in 30 out of 76 Tuberosum cultivars from Northern Hemisphere as well as in 3 Chilean Tuberosum cultivars, lacks in the 258 Andigena genotypes sampled, suggesting

that Chilean germplasm could have taken part in the origin of at least the 39% of the potato cultivars from Europe and North America analyzed here. -The distance WAGNER procedure provides an estimate of a 30% of heterogeneity in the evolutionary divergence shown by different groups of cultivated potatoes. Diploid groups show a higher (22.5%) evolutionary rate than tetraploids, which can be attributed to both tetrasomic inheritance and facultative autofecundation that exists in Andigena and Tuberosum groups. Thus, artificial selection acting since 10 000 years has not resulted in a higher rate of molecular evolution at the isozyme level in the tetraploids.

Despite the large series of historical, biogeographical, morphological, cytogenetical and biochemical studies which have been carried out on *Solanum* subsect. *Potatoe* D'ARCY (see SWAMINATHAN & MAGOON 1961, HOWARD 1970, 1978, UGENT 1970, HAWKES 1978a, b for revisions), a wide controversy still remains about the origin, the geographical distribution, and the phylogenetic relationships of the different taxa of cultivated potatoes *(Solanum tuberosum* L.), reflected in the different systematic classifications of the species. Here we use the terminology of DODDS (1962), which appears to conform closely with the conclusions of the present study.

The complex pattern of genetic variability, in addition to the high degree of phenotypic plasticity, makes it difficult to study biosystematic relationships among potatoes. A number of studies dealing with morphology and chemotaxonomy attempted to resolve this question. The basic problem with most of these traits is the lack of equivalence between phenotype and genotype due to complications introduced by varying heritability, dominance, epistasis, and pleiotropy. Cytogenetic analyses were also used in phylogenetic studies on potatoes. However, since most diploid potato species hybridize readily and produce fertile F l's, genome differentiation seems to have not progressed very far (HAWKES 1978b), thus rendering cytological studies inconclusive in revealing the phylogenetic history (SWAMINATHAN & MAGOON 1961).

Isozymes have been succesfully used in the analysis of animal and plant populations, including some solanaceous groups (RICK & FOBES 1975, RICK & al. 1977, WHALEN 1979, MCLEOD & al. 1983). In order to estimate the genetic variability in potatoes, we have undertaken an electrophoretic analysis of several genetically controlled enzyme systems in the most important cultivated groups of *S. tuberosum* as well as in one of the most related wild species, S. *sparsipilum.* Gene frequencies at 13 isozyme loci were used to trace the phylogenetic relationships among these taxa of potatoes.

Material and Methods

Collections. The cultivated potato *S. tuberosum* L. (group Stenotomum including the subgroup Goniocalyx group Andigena, and group Tuberosum) and

the diploid weed S. *sparsipilum* (BITT.) Juz. et BUK. were analyzed. The collections were of three kinds. The material received from Centro Internacional de la Papa (Lima, Peru) was composed of seeds obtained from different cultivated varieties (Table 1). The material from the Inter-Regional Potato Introduction Station, Sturgeon Bay (Wisconsin) consisted of tuber families (Table 1). With respect to group Tuberosum we analyzed tubers of 76 cultivars from the Northern Hemisphere (listed in MARTINEZ ZAPATER & OLIVER 1984 a) including those of most agronomic interest in Europe and North America, derived from different sources (Estacion de Mejora de la Patata, Vitoria, Spain; Instituto Nacional de Semillas y Plantas de Vivero, Madrid, Spain; Government Institute for Research on Varieties of Cultivated Plants, Wageningen, Holland). In addition, we also analyzed plantlets derived from seeds of 8 Tuberosum cultivars from Chile (Universidad Austral de Chile, Valdivia; see Table 3). Both tubers and seeds were grown in standard conditions in the greenhouse.

We included also *S. pinnatisectum* DUN. in the study (Table 1) because this species is also in the section *Petota* of the genus *Solanum*, but is not especially closely related; it thus serves as an "outgroup" in tree construction.

Electrophoretic Methods. Four organs of the plant were analyzed: young and mature leaves, tubers, and shoots. Enzyme extraction procedures and horizontal starch gel electrophoresis conditions were as described previously by OLIVER & al. (1983). Samples of cv. 'Desiree' were included in all the slab gels as internal markers to determine the electrophoretic mobilities of the different allozyme bands.

Different gel slices were assayed for 10 consistently scorable enzymes: Esterases (EST, E.C. 3.1.1. 1), Alcohol dehydrogenase (ADH, E.C. 1.1.1.1), Glutamate oxaloacetate transaminase (GOT, E.C. 2.6.1.1), Phosphoglucose isomerase (PGI, E.C. 5.3.1.9), Phosphoglucomutase (PGM, E.C. 2.7.5.1), Peroxidases (POX, E.C. 1.11.1.7), Malic enzyme (Me, E.C. 1.1.1.40), Glutamate dehydrogenase (GDH, E.C. 1.4.1.3), Malate dehydrogenase (MDH, E.C. 1.1.1.37), and 6-Phosphogluconate dehydrogenase (PGD, E.C. 1.1.1.43). For most enzymes standard staining methods (BREWER 1970, SHAW & PRASAD 1970) were used; detailed references will be found elsewhere (OLIVER & al. 1983, MARTÍNEZ ZAPATER & OLIVER 1984 b).

Estimation of Gene Frequencies. A computer program for general maximum likelihood estimation (MAXLIK) written by T. E. REED, University of Toronto, was used to estimate gene frequencies for each locus. In those accesions of gp. Stenotomum and Andigena grown from seeds (Table 1), we directly computed electromorph frequencies in each accession; the genotypes found in the remaining accessions, composed by tuber families (Table 1), were pooled by taxa before computing electromorph frequencies. The 76 cultivars of gp. Tuberosum from Northern Hemisphere were used as a whole to estimate gene frequencies in this group. Owing to reasons which we shall see below, the sample of gp. Tuberosum from Chile was only analyzed for the Pgm-B locus; gene frequencies at other isozyme loci were not computed and, therefore, Chilean Tuberosum was not used in computing variability measures, genetic distances of phylogenetic trees. In the tetraploid taxa analyzed here, isozyme loci were expressed in duplicate, originating asymmetrical banding intensities in the heterozygotes due to gene dosage effects (MARTÍNEZ ZAPATER & OLIVER 1984 b; see also OLIVER & al. 1983 for details about the criteria employed in the determination of duplicate expression of isozyme loci); these asymmetrical bands can be readily detected on the gels, allowing us to compute allelic frequencies in the duplicated loci of tetraploids.

Table 1. Accessions of different *Solanum* taxa analyzed in this study. The origin and type of material received (tuber families or seeds) are indicated

Taxon (1)	Accession (2)	Country of collection	Collector or donor number (3)	Material received
STN	C.I.P. 702979	Peru-Junin	–	seeds
STN	C.I.P. 701243	Peru-La Libertad		seeds
STN	C.I.P. 703225	Peru-Pun0	–	seeds
STN	C.I.P. 701503	Peru-Junin		seeds
STN	C.I.P. 702249	Peru-Ayacucho		seeds
STN	C.I.P. 702505	Peru-Cuzco	–	seeds
STN	U.S.D.A. 205526	Peru	CPC 1839	tubers
STN	U.S.D.A. 205527	Peru	CPC 1782	tubers
STN	U.S.D.A. 234007	Bolivia	CAN 29	tubers
STN	U.S.D.A. 234008	Bolivia	GAN 30	tubers
STN	U.S.D.A. 234009	Bolivia	GAN 56	tubers
GON	U.S.D.A. 195188	Peru	CPC 1514	tubers
GON	U.S.D.A. 195214	Peru	CPC 1793	tubers
GON	U.S.D.A. 230512	Peru	OCH 1922	tubers
SPL	U.S.D.A. 246536	Peru	COR P23 1	tubers
SPL	U.S.D.A. 275153	Peru	HJE 1534	tubers
SPL	U.S.D.A. 365343	–	–	tubers
ADG	C.I.P. 702499	Peru-Cuzco	–	seeds
ADG	C.I.P. 701815	Peru-Huanuco	–	seeds
ADG	C.I.P. 702844	Peru-Pun0	–	seeds
ADG	C.I.P. 702300	Bolivia-La Paz		seeds
ADG	C.I.P. 702573	Bolivia-Potosi	–	seeds
ADG	U.S.D.A. 230499	Peru	OCH 1226	tubers
ADG	U.S.D.A. 233985	Bolivia	GAN 12	tubers
ADG	U.S.D.A. 233990	Bolivia	GAN41	tubers
ADG	U.S.D.A. 233993	Bolivia	GAN 26	tubers
ADG	U.S.D.A. 233999	Bolivia	GAN 37	tubers
ADG	U.S.D.A. 243362	Colombia	CCC 8	tubers
ADG	U.S.D.A. 243369	Colombia	ccc 37	tubers
ADG	U.S.D.A. 243372	Colombia	ccc 44	tubers
ADG	U.S.D.A. 243375	Colombia	CCC 52	tubers
ADG	U.S.D.A. 243378	Colombia	ccc 59	tubers
PNT	U.S.D.A. 275231	Mexico	HAW 1426	tubers
PNT	U.S.D.A. 275232	Mexico	HAW 1435	tubers
PNT	U.S.D.A. 275233	Mexico	HAW 1455	tubers

(1) Abbreviations of potato names (SIMMONDS 1963): STN = S. *tuberosum* (Group Stenotomum); GON = S. *tuberosum* (Subgroup Goniocalyx); ADG = S. *tuberosum* (Group Andigena); SPL = S. *sparsipilum;* PNT = S. *pinnatisectum;* TBR = S. *tuberosum* (Group Tuberosum) from Northern Hemisphere. – (2) C.I.P. = Centro Internacional de la Papa, Lima, Peru; U.S.D.A. = United States. Department of Agriculture. Inter-Regional Potato Introduction Station, Sturgeon Bay, Wisconsin, U.S.A. – (3) CCC = Coleccion Central Colombiana; COR = Correll, D.S.; CPC = Commonwealth Potato Collection; GAN = Gandarillas, H.; HAW = Hawkes, J.G.; HJE = Hjerting, J.P.; OCH = Ochoa. C.M.

Genetic Variability Measures and Estimation of Genetic Distances. Average heterozygosity in the different taxa was estimated by the proportion of individuals sampled that are actually heterozygous ("direct-count") in the different loci. Other variability estimates, Prevosti distance (PREVOSTI & al. 1975) and NEI (1978) unbiased genetic distance for all pairwise comparisons were performed with the program BIOSYS-1 (SWOFFORD & SELANDER 1981).

Estimation of Pbylogenetic Trees. We have used the distance WAGNER analysis for the estimation of phylogenetic relationships among different taxa of potatoes. S. *pinnatisectum* was used as an outgroup; the corresponding distance matrix was subjected to the modified distance WAGNER procedure of SWOFFORD (1981) by means of the program WAGPROC, which generates a series of unrooted trees. Different network optimization procedures (averaging method of Swofford, least-squares, L1 approximation, and linear programming) were attempted by means of the program NETOPT; the results were evaluated using several goodness of fit statistics provided by this program.

BIOSYS-1, WAGPROC, and NETOPT were provided by D. L. SWOFFORD & R. B. SELANDER, University of Illinois. All computer programs are written in FORTRAN and were run on a DEC VAX 1 1/780 computer at CC/UAM.

Results

Formal genetic analysis of seed progenies from crosses between tetraploid Tuberosum cultivars were carried out for most of the variable isozymes analyzed here, revealing duplicate expression of isozyme loci, in some of which we have detected tetrasomic inheritance (MARTÍNEZ ZAPATER & OLIVER 1984 b). These analyses and the different patterns of tissue expression (MARTÍNEZ ZAPATER & OLIVER 1984 a, OLIVER & MARTÍNEZ ZAPATER 1984), were the criteria we employed in determining the number of isozyme loci in each enzyme and taxon. Genes were designated by a hyphenated capital letter added to the symbol for each enzyme; the locus coding the isozyme with the most anodal migration was designated A, the next B, and so forth. At each isozyme, the electromorph with the greatest relative mobility was called a, and then b, c, d, etc. The 10 enzyme systems examined showed the same number of isozymes in all of the taxa. Species identification of isozyme and electromorph homologies were based on electrophoretic mobilities. On this basis, all the isozymes show a similar pattern of tissue expression in all taxa of potatoes.

The electromorphs found at 11 variable isozymes in groups Stenotomum, Andigena, and Tuberosum from Northern Hemisphere as well as in S. *sparsipilum* are shown in Table 2. Table 3 shows the accesions of Chilean Tuberosum which were analyzed for Pgm-B locus, the sample size, and the number of plantlets in which the allele c of this locus was detected.

Thirteen out of 25 isozymes revealed by gel electrophoresis were selected to compute electromorph frequencies in the accessions analyzed

Table 2. Electromorphs found at 11 variable isozyme loci in some species, groups, and accessions of potatoes. (*) See legend of Table 1. -(**) Accession U.S.D.A. 243362 of ADG. – (***) Remaining accessions of ADG

Taxon(*)	Adh-A	Est-B	Got-A	Got-B	Mdh-A	Pgd-C
SPL	b	abcd	ab	cd	bc	ab
STN	abc	cd	a	d	b	ab
ADG(**)	bc	d	a	d	b	ab
ADG(***)	abc	abcd	abc	cde	ab	abc
TBR	bc	abcd	ab	cde	ab	abc

Taxon (*)	Pgi-B	Pgm-A	Pgm-B	POX-C	Pox-E
SPL	bc	abc	b	a cd	a
STN	bcd	abc	ab	abcd	ab
ADG (**)	c	a c	b	a	ab
ADG(***)	abcd	abc	b	abcd	ab
TBR	abcd	abc	bc	abcd	a

Table 3. Accessions of group Tuberosum from Chile which were analyzed for Pgm-B locus, sample size, and number of plantlets in which the allele c of this locus was found

Accession No.	Sample size	No. of plantlets with allele c of Pgm-B
UA-1333	17	0
UA-1210	8	0
UA- 1049	7	0
UA-1387	4	1
UA- 1270	5	0
UA- 1047	5	1
UA-1338	12	0
UA-1369	10	1

here. Those isozymes with no clear pattern of tissue expression or poorly resolved on the gels were not taken into account for this subject. The differences in substrate specificity among esterase isozymes are now under study; they also were not used in computing electromorph frequencies. Me-B showed the same electrophoretic mobility in all tested individuals and was considered to be coded by a monomorphic locus. The remaining 12 isozyme loci were variable, although some of them can be monomor-

phic in particular taxa (Tables 4 and 5). Mean number of alleles per locus, percentage of loci polymorphic (0.95 criterion) and heterozygosity averaged for the 13 loci are shown in Table 6.

Prevosti distance and Nei unbiased genetic distance among accesions were computed for all pairwise comparisons and averaged by taxa (Table 7). In inferrying phylogenetic relationships from isozyme data we employed a modified distance Wagner analysis (FARRIS 1972, SWOFFORD 1981) on the Prevosti distance matrix. The tree topology showing the best fit to this distance matrix was obtained through optimization using linear programming, minimizing the weighted F-value (Fig. 1). Since Prevosti distance shows properties of a Manhattan metric, making no assumptions about the rates of evolution (BERLOCHER & BUSH 1982), this tree-constructing method allowed us to test if the rate of evolutionary divergence is homogeneous over phyletic lines. The estimates of divergence, as calculated from the branch lengths of the tree of Fig. 1, are shown in Table 8.

Discussion

Levels of Genetic Variability in Diploid and Tetraploid Potatoes. The levels of genetic variability (mean number of alleles per locus, percentage of polymorphic loci, and mean heterozygosity) revealed by gel electrophoresis in diploid potatoes (Table 6), were similar to those found in other outcrossing diploid plant species (DOBZHANSKY & al., 1977, GOTTLIEB 1981).

All the measures of genetic variability were higher in tetraploid than diploid potatoes (Table 6), which may be due to both gene duplication and hybridization; this result was in agreement with the data obtained in both allopolyploids (ROOSE & GOTTLIEB 1976) and autopolyploids (RALIN & SELANDER 1979, QUIRÓS 1983). The increase in the mean number of alleles per locus showed by the tetraploid potatoes was similar to that found by ROOSE & GOTTLIEB (1976) in allopolyploid species of *Tragopogon*. The greater yield potential showed by tetraploid potatoes as compared with the diploid ones (MENDOZA & HAYNES 1976, MENDIBURU & PELOQUIN 1977), has been attributed to the greater number of alleles per locus possible in the polyploid forms (ROWE 1967). This was in agreement with our observation of a higher number of alleles per locus in Andigena and Tuberosum than in Stenotomum (Table 6).

Heterozygosity showed a two-fold increase in Andigena in respect to Stenotomum (Table 6); it was even higher in Tuberosum, where the 38% of the genome was heterozygous. These values of genic variability are exceptionally high; even so, they seem to be conservative estimates, since most of the other isozymes we have analyzed, but which were not included

Table 4. Electromorph frequencies in accessions of group Stenotomum (STN), subgroup Goniocalyx (GON), and *S.sparsipilum* (SPL). Seed accessions named by the three last numbers of their respective accession number (see second column in Table 1); STP = accessions of tuber families pooled together

	STN							GON	SPL
LOCUS	979	243	225	503	249	505	STP		
Adh-A									
(N)	30	29	25	30	30	30	45	20	24
a	0.07	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
b	0.50	0.64	0.94	0.88	0.68	0.50	0.33	0.82	1.00
c	0.43	0.36	0.06	0.12	0.25	0.50	0.67	0.18	0.00
Gdh-A									
(N)	39	39	25	29	38	33	46	23	27
a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Got-A									
(N)	32	33	27	35	31	31	46	23	26
a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.21
b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.79
c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Got-B									
(N)	32	29	27	35	31	31	46	23	26
a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.79
d	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.21
e	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mdh-A									
(N)	39	40	30	35	36	33	46	23	24
a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.81
c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19
Mdh-D									
(N)	39	40	30	35	36	33	46	23	24
a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pgd-C									
(N	39	40	30	34	38	33	46	23	27
a	0.45	0.00	0.48	0.60	0.78	0.79	0.61	0.54	0.19
b	0.55	1.00	0.52	0.40	0.22	0.21	0.39	0.46	0.81
c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pgi-B									
(N)	35	41	44	36	30	38	46	23	27
a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
b	0.29	0.00	0.09	0.08	0.02	0.38	0.12	0.09	0.76
c	0.53	1.00	0.16	0.42	0.27	0.43	0.57	0.02	0.24
d	0.19	0.00	0.75	0.50	0.72	0.18	0.32	0.89	0.00
e	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pgm-A									
(N)	42	20	30	34	40	27	43	22	25
a	0.00	0.00	0.17	0.37	0.32	0.04	0.00	0.09	0.14
b	0.00	0.00	0.47	0.07	0.00	0.11	0.13	0.02	0.76
c	1.00	1.00	0.37	0.56	0.68	0.85	0.87	0.89	0.10
Pgm-B									
(N)	44	23	30	40	42	33	43	22	25
a	0.00	0.00	0.02	0.01	0.01	0.06	0.00	0.05	0.00
b	1.00	1.00	0.98	0.99	0.99	0.94	1.00	0.95	1.00
c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pox-C									
(N)	29	29	25	29	29	29	43	23	26
a	0.81	0.86	0.96	0.84	0.64	0.62	0.88	0.85	0.13
b	0.10	0.00	0.00	0.02	0.00	0.03	0.03	0.00	0.00
c	0.02	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.83
d	0.07	0.14	0.04	0.14	0.34	0.34	0.08	0.15	0.04
Pox-E									
(N)	35	35	27	34	32	30	46	23	25
a	1.00	1.00	1.00	1.00	1.00	1.00	0.90	0.98	1.00
b	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.02	0.00

Table 5. Elcctromorph frequencies in accessions of groups Andigena (ADG), Tuberosum from Northern Hemisphere (TBR), and S. *pinnatisectum* (PNT). Seed accessions named by the three last numbers of their respective accession number (see second column in Table 1); ADP = accessions of tuber families which were pooled together

	ADG						TBR	PNT
LOCUS	499	815	844	300	573	ADP		
Adh-A								
(N)	32	31	28	31	32	83	76	26
a	0.00	0.01	0.00	0.00	0.02	0.00	0.00	0.00
b	0.73	0.98	0.61	1.00	0.84	0.72	0.95	0.00
c	0.27	0.02	0.39	0.00	0.14	0.28	0.05	1.00
Gdh-A								
(N)	44	42	26	26	21	83	76	24
a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
Got-A								
(N)	37	38	38	36	37	83	75	26
a	0.99	0.99	0.93	1.00	0.86	0.95	0.73	0.94
b	0.01	0.01	0.07	0.00	0.12	0.05	0.27	0.06
c	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
Got-B								
(N)	35	33	35	34	34	83	75	26
a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.38
b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.62
c	0.01	0.02	0.12	0.20	0.18	0.13	0.28	0.00
d	0.99	0.76	0.69	0.77	0.72	0.76	0.71	0.00
e	0.00	0.23	0.19	0.03	0.10	0.11	0.00	0.00
Mdh-A								
(N)	36	54		36	29	81	75	26
a	0.42	0.00	0 %	0.01	0.00	0.13	0.01	0.00
b	0.58	1.00	0.99	0.99	1.00	0.87	0.99	1.00
c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mdh-D								
(N)	36	54	27	36	29	73	75	26
a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
b	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Pgd-C								
(N	44	64	27	37	28	77	74	26
a	0.57	0.59	0.74	0.33	0.57	0.58	0.49	1.00
b	0.28	0.41	0.25	0.49	0.38	0.39	0.48	0.00
c	0.14	0.00	0.01	0.18	0.04	0.03	0.04	0.00
Pgi-B								
(N)	73	87	48	69	60	81		26
a	0.01	0.01	0.02	0.00	0.09	0.00	0 %	0.00
b	0.23	0.31	0.02	0.01	0.35	0.14	0.11	0.00
c	0.51	0.66	0.60	0.70	0.56	0.81	0.84	0.35
d	0.25	0.02	0.36	0.29	0.00	0.05	0.04	0.00
e	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.65
Pgm-A								
(N)	41	44	21	31	24	78	72	26
a	0.02	0.19	0.32	0.00	0.15	0.27	0.24	0.00
b	0.52	0.31	0.27	0.25	0.23	0.12	0.25	1.00
c	0.46	0.50	0.40	0.75	0.63	0.61	0.51	0.00
Pgm-B								
(N)	44	46	26	32	32	78	76	26
a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
b	1.00	1.00	1.00	1.00	1.00	1.00	0.87	1.00
c	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00
Pox-C								
(N)	30	29	27	28	30	74	75	23
a	0.69	0.56	0.22	0.83	0.56	0.68	0.81	1.00
b	0.00	0.00	0.03	0.02	0.00	0.01	0.06	0.00
c	0.00	0.00	0.08	0.12	0.12	0.10	0.07	0.00
d	0.31	0.44	0.67	0.04	0.33	0.21	0.06	0.00
Pox-E								
(N)	35	33	28	33	34	82	75	23
a	1.00	1.00	0.91	1.00	0.88	0.97	1.00	0.37
b	0.00	0.00	0.09	0.00	0.13	0.03	0.00	0.63

Table 6. Several measures of genetic variability in different taxa of *Solanum* (standard errors in parentheses). (*) See legend of Table 1.—(**) A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95

Taxon(*)	Mean sample size per locus	Mean No. of alleles per locus	Percentage of loci polymorphic(**)	Mean heterozygosity (direct-count)
PNT	25.4 (0.3)	1.4 (0.1)	38.5	0.09 (0.04)
SPL	25.6 (0.3)	1.7 (0.2)	53.8	0.14 (0.04)
STN	34.8 (2.0)	1.6 (0.1)	35.2	0.16 (0.02)
GON	22.6 (0.2)	1.7 (0.2)	38.5	0.14 (0.07)
ADG	43.5 (8.4)	2.1 (0.1)	50.0	0.36 (0.02)
TBR	75.1 (0.3)	2.2 (0.3)	53.8	0.38 (0.01)

in computing these figures, were also variable. Thus, the claims on a lack of genetic variability in gp. Tuberosum, due to the small amount of basic material from which most varieties have been bred (see, for example, SIMMONDS 1962) were not supported by molecular data.

Our observations were in agreement with previous reports (SWAMINATHAN & MAGOON 1961, UGENT 1970, LANDEO & HANNEMAN 1982) about the complex pattern of variability at morphological and physiological levels in cultivated potatoes. These high levels of genetic variability may be due to the interaction of several evolutionary factors: (1) natural and artificial selection acting from 10 000 years ago (HAWKES 1978 b); (2) sexual polyploidization, allowing transmission of heterozygosity of the diploid parents to the polyploids (IWANAGA & PELOQUIN 1982); (3) introgression from the related wild or weedy species (UGENT 1970, HAWKES 1978 b) via 2 n gametes (IWANAGA & PELOQUIN 1982); and (4) the dual system of reproduction (sexual and asexual) available to them (HAWKES 1978b).

Since heterozygosity at each cultivar showed a high uniformity in both Andigena (0.36 ± 0.02) and Tuberosum (0.38 ± 0.01), an optimum level of genetic variability seems to exist in tetraploid potatoes. SANFORD & HANNEMAN (1982) have postulated the existence in potatoes of a heterotic threshold, beyond which more heterozygosity does not result in more yield. If so, an equilibrium among the evolutionary factors which increases genetic variability (see above) and artificial selection for maximum yield would result in similar levels of heterozygosity at each potato cultivar.

Genetic Differentiation at the Diploid Level. S. *pinnatisectum*, the species we have used as an "outgroup" in tree construction, was clearly

differentiated from series *Tuberosa* RYDB. (Table 7); the averaged Nei unbiased genetic distance between S. ***pinnatisectum*** (series ***Pinnatisecta*** RYDB.) and the remaining taxa (series ***Tuberosu)*** was 0.642.

The distance between gp. Stenotomum and S. ***sparsipilum (0.325)*** is similar to the averaged figure of 0.40 found for pair of outcrossing diploid plant species (GOTTLIEB 1981). However, the genetic distance between group Stenotomum and Subgroup Goniocalyx (0.044) is very closed to the mean value found among accesions of Stenotomum (0.048). Thus, isozyme data does not support the status of species proposed for S. *goniocalyx* Juz. et BuK., being however in agreement with the view of DODDS & PAXMAN (1962). The production of fertile hybrids (DODDS & PAXMAN 1962) and the high chromosomal similarity between Stenotomum and Goniocalyx (HAWKES 1978 b) ruled out the possibility of that quantum speciation may be in the origin of both forms. Noteworthy, HAWKES (pers. comm.) has recently completed a morpho-numerical study, from which it also appears that S. ***goniocalyx*** should be included within S. ***stenotomum.***

Table 7 also shows that the genetic distances of S. ***sparsipilum*** with the tetraploid potatoes (0.214 in average) are lower than with the diploid ones (0.336 in average), which may be due to the participation of S. ***sparsipilum*** in the origin of tetraploid cultivars (see below).

Origin of S. tuberosum gp. Andigena. Autoploidy from Stenotomum (HAWKES 1956), intervarietal autoploidy (STEBBINS 1957), segmental allopolyploidy (MATSUBAYASHI 1960), or amphidiploidy from Stenotomum and S. ***sparsipilum*** (HAWKES 1967, HOWARD 1973; but see WOODCOCK & HOWARD 1975) and from Stenotomum and S. *vernei* (BRÜCHER 1964), have been suggested to be implied in the origin of gp. Andigena of S. ***tuberosum.***

In most isozyme loci, the electromorphs observed in the gp. Andigena were a combination of those found in gp. Stenotomum and S. ***sparsipilum*** (Table 2). This is particularly evident in Est-B, Got-A, and Got-B. In the gp. Andigena, the electromorph in highest frequency at each of its loci was also the one in highest frequency in one or both of the other taxa (Tables 4 and 5). This suggests an amphidiploid origin for most accesions of Andigena from Stenotomum and S. ***sparsipilum.*** In a recent study, HAWKES (1979 and pers. comm.) using morphological and biochemical analyses, shows that Stenotomum × S. ***sparsipilum*** tetraploid hybrids cannot be distinguished from Andigena.

Table 2 also reveals in the gp. Andigena unique electromorphs in several isozyme loci (Got-A, Got-B, Mdh-A, Pgd-C, and Pgi-B), which were lacking in both S. ***sparsipilum*** and gp. Stenotomum. Although mutation cannot be rejected, this suggests that other species could be also implied in the origin of gp. Andigena, as it was proposed by UGENT (1970).

Also the autopolyploidy seems to have played a role in the origin of gp. Andigena. This group was more related to Stenotomum (D = 0.052) than to S. ***sparsipilum*** (D = 0.241), indicating that gene flow may be higher between the two former taxa. Several mechanisms of introgressive hybridization between both ploidy levels have been proposed by UGENT (1970). One of these is the autopolyploidization of Stenotomum individuals and the subsequent hybridization with gp. Andigena. The low genetic distance between Stenotomum and Andigena can indicate that this mechanism may act with relative frequency. Noteworthy, we have found an Andigena tuber family (U.S.D.A. P1243362) in which the electromorph combinations at 11 variable isozymes were consistent with an autoploid origin from Stenotomum (Table 2). SWAMINATHAN & MAGOON (1961) reported the close morphological resemblance of autotetraploid Stenotomum to varieties of Andigena.

Thus, our study suggests that in the origin of gp. Andigena could have taken part several mechanisms: amphidiploidy, autoploidy, and hybridization at tetraploid level. A similar view was already advanced by UGENT (1970), who considers that the multiple origin of Andigena may be due to the low degree of genomic differentiation which exists among the weedy related species, the tendency toward polyploidy, and the high incidence of natural interspecific hybridizations. The hypothesis of a multiple origin for Andigena could explain the opposed results obtained in both morphological and cytological studies. Thus, it explains the morphological similarity of Andigena with the autoploids Stenotomum (SWAMINATHAN & MAGOON 1961) or with Stenotomum × S. ***sparsipilum*** tetraploid hybrids (HAWKES 1979 and pers. comm.). It would also explain the unlike quadrivalent frequencies found in different Andigena and Tuberosum varieties (SWAMINATHAN & MAGOON 1961, HOWARD 1970). It is interesting to note that was this variability in the extent of multivalent associations formed in different varieties, what leads STEBBINS (1957) to propose that the nature of polyploidy in the commercial potato could be considered to vary from autotetraploidy toward segmental allotetraploidy.

Origin of *S. tuberosum* gp. Tuberosum. The most generalized view about the origin of gp. Tuberosum is that this group was derived from gp. Andigena on two separate occasions, in Chile and Europe, by a process of parallel evolution. Tubers of gp. Andigena arrived at southern Spain (Sevilla) about 1570 (SALAMAN 1949). Strong artificial selection, always aiming to adaptation at long days of Europe, would have changed gp. Andigena to gp. Tuberosum, just as occurred in the previous millenia when Andigena migrated southward to Chile (HAWKES 1978 a). After the late blight epiphytotics of the 1840s, which almost totally decimated the

potatoes then raised in Europe and North America, mass selection for late blight resistance coupled with continued selection for desirable agronomic characters, would have accelerated this change. SIMMONDS (1966) and GLENDINNING (1975) through very few generations of artificial selection for earliness seem to have repeated the process for a third time, obtained a potato material, named Neo-Tuberosum, which resembles Tuberosum in a series of agronomic characteristics (see, however, GRUN 1979).

A different view about the origin of our present potato cultivars was provided by GRUN (1970, 1973, 1979); on the basis of the similarity between Tuberosum from Northern Hemisphere and Tuberosum from Chile in both morphology and nature of its cytoplasmic factors, this author proposes that the evolution of Tuberosum from Andigena occurred but once, in Chile, and the product raised today in the Northern Hemisphere was simply imported from that region after the late blight epiphytotics of the 1840s. An example may be the variety "Rough Purple Chile", for which historical evidence exists about its introduction in 1851 into North America (GRUN 1970, 1979, HAWKES 1978a, HOWARD 1978). The lineage of the 25–28% of present day potato cultivars from North America can be traced to this Chilean variety (GRUN 1970).

Allozyme data allowed us to assess the relative roles played by Andean and Chilean potatoes in the evolution of S. *tuberosum* in the Northern Hemisphere. Most of the electromorphs present in Tuberosum from Europe and North America were found in Andigena, even those that were uniques in the last group (Table 2). Furthermore, the genetic distance (0.036) found between the two tetraploid groups of S. *tuberosum* (Table 7) is very closed to the average distance among accesions of Andigena (0.033). Both the direct derivation of Tuberosum from Andigena and the repeated introgression provided by breeding programmes could explain these results.

However, the allele c of Pgm-B, present in 30 out of 76 cultivars of Tuberosum from Northern Hemisphere, lacks in the 258 genotypes of Andigena sampled for this isozyme locus (Table 5). Since we have found this allele segregating in 3 Tuberosum cultivars from Chile (Table 3), Chilean Tuberosum germplasm seems to have taken part in the origin of at least the 39% of the potato cultivars from Europe and North America analyzed here.

Evolutionary Rates in Different **Taxa** of **Potatoes.** The patristic differences estimated by the distance Wagner procedure, provide approximations to the amounts of evolution in the different phyletic lines, allowing us to test the hypothesis of homogeneity in their rates of molecular evolution (FARRIS 1972).

Table 8 and Fig. 1 clearly show that heterogeneity in evolutionary

Table 7. Distance coefficients averaged by taxon in *Solanum*. Above: Prevosti distance; below: Nei unbiased genetic distance. – (*) See legend of Table 1

Taxon (*)	1	2	3	4	5	6
1 STN	–	0.103	0.364	0.146	0.165	0.507
2 GON	0.044	–	0.375	0.161	0.173	0.546
3 SPL	0.325	0.347	–	0.322	0.280	0.633
4 ADG	0.052	0.073	0.241	–	0.129	0.520
5 TBR	0.062	0.093	0.187	0.036	–	0.541
6 PNT	0.568	0.644	0.855	0.554	0.589	–

Table 8. Estimated patristic differences between each taxon of potatoes and the estimated root of the tree shown in Fig. 1. (See legend of Table 1 for abbreviations)

STN	GON	SPL	ADG	TBR
0.146	0.157	0.218	0.110	0.125

divergence exists among the different taxa of potatoes. S. ***sparsipilum*** and gp. Tuberosum showed, respectively, the maximal and the minimal divergence, which corresponds to a heterogeneity of 50% in the overall divergences. Within cultivated potatoes, a heterogeneity of 30% was found.

The evolutionary divergence was on average 38.5% greater in *S. **sparsipilum*** than in cultivated potatoes. The high evolutionary rate of this highly polymorphic weed diploid species could be related with their multiple hybrid origin (UGENT 1970).

The diploids Stenotomum and Goniocalyx show a higher (22.5%) evolutionary divergence than tetraploids Andigena and Tuberosum. This may be due in part to the amphidiploid nature (between Stenotomum and S. ***sparsipilum)*** of most of tetraploid cultivars, which makes them more similar to the common root of all the phyletic lines. Tetrasomic inheritance (HOWARD 1970, MARTÍNEZ ZAPATER & OLIVER 1984 b) and facultative autofecundation in the tetraploids can also account for their lower evolutionary rate. In any event, artificial selection acting from 10 000 years ago (HAWKES 1978 b, UGENT 1983), aiming to increase vigor, yield, and, lately, adaptation to long days, have not resulted in the tetraploids in a higher rate of molecular evolution at isozyme level.

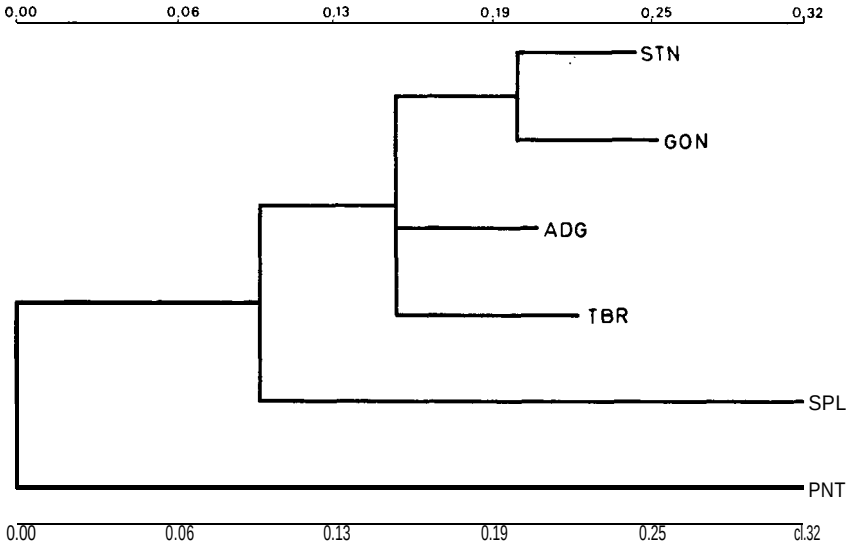

Fig. 1. Wagner tree rooted using *S. pinnatisectum* as an outgroup. Optimization was carried out using linear programming, minimizing weighted F-value. — Goodness of fit statistics: FARRIS (1972) "F" = 0.164. PRAGER & WILSON (1976) "F" = 3.303. -Weighted F = 0.458. -Per cent standard deviation (FITCH & MARGOLIASH 1976) = 6.885. — Cophenetic correlation = 0.994. -Total length of tree = 0.965

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References

BERLOCHER, S. H., BUSH, G. L., 1982: An electrophoretic analysis of *Rhagoletis (Diptera: Tephritidae)* phylogeny. — Syst. Zool. 31, 136 — 155.

BREWER, G. J., 1970: An introduction to isozyme techniques. — London: Academic Press.

BRÜCHER, H., 1964: El origen de la papa *(Solanum tuberosum).* — Physis 24, 439 — 452.

DOBZHANSKY, TH., AYALA, F. L., STEBBINS, G. L., VALENTINE, J. W., 1977: Evolution. — San Francisco: Freeman and Company.

DODDS, K. S., 1962: Classification of cultivated potatoes. – In CORRELL, D. S., (Ed.): The Potato and Its Wild Relatives. – Renner, Texas: Texas Research Foundation.

– PAXMAN, G. J., 1962: The genetic system of cultivated diploid potatoes. – Evolution 16. 154 – 167.

FARRIS, J. S., 1972: Estimating phylogenetic trees from distance matrices. – Am. Nat. 106, 645 – 668.

FITCH, W. M., MARGOLIASH, E., 1967: Construction of phylogenetic trees. – Science 155, 279 – 284.

GLENDINNING, D. R., 1975: Neo-Tuberosum: New potato breeding material. I. The origin, composition, and development of the Tuberosum and Neo-Tuberosum gene pools. – Pot. Res. 18, 256 – 261.

GOTTLIEB, L. D., 1981: Electrophoretic evidence and plant populations. – Progr. Phytochem. 7, 1-46.

GRUN, P., 1970: Cytoplasmic sterilities that separate the cultivated potato from its putative diploid ancestors. – Evolution 24, 750 – 758.

– 1973: Cytoplasmic sterilities that separate the group Tuberosum cultivated potato from its putative tetraploid ancestor. – Evolution 27, 633 – 643.

– 1979: Evolution of the cultivated potato: A cytoplasmic analysis. In HAWKES, J. G., LESTER, R. N., SKELDING, A. D., (Eds.): The Biology and Taxonomy of the *Solanaceae*. – London: Academic Press.

HAWKES, J. G., 1956: Taxonomic studies on the tuber-bearing *Solanums*. *I. Solanum tuberosum* and the tetraploid species complex. – Proc. Linn. SOC. London 166, 97 – 144.

1967: The history of the potato. – J. R. Hort. Soc. 92, 207 – 224; 249 – 262; *288-302*.

1978a: History of the Potato. – In HARRIS, P. M., (Ed.): The Potato Crop. – London: Chapman and Hall.

1978b: Biosystematics of the Potato. – In HARRIS, P. M., (Ed.): The Potato Crop. – London: Chapman and Hall.

1979: Evolution and polyploidy in potato species. – In HAWKES, J. G., LESTER, R. N., SKELDING, A. D., (Eds.): The Biology and Taxonomy of the *Solanaceae*. – London: Academic Press.

HOWARD, H. W., 1970: Genetics of the potato *Solanum tuberosum*. – London: Logos Press.

– 1973: Calyx forms in dihaploids in relation to the origin of *Solanum tuberosum*. – Potato Res. 16, 43 – 46.

– 1978: The production of new varieties. – In HARRIS, P. M., (Ed.): The Potato Crop. – London: Chapman and Hall.

IWANAGA, M., PELOQUIN, S. J., 1982: Origin and evolution of cultivated tetraploid potatoes via 2 n gametes. – Theor. Appl. Genet. 61, 161 – 169.

LANDEO, J. A., HANNEMAN, R. E., Jr., 1982: Geneticvariation in *Solanum tuberosum* Andigena haploids. – Theor. Appl. Genet. 62, 311 – 315.

MARTÍNEZ ZAPATER, J. M., OLIVER, J. L., 1984a: Identification of potato varieties: An isozyme approach. – In D'ARCY, W. G., (Ed.): *Solanaceae:* Biology and Systematics. – New York: Columbia University Press.

– 1984 b: Genetic analysis of isozyme loci in tetraploid potatoes *(Solanum tuberosum* L.). – Genetics 108, 669-679.

MATSUBAYASHI, M., 1960: Studies on the haploid plants of *Solanum tuberosum*. II. Meiotic chromosome pairing in the polyhaploid plants. – Jap. J. Breed. 10, 195 – 202.

McLEOD, M. J., GUTTMAN, S. I., ESHBAUCH, W. H., RAYLE, R. E., 1983: An electrophoretic study of evolution in ***Capsicum*** (*Solanaceae*). – Evolution 37, 562 – 574.

MENDIBLJRU, A. O., PELOQUIN, S. J., 1977: Bilateral sexual polyploidization in potatoes. – Euphytica 26, 573 – 583.

MENDOZA, H. A., HAYNES, F. L., 1976: Variability for photoperiodic reaction among diploid and tetraploid potato clones from three taxonomic groups. – Amer. Pot. J. 53, 319 – 332.

NEI, M., 1978: Estimation of average heterozygosity and genetic distance from a small number of individuals. – Genetics 89, 583 – 590.

OLIVER, J. L., MARTÍNEZ ZAPATER, J. M., 1984: A genetic classification of potato cultivars based on allozyme patterns. – Theor. Appl. Genet. (In press.)

– – PASCUAL, L., ENRIQUEZ, A. M., Rurz REJÓN, C., RUIZ REJÓN, M., 1983: Different genome amplification mechanisms and duplicate gene expression in ***Liliaceae.*** – In RATAZZI, M. C., SCANDALIOS, J. G., WHITT, G. S., (Eds.): Isozymes: Current Topics in Biological and Medical Research 10, pp. 341 – 363. – New York: Alan R. Liss.

PRAGER, E. M., WILSON, A. C., 1976: Congruency of phylogenies derived from different proteins. A molecular analysis of phylogenetic position of cracid birds. – J. Mol. Evol. 9, 45 – 57.

PREVOSTI, A., OCAÑA, J., ALONSO, G., 1975: Distances between populations of ***Drosophila*** *subobscura*, based on chromosome arrangement frequencies. – Theor. Appl. Genet. 45, 231 – 241.

QUIRÓS, C., 1983: Perennials: Alfalfa and its closely related species. In: TANKSLEY, S. D., ORTON, T. J., (Eds.): Isozymes in Plant Genetics and Breeding. – Amsterdam: Elsevier .

RALIN, D. B., SELANDER, R. K., 1979: Evolutionary genetics of diploid-tetraploid species of treefrogs of the genus *Hyla*. – Evolution 33, 595 – 608.

RICK, C. M., FOBES, J. F., 1975: Allozymes of Galapagos tomatoes: polymorphism, geographic distribution, and affinities. – Evolution 29, 443 – 457.

– – HOLLE, M., 1977: Genetic variation in ***Lycopersicon*** *pimpinellifolium*: evidence of evolutionary change in mating systems. – Plant Syst. Evol. 127, 139 – 170.

ROOSE, M. L., GOTTLIEB, L. D., 1976: Genetic and biochemical consequences of polyploidy in ***Tragopogon.*** – Evolution 30, 818 – 830.

ROWE, P. R., 1967: Performance of diploid and vegetatively doubled clones of Phureja-haploid Tuberosum hybrids. – Amer. Pot. J. 44, 195 – 203.

SALAMAN, R. N., 1946: The early European potato: its characters and place of its origin. – J. Linn. Soc. (Bot.) 53, l-27.

– 1949: The history and social influence of the potato. – London: Cambridge Univ. Press.

– HAWKES, J. G., 1949: The character of the early European potato. – Proc. Linn. Soc. 161, 71 – 84.

SANFORD, J. C., HANNEMAN, R. E., Jr., 1982: A possible heterotic threshold in the potato and its implications for breeding. – Theor. Appl. Genet. 61, 151 – 159.

SHAW, C. R., PRASAD, R., 1970: Starch gel electrophoresis of enzymes. A compilation of recipes. – Biochem. Genet. 4, 297-320.

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

– 1963: Abbreviations of potato names. – Europ. Potato J. 3, 186 – 190.

– 1966: Studies of the tetraploid potatoes. III. Progress in the experimental re-creation of the Tuberosum group. – J. Linn. Soc. (Bot.) 59, 279-288.

STEBBINS, G. L., 1957: Genetics, evolution and plant breeding. – Indian J. Genet. and Plant Breeding 17, 129 – 141.

SWAMINATHAN, M. S., MAGOON, M. L., 1961: Origin and cytogenetics of the commercial potato. – Advan. Genet. 10, 217-256.

SWOFFORD, D. L., 1981: On the utility of the distance Wagner procedure. – In FUNK, V. A., BROOKS, D. R., (Eds.): Advances in Cladistics: Proceedings of the First Meeting of the Willi Hennig Society. – Bronx, N. Y.: New York Botanical Garden.

– SELANDER, **R. B., 1981: BIOSYS-1:** a **FORTRAN** program for the comprehensive analysis of electrophoretic data in population genetics and systematics. – J. Hered. 72, 281 – 283.

UGENT, D., 1970: The potato. – Science 170, 1161 – 1166.

– POZORSKY, S., POZORSKY, T., 1983: Restos arqueolbgicos de tubérculos de papas y camotes en el valle de Casma en el Perú. – Boletín de Lima 25, 1 – 16.

WHALEN, M. D., 1979: Allozyme variation and evolution in *Solanum* section *androceras.* – Syst. Bot. 4, 203 – 222.

WOODCOCK, K. M., HOWARD, H. W., 1975: Calyx types in *Solanum tuberosum* dihaploids, S. *stenotomum, S. sparsipilum* and their hybrids. – Potato Res. **18,** 460 – 465.

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