

Identification of Potato Varieties: An Isozyme Approach

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We propose here a method for potato variety identification based on the isozyme pattern that each variety displays. Using seven different isozymes from tubers and sprouts, we have been able to identify 65 out of 67 varieties. We also discuss the possible origin of the isozyme phenotype similarities found among the cultivars studied.



Identification of potato varieties is normally based on visual descriptions of morphological and physiological characters of tubers, sprouts, and adult plants. The variation shown by these characters under different environmental changes raises the question of finding an objective means of identification. Several attempts were made to identify varieties of potato using total protein electrophoretic profiles (Zwartz 1966; Stegemann and Loeschke 1976). However, total protein profiles are affected by a series of environmental and culture conditions (Stegemann and Loeschke 1977; Stegeman 1979), as well as by physiological changes with tuber maturation (Zwartz 1966; Stegeman, Francksen, and Macko 1973).

Genetic identification through isozyme analysis has the advantage that each cultivar line shows a unique isozyme phenotype under any set of culture conditions (Schwartz 1960; Loeschke and Stegemann 1966), although some

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laboratory manipulations (freezing of the whole tubers or storage of their crude extracts) can affect specific isozyme patterns, particularly the phosphorilases (Gerbrandy et al. 1975). Furthermore, genetic isozyme characterization of the different varieties allows better breeding program planning (Stegemann 1979). The use of isozymes as genetic markers for cultivar identification has been reported in many food crops and related plants (Almgard and Landegren 1974; Fedak 1974; Natarella and Sink 1975; Almgard and Clapham 1975, 1977; Wehner, Duich, and Watschke 1976; Wolfe 1976; Bassiri and Rouhani 1977; Valizadeh, Rivals, and Valdeyron 1977; Werner and Sink 1977; Kuhns and Fretz 1978; Santamour and Demuth 1980; Salinas, Pérez, and Benito 1982).

Desborough and Peloquin (1968) used soluble-protein profiles in combination with isozyme systems (esterases and peroxidases) to identify 45 potato varieties but made no attempts at a genetic interpretation of isozyme data. Furthermore, because esterases and peroxidases are subject to both substrate specificity and developmental changes, a deeper study of the genetic control and the tissue expression patterns of their isozymes is needed if we want an accurate and reliable method of identifying varieties. Along these lines May, Jack, and Kuhns (1982) have recently pointed out the usefulness of genetic studies on isozymes for potato variety identification.

Potato varieties are suited to an isozyme identification program because each one is a unique genotype reproduced vegetatively, and therefore, no variability among plants of each cultivar may be expected. Furthermore, the interline variability may be greater in potato than in species where the different varieties are pure lines reproduced sexually; thus, isozyme techniques may also be expected to have greater power of discrimination.

In the course of the study on isozyme variability that we are carrying out in *Solanum tuberosum* and related species, we are now trying to characterize genetically different varieties of potato (*S. tuberosum* ssp. *tuberosum*). We report here the phenotypes of ten isozymes shown by a total of 67 potato varieties, including the most economically important ones in Spain and other European countries. With the isozyme phenotypes found in tubers and sprouts, we have been able to distinguish entirely 65 out of the 67 varieties analyzed.

Materials and Methods

A total of 67 potato varieties, 30 percent of which had more than one source, were analyzed (table 32.1). The term *variety* is used here to indicate named clonal selections. The potato tubers were maintained in a cool lighted room to avoid sprouting and put in darkness when sprouts were necessary. Roots, leaves, and flowers were obtained from tubers maintained in hydroponic culture with a standard nutritive solution.

To determine the tissue expression patterns of each isozyme, nine different tissues of the plants were analyzed: tuber (central zone), sprout (base and tip),

Table 32.1. Potato Varieties Analyzed and Their Sources

KEY	Cultivar	Source*	KEY	Cultivar	Source ^a
AB	Alberta	VI, MO	IT	Iturrieta	MO
ACK	Ackersegen	VI	JA	Jaerla	VI, MO
AD	Alda	VI	KD	King Edward	MO
AK	Abnaki	MO	KE	Kennebec	VI, MO
AL	Alava	VI, MO	LI	Libertas	VI
AP	Alpha	WA	LOA	Lora	MO
AR	Arran Banner	VI, MO	MA	Marike	MO
ARI	Ari	VI	MI	Mirka	VI
AV	Avenir	WA	NG	Netted Gem	MO
BA	Baraka	VI, MO	NI	Nipigon	MO
BEA	Bea	VI, WA	NO	Noorsak	MO
BI	Bintje	VI	NR	Norchip	MO
BKC	Blanka	MO	OL	Olalla	VI
BL	Belda	VI, MO	OS	Ostara	MO
BR	Burmania	VI	PA	Palogán	VI, MO
BS	Belle Isle	MO	PI	Pimpernel	VI
BT	Batoche	MO	PM	Pedro Muñoz	VI
BU	Buesa	VI, MO	PR	President	VI
BUT	Butte	MO	RCR	Red Craigs Royal	VI
CA	Cardinal	VI, MO	RE	Record	WA
CH	Chieftain	MO	RK	Royal Kidney	VI
CL	Claustar	VI, MO	RO	Rosalie	VI, MO
DE	Desiree	VI, MO	RP	Red Pontiac	VI, MO
DI	Diamant	MO	RR	Roja Riñon	VI
DR	Draga	MO	SE	Sebago	MO
DU	Duquesa	VI	SP	Spunta	VI, MO
ED	Edzina	VI, MO	ST	Saturna	WA
EL	Etoile du Leon	VI	SU	Superior	MO
FU	Furore	WA	TR	Triumph	WA
GA	Gauna	VI	TU	Turia	VI, MO
GM	Green Mountain	MO	UR	Urgenta	VI
GO	Goya	VI	VI	Victor	VI, MO
HE	Heida	VI	WA	Warseum	MO
IN	India	VI			

*WA—Government Institute for Research on Varieties of Cultivated Plants, Wageningen (Holland); VI—Estación de Mejora de la Patata, Victoria (Spain); MO—Instituto Nacional de Semillas y Plantas de Vivero, Servicio de la Patata de Siembra, Ministerio de Agricultura, Pesca y Alimentación, Madrid (Spain).

leaf, root, petal, anther, ovary, and calyx. Special care was taken to analyze the different organs at a similar developmental stage in all the varieties. Whole sprouts 1–2 cm long were usually analyzed, although we analyzed the tip and the base separately. In order to prevent browning, the enzyme extraction was accomplished by crushing the plant material in a buffered solution of several reducing agents (Valizadeh 1977). The enzyme extracts were absorbed directly onto paper wicks and subjected to horizontal starch gel electrophoresis, with LiOH/Borate (pH 8.1) electrode buffer and Tris/Citrate (pH 8.3) gel buffer

(Selander et al. 1971). Samples of var. 'Desiree' variety were included in all the slab gels in order to use them as internal markers to determine the electrophoretic mobilities of the different isozyme bands.

Different gel slices were assayed for seven enzymes: Esterases (EST, E.C. 3.1.1.1), using *N*-Naphthyl acetate 0.04M in a buffer of $\text{PO}_4\text{H}_2\text{K}$ 0.1M (pH 6.5) and staining with Fast-Blue RR; 10% alcohol dehydrogenase (ADH, E.C. 1.1.1.1) (Pasteur 1973); glutamate oxaloacetate transaminase (GOT, E.C. 2.6.1.1) (Gottlieb 1973); phosphoglucose-isomerase (PGI, E.C. 5.3.1.9) (Brewer 1970); phosphoglucomutase (PGM, E.C. 2.7.5.1) (Brewer 1970); peroxidases (POX, E.C. 1.11.1.7) (Shaw and Prasad 1970), with the pH modified to 4.5 according to Rick, Zobel, and Fobes (1974); and malic enzyme (Me, E.C. 1.1.1.40) (Brinkman and Van der Meer 1975), with Tris/HCl 0.2M (pH 8.0). After staining, the gels were fixed in methyl alcohol, acetic acid, and deionized water for EST and GOT; glycerine and deionized water for POX; and methyl alcohol, glycerine, and deionized water for dehydrogenase enzymes.

Results

The comparative analysis of the electrophoretic phenotypes shown by the different potato varieties and the differential patterns of tissue expression (table 32.2) were the criteria we employed in determining the number of isozymes in each enzyme. Inheritance studies through electrophoretic analysis of seed progenies derived from different crosses are under way to determine the genetic control of each isozyme. At least five tubers of each variety were analyzed; no differences were found among plants of each variety, although tubers from different sources were analyzed.

Table 32.2. Tissue Expression Patterns of the Different Isozymes in Potato Varieties

Isozyme	No. of Mobility	Expression								
		TUB	SP(B)	SP(T)	LE	RO	PET	ANT	OV	CAL
ADH-A	2	+	+	+	-	+	-	-	-	-
POX-C	4	-	+	+	+	+	+	+	+	+
POX-E	2	-	+	-	+	-	-	-	-	+
GOT-A	2	+	+	+	+	+	+	+	+	+
GOT-B	4	+	+	+	+	+	+	+	+	+
EST-C	7	+	+	-	-	-	-	-	-	-
PGI-A	1	+	+	+	+	+	+	+	+	+
PGI-B	7	+	+	+	+	+	+	+	+	+
PGM-B	2	+	+	+	+	+	+	+	+	+
ME-A	1	+	+	+	+	+	?	?	?	?

NOTE: TUB—tuber; SP(B)—sprout (base); SP(T)—sprout (tip); LE—leaf; RO—root; PET—petal; ANT—anther; OV—ovary; CAL—calyx.

We also studied the isozyme expression patterns during sprout development. When whole sprouts, developed both in darkness and in daylight, were analyzed at different times (with two-day intervals), no measurable differences were found in most of the isozymes; exceptions were EST-C and POX-F isozymes, which begin expression later in the development of the sprout, at approximately the 15th day of sprouting, without any effect from the lighting conditions.

The electrophoretic phenotypes shown by the different isozymes were as follows:

GOT. Two isozymes (GOT-A and GOT-B) were expressed in all the analyzed tissues. In GOT-A three electrophoretic mobilities (0.46, 0.43, and 0.40) were detected, one of which (0.46) is present in all the analyzed varieties. Four electrophoretic bands (0.22, 0.18, 0.14, and 0.10) in five phenotype combinations were found in GOT-B (figure 32.1).

Figure 32.1. Ordered classification table indicating the presence (1) or absence (0) of each electrophoretic mobility at 67 potato varieties. At each isozyme, the electromorphs are ordered from the left according higher mobilities. All but Cardinal and Diamant varieties show a differential array of electrophoretic phenotypes.

VAR	ADH-A	PGI-B	GOT-B	EST-C	POX-C	POX-F	PGM-B
BT	01	0000100	0110	0120211	1010	11	11
DE	10	0000100	0010	0000101	1000	10	10
GA	10	0000100	0010	0010201	1010	10	11
AV	10	0000100	0010	0020201	1100	11	10
DI	10	0000100	0010	0110111	1001	10	10
CA	10	0000100	0010	0110111	1001	10	10
RR	10	0000100	0011	0120211	1000	10	10
RO	10	0000100	0110	0000111	1001	10	10
VI	10	0000100	0110	0001110	1000	11	10
OL	10	0000100	0110	0010201	1001	10	10
CH	10	0000100	0110	0010201	1010	10	10
DU	10	0000100	0110	0011111	1000	11	10
NI	10	0000100	0110	0011111	1010	10	10
AK	10	0000100	0110	0020201	1010	10	11
TR	10	0000100	0110	0020201	1010	11	10
AB	10	0000100	0110	0022211	1000	10	11
RP	10	0000100	0110	0022211	1010	10	11
LOA	10	0000100	0110	0110101	1100	10	10
BA	10	0000100	0110	0110101	1100	10	11
UR	10	0000100	0110	0110111	1000	10	10
LI	10	0000100	0110	0110111	1000	11	10
DR	10	0000100	0110	0111111	1000	10	10

(continued)

Figure 32.1 (continued)

VAR	ADH-A	PGI-B	GOT-B	EST-C	POX-C	POX-F	PGM-B
OS	10	0000100	1110	0010201	1000	10	11
PM	10	0000100	1110	0010201	1010	11	10
GO	10	0000100	1110	0020201	1000	10	11
SP	10	0000100	1110	0101111	1000	10	11
BS	10	0000100	1110	0111111	1000	11	11
PI	10	0000100	1110	0120211	1000	10	10
MI	10	0000111	0110	0010100	1000	11	10
RCR	10	0000111	0110	0010201	1000	10	10
AP	10	0000111	0110	0020201	1100	11	10
FU	10	0000111	0110	0110111	1010	10	10
NR	10	0000111	1100	0020201	1010	11	10
CL	10	0000111	1110	0011111	1000	01	10
HE	10	0000111	1110	0110111	1000	10	11
RE	10	0000111	1110	0110111	1000	11	10
ACK	10	0000111	1110	0111111	1100	10	11
BKC	10	0011100	0010	0001011	1000	10	10
IN	10	0011100	0010	0011111	1000	11	11
BEA	10	0011100	0110	0001011	1000	10	10
NO	10	0011100	0110	0011111	1010	10	11
SE	10	0011100	0110	0020201	1010	11	11
BUT	10	0011100	0110	0020201	1100	11	10
AR	10	0011100	0110	0110101	1100	10	10
AD	10	0011100	0110	0110111	1000	10	11
GM	10	0011100	0110	0110111	1000	11	11
PR	10	0011100	0110	0110111	1010	10	10
TU	10	0011100	0110	0111111	1000	10	10
NG	10	0011100	0110	0111111	1100	10	10
JA	10	0011100	1100	0001110	1000	11	10
ARI	10	0011100	1110	0011111	1010	10	11
KE	10	0011100	1110	0011111	1100	10	11
BR	10	0011100	1110	0020201	1000	10	10
SU	10	0011111	1110	0011111	1000	11	11
WA	10	1111100	0010	0010201	1001	10	11
MA	10	1111100	0110	0101111	0101	11	10
BI	11	0000100	0010	0001110	1000	10	11
BL	11	0000100	0110	0101111	1000	10	11
AL	11	0000100	0110	0111111	1001	10	10
IT	11	0000100	1110	0010201	1000	10	11
ED	11	0000100	1110	0011100	1000	01	11
ST	11	0000100	1110	0101010	1000	11	10
PA	11	0000100	1110	0110111	1001	10	10
BU	11	0000100	1110	0110111	1001	10	11
KD	11	0011100	0010	0011111	1101	01	10
EL	11	0011100	0110	0110101	1100	11	10
RK	11	0011100	0110	1101100	0110	10	10

NOTE ADDED IN PROOF: We have now analyzed more tissues and organs from commercial potato varieties. The study was also extended to other tetraploid and diploid groups of cultivated and wild potatoes. An updated characterization table (number and relative mobilities of different allozymes, epigenetic modifications, subcellular localization, and subunit number) of different potato isozymes is available from the authors.

Me. Only one electrophoretic mobility (0.32) was found in all the analyzed tissues (the flower organs have not yet been analyzed for Me) and in all the potato varieties. Consequently, this enzyme was not useful for identification purposes.

ADH. A unique isozyme (ADH-A) was found. Two electrophoretic mobilities (0.51 and 0.49) and three phenotype combinations were found (figure 32.1).

EST. Although we were able to detect at least the presence of seven esterase isozymes in the potato plant, only one (EST-C) was detected in the tuber with the staining method we employed. This isozyme is also expressed in the sprout base (see table 32.2). Seven electrophoretic mobilities (0.68, 0.66, 0.63, 0.61, 0.59, 0.56, and 0.53) were found in the EST-C isozyme zone, providing great richness of phenotype combinations (17 phenotypes were found in the 67 varieties analyzed; see figure 32.1); thus, the esterases are an important tool for cultivar identification in the potato.

PGI. Three PGI isozymes (PGI-A, PGI-B, and PGI-C) were present in all the analyzed tissues. The fast-migrating isozyme, PGI-A, with only one electrophoretic mobility (0.57), seems to be a plastid enzyme as in the tomato (Tanksley 1980) and in other plant species (Weeden and Gottlieb 1980; Gottlieb and Greve, 1981). Five phenotype combinations of a total of seven electrophoretic bands (four electromorphs, 0.41, 0.37, 0.33, 0.27 plus three presumable heterodimeric bands, 0.39, 0.35 and 0.30) were shown by PGI-B (figure 32.1). The presence of three-banded phenotypes, with the intermediate band more intensely stained, suggests a dimeric structure for this isozyme like in other plants (Tanksley 1980; Gottlieb and Greve 1981). The PGI-B electrophoretic patterns of certain potato varieties have recently been reported by May, Jack, and Kuhns (1982). Although a different method has been used, it is important to point out that the number of electromorphs is the same and the phenotypes of the varieties analyzed coincides in both studies. PGI-C was not included in the study due to its poor resolution.

POX. At least six anodic peroxidase isozymes were detected in the potato plants. The expression patterns of some of them, mainly the fast-migrating ones, were in accordance with the stage of growth of the tissue analyzed (unpublished results). Apparently their activity increases with the age of the tissue, as has been observed in roses (Kuhns and Fretz 1978) and cotton (Wise and Morrison 1971). This could be related to the indolacetic acid oxidase activity of these isozymes (Scandalios 1969; Lee 1972). The POX-C isozyme was expressed in all the analyzed tissues except the tuber, being active in both the root and the sprout; seven phenotype combinations of four electrophoretic mobilities (0.54, 0.52, 0.50, and 0.48) were present in the potato varieties we studied. POX-F

isozyme presented a different tissue expression pattern (table 32.2); two electrophoretic mobilities (0.17 and 0.08) and three possible phenotype combinations were found.

PGM. As has been previously reported by other authors (Takamiya and Fukui 1978), two PGM isozymes were detected in potato. The fast-migrating PGM-A was slightly stained; it seems to be a plastid enzyme, resembling that in the tomato (Tanksley 1979) but not the one found in peas, where the chloroplast isozyme is the slow-migrating PGM-2 (Weeden and Gottlieb 1980). PGM-B isozyme was expressed in all the tissues that we analyzed (table 32.2); the two electrophoretic mobilities (0.40 and 0.34) were found in only two phenotype combinations, the band 0.40 being present in all the potato varieties. The two-banded phenotypes observed in many potato varieties suggest a monomeric structure for this isozyme, as it happens in other species (Weeden and Gottlieb 1980).

In scoring these electrophoretic data, we considered the absence (0) or the presence (1) of each of the isozyme bands in the different potato varieties; for esterases, in which conspicuous and reproducible differences in staining intensities exist, we scored the absence (0), the normal intensity (1), and the strong intensity (2) of each isozyme band. The isozyme data of the 67 varieties analyzed were sorted in a computer. We excluded Me and PGI-A isozymes, since they had a fixed phenotype. The GOT-A phenotypes do not contribute to a better identification of the different varieties either, so they were also excluded from the classification table.

Discussion

The ordered classification table of figure 32.1 shows that 65 out of 67 potato varieties analyzed were entirely identified by their electrophoretic phenotype arrays of seven isozymes. Only the Diamant and Cardinal varieties show an identical phenotype in all the isozymes studied; nevertheless, these two varieties are easily distinguishable by their skin color: Cardinal skin is red, whereas Diamant is yellow. Increasing the number of isozymes studied will probably permit the separation of these varieties.

The simplicity of the method, based mostly on the presence or absence of each isozyme band, eliminates the errors that could be introduced if the determination were based on the different band intensities and provides an easy way to score the results. Besides, it is interesting to point out that the use of a sorting program is a simple and quick method of arranging the different phenotypes found and comparing a new variety with those previously studied. Thus, isozyme identification is revealed as an effective and reliable method for variety identification in potato.

In most of the isozymes there exists an electrophoretic mobility that is either the most frequent or fixed in all the varieties (table 32.3). Two mechanisms can

Table 32.3. Most Frequent or Fixed Isozyme Bands in Potato Varieties

<i>Isozyme</i>	<i>Electrophoretic mobility</i>	<i>No. of varieties in which present</i>
ADH-A	0.51	
EST-B	0.59	66
GOT-A	0.46	64
GOT-B	0.14	67
POX-D	0.54	65
POX-G	0.17	65
PGI-B	0.33	64
PGM-B	0.40	67
		67

NOTE: 67 varieties analyzed.

account for the high frequencies of these electrophoretic variants in potato varieties: (1) A founder effect, since most of the cultivated potato varieties are descendants of few individuals of the short-day tetraploid *S. tuberosum* ssp. *andigena* introduced in Europe in the sixteenth century (Salaman 1949; Hawkes 1978). *S. tuberosum* ssp. *tuberosum* is thought to have derived from this restricted genetic base. (2) The selective significance of these electromorphs with respect to the artificial selective pressures undergone by the potato cultivars (Simmonds 1962), always aiming for adaptation to long days and for increased yield (Mendoza and Haynes, 1974). The comparative isozyme analysis that we are carrying out among European and South American varieties will contribute to the determination of the respective roles played by these two mechanisms in originating the phenotype combinations now found in potatoes. The genetic characterization through isozyme analysis of cultivated potato varieties will also permit a relating of the genotypes or genotype arrays to different disease resistances or yield traits (Rick and Fobes 1974; Gelderman 1976), allowing a better-planned breeding program (Stegeman 1979).

References

- Almgard, G. and D. Clapham. 1975. Isozyme variation distinguishing 18 *Avena* cultivars grown in Sweden. *Swed. J. Agric. Res.* 5:61-67.
- Almgard, G. and D. Clapham. 1977. Swedish wheat cultivars distinguished by content of gliadins and isozymes. *Swed. J. Agric. Res.* 7:137-142.
- Almgard, G. and U. Landegren. 1974. Isoenzymatic variation used for the identification of barley cultivars. *Z. Pflanzenzücht.* 72:63-73.
- Bassiri, A. and I. Rouhani. 1977. Identification of broad bean cultivars based on isozyme patterns. *Euphytica* 26:279-286.
- Brewer, G. J. 1970. *An Introduction to Isozyme Techniques*. London: Academic Press.
- Brinkman, F. G. and L. J. Van der Meer. 1975. Dehydrogenases in the potato tuber (*S. tuberosum*). Identity, coenzyme-specificity, and isoenzyme composition of malic enzyme malate dehydrogenase, and lactate dehydrogenase. *Pflanzenphysiol.* 75(4):322-331.

- Desborough, S. and S. J. Peloquin. 1968. Potato variety identification by use of electrophoresis patterns of tuber proteins and enzymes. *Amer. Potato J.* 45:220-229.
- Fedak, J. G. 1974. Allozymes as aids to Canadian barley cultivar identification. *Euphytica* 23:166-173.
- Geldermann, H. 1976. Untersuchung der Milchleistungsvererbung beim Deutschen Schwarzbunten Rind mit Hilfe von Marker-Genen. Universität Göttingen. Habilitation-Schrift.
- Gerbrandy, S. J., V. Sankar, K. N. Shivaran, and H. Stegemann. 1975. Conversion of potato phosphorilase isozymes. *Phytochemistry* 14:2331-2333.
- Gottlieb, L. D. 1973. Genetic control of glutamate oxaloacetate transaminase isozymes in the diploid plant *Stephanomeria exigua* and its allotetraploid derivative. *Biochem. Genet.* 9:97-107.
- Gottlieb, L. D. and Greve L. C. 1981. Biochemical properties of duplicated isozymes of phosphoglucose isomerase in the plant *Clarkia xantiana*. *Biochem. Genet.* 19:155-174.
- Hawkes, J. G. 1978. History of the potato. In P. M. Harris, ed., *The Potato Crop: The Scientific Basis for Improvement*, pp. 2-14 London: Chapman and Hall.
- Kuhns, L. J. and T. A. Fretz. 1978. Distinguishing rose cultivars by polyacrylamide gel electrophoresis. II. Isozyme variation among cultivars. *J. Amer. Soc. Hort. Sci.* 103:509-516.
- Lee, T. T. 1972. Interaction of cytokinin, auxin, and gibberellin on peroxidase isoenzymes in tobacco tissues cultured in vitro. *Can. J. Bot.* 50:2471-2477.
- Loeschcke, V. and H. Stegemann. 1966. Proteine der Kartoffelknollen in Abhängigkeit von Sorbe von Vivoren (Polyacrylamideelektrophorese). *Phytochemistry* 5:985-991.
- May, B., E. S. Jack, and L. J. Kuhns. 1982. Potato cultivars: Genetic variation within putative clones. *Amer. Potato J.* 59:179-187.
- Mendoza, H. A. and F. L. Haynes. 1974. Genetic relations among potato cultivars grown in the United States. *HortScience*, 9:328-330.
- Natarella, N. J. and K. C. Sink. 1975. Electrophoretic analysis of proteins and peroxidases of selected *Petunia* species and cultivars. *Bot. Gaz.* 136:20-26.
- Pasteur, N. 1973. Microelectrophoretic analysis of enzymes and other proteins during development of *Drosophila pseudoobscura*. Ph.D. diss., University of Texas, Austin, Texas.
- Rick, C. M. and J. F. Fobes. 1974. Association of an allozyme with nematode resistance. *Rep. Tomato Genet. Crop.* 24:25.
- Rick, C. M., R. W. Zobel, and J. F. Fobes. 1974. Four peroxidase loci in red-fruited tomato species: Genetics and geographic distribution. *Proc. Natl. Acad. Sci. U.S.A.* 71:835-839.
- Salaman, R. N. 1949. *The History and Social Influence of the Potato*. Cambridge: Cambridge University Press.
- Salinas, J., M. Pérez de la Vega, and C. Benito. 1982. Identification of hexaploid wheat cultivars based on isozyme patterns. *J. Sci. Food Agric.* 33:221-226.
- Santamour, F. S. and P. Demuth, 1980. Identification of Callery pear cultivars by peroxidase isozyme patterns. *J. Hered.* 71:447-449.
- Scandalios, J. G. 1969. Genetic control of multiple molecular forms of enzymes in plants: A review. *Biochem. Genet.* 3: 37-79.
- Schwartz, D. 1960. Genetic studies on mutant enzymes in maize: Synthesis of hybrid enzymes by heterozygotes. *Proc. Natl. Acad. Sci. U.S.A.* 46:1210-1215.
- Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, and J. B. Gentry. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). *Univ. Texas Publ.* No. 7103:49-90.
- Shaw, C. R. and R. Prasad. 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. *Cambridge Phil. Soc. Biol. Rev.* 37:422-465.

- Stegemann, H. 1979. Characterization of proteins from potatoes and the "Index of European Varieties." In J. G. Hawkes, R. N. Lester, and A. D. Skelding, eds., *The Biology and Taxonomy of the Solanaceae*, pp. 279-284. London: Academic Press.
- Stegemann, H., H. Francksen and V. Macko. 1973. Potato proteins: Genetic and physiological changes, evaluated by one- and two-dimensional PAA-gel techniques. *A. Naturforsch.* 286:722-732.
- Stegemann, H. and V. Loeschke. 1976. Index of European potato varieties, based on electrophoretic spectra (in German). *Mitteilungen der Biologischen Bundesanstalt Für Land- und Forstwirtschaft* 168:1-215.
- Takamiya, S. and T. Fukui. 1978. Purification and multiple forms of phosphoglucumutase from potato tubers. *Plant Cell Physiol.* 19:759-768.
- Tanksley, S. D. 1979. Linkage, chromosomal association, and expression of Adh-1 and Pgm-2 in tomato. *Biochem. Genet.* 17:1159-1167.
- Tanksley, S. D. 1980. PGI-1, single gene in tomato responsible for a variable number of isozymes. *Can. J. Genet. Cytol.* 22:271-278.
- Valizadeh, M. 1977. Esterase and acid phosphatase polymorphism in the fig tree (*Ficus carica* L.). *Biochem. Genet.* 15:1037-1048.
- Valizadeh, M., P. Rivals, and G. Valdeyron. 1977. Utilisation du polymorphisme protéique pour l'étude des variétés de figuier (*Ficus carica* L.). *C. R. Acad. Agric. France* 63:647-655.
- Weeden, N. F. and L. D. Gottlieb. 1980. The genetics of chloroplast enzymes. *J. Hered.* 71: 392-396.
- Wehner, D. J., J. M. Duich, and T. L. Watschke. 1976. Separation of Kentucky blue-grass cultivars using peroxidase isoenzyme banding patterns. *Crop Sci.* 16:475-480.
- Werner, D. J. and K. C. Sink. 1977. Identification of poinsettia cultivars by electrophoretic analysis of proteins and peroxidases. *J. Hered.* 68:35-40.
- Wise, B. and M. Morrison. 1971. Localization of isozyme forms of peroxidase in the cotton plant. *Phytochemistry* 10:2355-2359.
- Wolfe, W. H. 1976. Identification of grape varieties by isozyme banding patterns. *Amer. J. Viticult.* 272:68-73.
- Zwartz, J. A. 1966. Potato varieties and their protein electrophoregram characteristic. *Eur. Potato J.* 9:111-128.