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Genetic diversity in cucumber (*Cucumis sativus* L.): II. An evaluation of selected cultivars released between 1846 and 1978

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Abstract

Genetic variation among 155 U.S. modern and heirloom cultivars was assessed from assays of 21 polymorphic isozyme loci. Four loci (*Fdp-1, Mdh-1, Mpi-1* and *Pgd-1*) were monomorphic. Multivariate analyses partitioned cultivars into two distinct groups: those released before 1968, and those released after 1968. Cluster analysis produced a dendrogram with 14 nodes and 28 groups. Modern U.S. and European cultivars released after 1968 differed in isozyme frequencies. Isozymic profiles clearly discriminated some cultivars with unique attributes and/or pedigrees [e.g., 'Windermoor Wonder' (USA), 'Gergana' (The Netherlands), 'Seiram' (The Netherlands), 'Fancy Pak' (USA), 'Dasher 2' (USA), and WI 2757 (USA)].

Introduction

Cucumber (*Cucumis sativus* var. *sativus* L.) is grown in nearly all temperate regions and is one of the ten most widely cultivated vegetable species, ranking fourth after tomato, onion and cabbage (Tatlioglu, 1993). In 1992, approximately one million hectares of processing cucumbers were planted worldwide, yielding an estimated 15 million metric tons of fresh product (FAO, 1993).

Cucumber is indigenous to India and was domesticated there approximately 3,000 years ago (Whitaker & Davis, 1962; Brothwell and Brothwell, 1969). Evidence from excavation of two sites ("Spirit Cave") in northern Thailand near the Burmese border, however, suggests that cucumber was used by man roughly 9750 B.C., almost 2000 years before true agriculture began in the Near East or in Central America (Tannanhill, 1973; Solheim, 1972). Its cultivation appears to have spread rapidly from India to western Asia, and then to southern Europe (Brothwell & Brothwell, 1969). Curiously, cucumber was not cultivated in China until the second century B.C. It was part of the Sumerian diet (2,500 B.C.; garden of Ur-Nammu at Ur, *c.* 2100 B.C.), and was widely grown by ancient Greeks and Romans (Brothwell & Brothwell, 1969; Tannanhill, 1973). Although the existence of ancient names for cucumber indicates that this plant was known in the Caucasus region before it was known by Sanskrit-speaking people (1,500 B.C. to 1,100 A.D.; in Sanskrit as "chirbhita", "urvaruka" and "sukasa"), it is uncertain whether the ancient Egyptians in the earliest part of this period knew it (Achaya, 1994; Candolle, 1886; Darby et al., 1977; Erman, 1996; Sturtevant, 1919; Tapley et al., 1937). Cucumber was cultivated in pre-Renaissance France (9th century; "French salad") and England (15th century), and may have been brought to colonial North America as early as the end of the 15th century (Levenstein, 1988; Tatlioglu, 1993; Wilson, 1974). Cucumbers were grown on a considerable scale in England during the sixteenth century, but unlike their modern counterparts, these cucumbers where pear-shaped or nearly round (Wilson, 1974). In colonial North America, consumption of cucumber was limited relative to present-day standards. New England colonists used cucumber as sauces to accompany meats (Levenstein, 1988), and it was grown by Iroquois Indians near Montreal, Canada (1535), and

by Seminoles in Florida (1539) and by Powhatans in Virginia (1584) (Sturtevant, 1919).

In cucumber improvement programs, plants are selected for improved performance in specific environments (greenhouse, field, single or multiple harvest), as well as for intended use (processing, fresh market), and consumer preference (fruit shape and quality). Many breeding projects select plants with pest and disease resistance, abiotic stress tolerance (e.g., low growing temperatures) and high fruit yield and quality (Lower & Edwards, 1986). Fruit length:diameter ratio of the U.S. processing varieties has increased to meet consumer and processor demands. Likewise, fruit of modern varieties are darker green than their predecessors and in contrast to earlier black-spined types possess white spines.

Most modern American cucumber cultivars are derived from European germplasm, either as direct selections or from more intensive breeding efforts. In 1872, the first American-bred cultivar, 'Tailby's Hybrid', was exhibited at the annual meeting of the Massachusetts Horticultural Society. It was green-fruited, white spined, relatively high yielding, with the smooth skin texture of English cultivars. There had been little interest before that time in developing new cultivars for the U.S. market. Nevertheless, since its introduction there have been many releases of new market and processing cucumber cultivars. Some of the earliest open-pollinated cucumber cultivars included 'China Long' and 'Chicago Pickling' which were sold as early as 1882 and 1888, respectively (Tapley, 1937). By 1920, 'Adams', 'National Pickling' and 'President', along with 19 other new cultivars, had been introduced (Minges, 1972). In the 1930s two market cultivars, 'Colorado' and 'Straight 8', were popular because of their superior fruit shape and color.

Genetic improvements for yield resulted mainly from the incorporation of gynoecy and disease resistance (tolerance) identified in exotic germplasm of diverse origin (Peterson, 1960, 1975; Provvidenti, 1989) and the improvement of cultural practices (Lower & Edwards, 1986). Resistance to cucumber mosaic virus (CMV) in exotic germplasm was first used by R. H. Porter at the Iowa Agricultural Experiment Station, Ames ('Chinese Long') and then subsequently by S. P. Doolittle ('Tokyo Long Green') (1939). The incorporation of such exotic germplasm (e.g., 'Expo'; glasshouse type) led to the development of disease-resistant germplasm adapted to cultivation in North America (e.g., Wisconsin SMR-18, 'Tablegreen' and 'Marketmore').

Gynoecious hybrids were made possible in 1954 when E.M. Meader of the New York Agricultural Experimental Station at Geneva acquired the Korean cucumber 'Shogoin' (PI 220860) which segregated for gynoecy (Wehner & Robinson, 1991). The first gynoecious processing cucumber inbred line, 'MSU 713–5' (released in 1960), was developed by selecting 'Shogoin' for predominately pistillate flowers and backcrossing the selection to 'Wisconsin SMR-18' (Peterson, 1960; 1975). This resulted in the first modern gynoecious x monoecious hybrid cucumber, Spartan Dawn, in 1963 (Peterson & Andher, 1960; Peterson & DeZeeuw, 1963).

Although cucumber cultivars are often morphologically distinct, many of them share traits (genes) incorporated from the same germplasm sources (Peterson, 1975). It has been apparent that the genetic base of commercial cucumber germplasm is not extremely heterogenous (Staub & Meglic, 1993; Pierce & Wehner, 1990). Moreover, the historical reservoirs of genetic variation for cucumber, such as India (primary center) and Burma and Southern China (secondary center), are subject to genetic erosion (Tatlioglu, 1993). Often, unadapted cultivars or wild relatives having desirable traits must be introduced into breeding pools to increase the latter's genetic diversity (Duvick, 1990). Genetic diversity in commercial cucumber has been increased by the introduction of genes (i.e., for disease resistance) from exotic germplasm (Peterson, 1975).

Genetic markers have been used to characterize genetic diversity. For example, studies of isozymic variation clarified genetic relationships within and among wild and cultivated *Cucumis* species (Dane, 1983; Esquinas-Alcazar, 1977; Staub et al., 1987 and 1992; Sujatha & Seshadri, 1989; Isshiki et al., 1992), and have described genetic differences among elite cucumber inbreds and hybrids (Staub et al., 1985). Recently, variability in RFLPs distinguished 35 elite lines (5 U.S. processing, 5 U.S. slicing, 2 European processing, 11 European glasshouse, 12 Mediterranean) that are currently cultivated (Dijkhuizen et al., 1996). Staub and Meglic (1993) assessed genetic differences among 590 commercial cucumber cultivars from six European (317) and five U.S. (273) seed companies by analyzing 14 mapped polymorphic isozyme loci. This array of cultivars is representative of the genetic variation present in recently released germplasm (>1980) and inbred lines currently under development in public and private breeding programs.

Modern U.S., European and Mediterranean cucumber types are genetically distinct (Dijkhuizen et al.,

1996), but the level of genetic diversity present in U.S. cucumber cultivars grown over the past century is unknown. Moreover, there have been no direct genetic comparisons of U.S. heirloom (i.e., open-pollinated germplasm past through generations) cultivars, modern European cultivars, and accessions in the U.S. National Plant Germplasm System (NPGS) germplasm collection. Therefore, this study was designed to evaluate genetic relationships among: 1) modern and heirloom U.S. cucumber cultivars, and 2) modern U.S. and European cultivars, and 3) the U.S. national germplasm collection to provide baseline information regarding changes in the genetic structure of commercial cucumber germplasm through time and to compare these results with previous studies (Staub & Meglic, 1993).

Material and methods

One hundred and fifty-five cultivars (107 U.S. and 48 European; Table 1) were surveyed for isozymic variation with horizontal starch gel electrophoresis procedures and techniques described by Meglic and Staub (1995; companion paper, this issue). Each accession and/or cultivar was represented by a random sample of 20 plants. The estimation of allelic frequency using the bulk sampling of plants within an accession possessing homozygous and heterozygous individuals can be inaccurate if alleles are not at or near Hardy-Weinberg equilibrium. During linkage studies of the isozymes used in this study, allelic frequencies were not significantly ($P = 0.05$) different from $p = 0.5$ and $q = 0.5$ (Knerr and Staub, 1992, Meglic & Staub, 1996). In addition, a Chi-square analysis of a random sample of 10 heterozygous PIs and breeding lines indicated that allelic frequencies at 10 loci were not significantly different ($P = 0.05$) than $p = q = 0.5 \pm 0.04$ (unpublished data). Thus, estimates of allelic frequencies were calculated according to Widrlechner et al. (1992).

Isozyme banding patterns observed in 15 enzyme systems for 21 loci (*Ak-2*, *Ak-3*, *Fdp-1*, *Fdp-2*, *Gpi*, *G2dh*, *Gr*, *Idh*, *Mdh-1*, *Mdh-3*, *Mdh-3*, *Mpi-1*, *Mpi-2*, *Pgd-1*, *Pgd-2*, *Per*, *Pep-la*, *Pep-pap*, *Pep-gl*, *Pgm*, and *Skdh*) were recorded for analysis. Genetic nomenclature for describing allozymic variation followed a modified form (Knerr & Staub, 1992; Staub et al., 1985; 1987) previously described by Richmond (1972).

Principal component analysis (PCA) and cluster analysis depicted genetic affinities among modern and heirloom cultivars from the U.S. and Europe. Modern and heirloom U.S. and European cultivars were separated into three groups for analysis: (1) 30 (29 U.S., 1 European) turn-of-the-century cultivars released or mentioned before 1937 (Tapley et al., 1937; Sturtevant, 1919); (2) 28 cultivars released between 1937 and 1968 (Minges, 1972); (3) 97 modern cultivars released after 1968 [U.S. (50) and European (47); Miller & Wehner, 1989] (Table 1). Although the cultivation and use of a particular cultivar depends upon several factors (e.g., quality characteristics, social preferences, regional tastes), the U.S. group consisted mainly of processing (~92 total; 29 1846–1937, 23 1937–1968, 40 > 1968) and market (~15 total; 1 1846–1937, 4 1937–1968, 11 > 1968) types. The European cultivars examined were glasshouse (~28) and processing types (~20) released after 1968. These cultivars were chosen to comprise a diverse sampling of commercial European cucumber germplasm. Allelic frequencies were estimated for each release interval (i.e., 1846–1937, 1937–1968 and > 1968) for all comparisons (Table 2).

The East Indies Gherkin (*Cucumis anguria* L.) and the European cultivar, Windermoor Wonder (released 1917), were used as reference germplasm for comparison to other accessions. *Cucumis anguria* is native to Africa and was brought to the Americas via the slave trade. The fruits are grown mainly by Africans and South Americans for pickling in the immature stage, and in soups and stews when the fruits are mature. 'Windermoor Wonder' was previously analyzed for genetic variation using isozyme analysis and is distinct from modern cucumber cultivars (Staub & Meglic, 1993).

Data were initially subjected to PCA in order to reduce the data matrix for further analysis (Harris, 1975). Cultivars were grouped for analysis according to year of release (3 groups) and region of development (U.S. and Europe). Eigenvalues measured the cumulative portions of the total variance accounted for by each principal component. Cultivars were ordered by overall variation and those with identical isozyme phenotypes were identified. One cultivar from each group with identical principal component scores was then subjected to cluster analysis (complete linkage analysis; Sorensen, 1948; SAS Institute, 1992). Individual cultivars and/or those grouped by release-date categories having similar isozyme phenotypes were clustered together on the resulting dendrogram.

Table 1. The seed source, origin and release date of cucumber (*Cucumis sativus* L.) cultivars analyzed.

Cultivar number	Name of cultivar	Seed source[1]	Origin[2]	Release date	Group in cluster analysis
1	A & C	13	1	1928	1
2	Addis	10	1	>1968	3
3	Arlington White Spine	14	1	1886	1
4	Armstrong Cluster	18	1	1920	6
5	Ashley	3	1	1956	1
6	Athens	18	1	1870	9
7	B 6423	22	1	>1968	1
8	Black Diamond	18	1	1920	9
9	Boston Pickling	14	1	1885	9
10	Brice	18	1	1920	9
11	Burpee Pickler	2	1	1957	7
12	Burpless Muncher	18	1	1940	7
13	Burpless 33	18	1	1933	9
14	Calypso	10	1	>1968	4
15	Carolina	1	1	>1968	8
16	Centurion	17	1	>1968	9
17	Challenger	13	1	1958	1
18	Chemset	1	1	>1968	4
19	Chicago Pickling	14	1	1889	9
20	Chipper	3	1	>1968	4
21	Clinton	10	1	>1968	10
22	Collier	18	1	1960	8
23	Coolgreen	1	1	>1968	7
24	County Fair 87	1	1	>1968	10
25	Cross Country	7	1	>1968	10
26	Crystal Apple	14	1	1933	4
27	Cubit	14	1	1943	10
28	Dasher II	15	1	>1968	20
29	Davis Perfect	14	1	1906	9
30	Delcrow	14	1	1936	9
31	Delicatesse	14	1	1920	8
32	Discover	1	1	>1968	6
33	Double Yield	14	1	1924	4
34	Dublin	20	1	1928	9
35	Early Cluster	14	1	1863	14
36	Early Fortune	14	1	1906	15
37	Early Green Cluster	14	1	1863	4
38	Early Michigan	18	1	1938	17
39	Earlipik 14	17	1	>1968	2
40	Early Russian	14	1	1859	9
41	Early Triumph	15	1	>1968	9
42	Early White Spine	14	1	1906	9
43	Everbearing	14	1	1888	1
44	Fancipak	1	1	>1968	22
45	Fletcher	10	1	1959	9
46	Flurry	1	1	>1968	8

Table 1. Continued

Cultivar number	Name of cultivar	Seed source[1]	Origin[2]	Release date	Group in cluster analysis
47	Galaxy	3	1	>1968	10
48	Geletros	18	1	1900	3
49	Gayheart	18	1	1920	7
50	Green Thumb	8	1	1952	14
51	Gy 3	3	1	1960	3
52	Gy 14	3	1	>1968	5
53	Gynomite	1	1	>1968	6
54	Helwa Prolific	18	1	1960	11
55	Highmark	1	1	>1968	2
56	Homegreen # 2	10	1	1960	13
57	Hylares	18	1	1920	7
58	Improved Burbone	18	1	1892	1
59	Klondike	14	1	1902	10
60	Longfellow	18	1	1927	16
61	M 21	10	1	>1968	7
62	M 41	10	1	>1968	13
63	Magic	1	1	>1968	8
64	Magnolia	14	1	1949	10
65	Marketmore	18	1	1968	1
66	Medaust	18	1	>1968	9
67	Model	14	1	1946	1
68	Morden Early	18	1	1956	8
69	MSU 9429M	9	1	>1968	10
70	Nappa 63	14	1	1963	4
71	National Pickling	14	1	1924	4
72	Packer	18	1	1946	10
73	Pick	3	1	>1968	1
74	Pickmaster	17	1	>1968	6
75	Pickalot	2	1	>1968	11
76	Pik Rite	7	1	>1968	6
77	Pixie	3	1	1963	9
78	PMR 551	4	1	>1968	9
79	Poinsett	3	1	1966	7
80	Poinsett 76	4	1	>1968	6
81	Polaris	3	1	1961	9
82	Producer	14	1	1945	9
83	Prolific	19	1	>1968	9
84	Regal	10	1	>1968	13
85	Richmond Green Apple	18	1	1920	18
86	Royal	8	1	>1968	14
87	Salvo	15	1	>1968	8
88	Samson	15	1	>1968	14
89	SC 10	3	1	1960	3
90	SC 57M	3	1	1960	10
91	Score	1	1	>1968	12
92	Sentry	15	1	>1968	14
93	Slice	3	1	>1968	9

Table 1. Continued

Cultivar number	Name of cultivar	Seed source[1]	Origin[2]	Release date	Group in cluster analysis
94	Slice Max	19	1	>1968	6
95	Space Master	4	1	>1968	9
96	Spartan Salad	9	1	1964	10
97	Sprint 440	1	1	>1968	6
98	Straight 8	22	1	1935	19
99	Sumter	3	1	>1968	8
100	Sunny South	14	1	1920	10
101	Tablegreen 72	4	1	1961	10
102	Tamor	1	1	>1968	8
103	Target	15	1	>1968	14
104	Transamerica	7	1	>1968	4
105	WI 1902	22	1	>1968	8
106	WI 1983	22	1	>1968	9
107	WI 2757	22	1	>1968	24
108	Zeppelin	18	1	1920	3
109	A 850945	12	2	>1968	23
110	Anushka	16	2	>1968	13
111	Arabel	11	2	>1968	13
112	Aricia	6	2	>1968	4
113	Aurelia	6	2	>1968	1
114	B 880027	12	2	>1968	21
115	Banza	6	2	>1968	10
116	Bella	11	2	>1968	6
117	Bellita	6	2	>1968	1
118	Bivugeel	11	2	>1968	1
119	Boloria	6	2	>1968	1
120	Caprice	6	2	>1968	4
121	Colias	6	2	>1968	7
122	Dugan	11	2	>1968	4
123	Elka	11	2	>1968	4
124	Euphya	6	2	>1968	1
125	Gergana	11	2	>1968	25
126	Girola	6	2	>1968	7
127	Ilonca	11	2	>1968	14
128	Indira	11	2	>1968	1
129	Jazzer	6	2	>1968	11
130	K 907287	12	2	>1968	22
131	Kamaron	6	2	>1968	9
132	Khalifa	6	2	>1968	11
133	Kivia	6	2	>1968	10
134	Levo	11	2	>1968	4
135	Lora	11	2	>1968	9
136	Lutra	6	2	>1968	11
137	Maresto	11	2	>1968	14
138	Marinda	16	2	>1968	14
139	Melani	16	2	>1968	8
140	Papilio	6	2	>1968	1

Table 1. Continued

Cultivar number	Name of cultivar	Seed source[1]	Origin[2]	Release date	Group in cluster analysis
141	Parker	11	2	>1968	8
142	Parmel	11	2	>1968	14
143	Paska	11	2	>1968	8
144	Pauca	16	2	>1968	8
145	Petita	6	2	>1968	4
146	Picobello	5	2	>1968	1
147	Profi	11	2	>1968	8
148	Radja	11	2	>1968	4
149	Sandra	11	2	>1968	6
150	Saskia	11	2	>1968	4
151	Seify	11	2	>1968	13
152	Seiram	11	2	>1968	26
153	Silor	11	2	>1968	14
154	Talgo	11	2	>1968	8
155	Tomara	11	2	>1968	14
156	West indian gherkin[3]	18	2	1846	28
157	Windermoor wonder[4]	18	20	1917	27

[1] 1 = Asgrow Seed Co., Kalamazoo, MI; 2 = Burpee Seed Co., Warminster, PA; 3 = Clemson University, Charleston, SC; 4 = Cornell University, Ithaca, NY; 5 = De Ruiter Zonen, Bleiswijk, The Netherlands; 6 = Enza Zaden, Einkhuizen, Holland; 7 = Ferry-Morse Seed Co., Modesto, CA; 8 = Harris Moran Seed Co., Davis, CA; 9 = Michigan State University, East Lansing, MI; 10 = North Carolina State University, Raleigh, NC; 11 = Nunhems Zaden BV, Haelen, The Netherlands; 12 = Nickerson-Zwaan, Barendrecht, The Netherlands; 13 = Niagara, Canada; 14 = National Seed Storage Laboratory, Fort Collins, CO; 15 = Petoseed Co., Saticoy, CA; 16 = Royal Sluis, Einkhuizen, Holland; 17 = Rodgers NK Seed Co., Naples, FL; 18 = Seed Savers Exchange, Decorah, IA; 19 = Sakata Seed America, Morgan Hill, CA; 20 = Stokes Seeds, Buffalo, NY; 21 = Sunseeds, Hollister, CA; 22 = U.S. Department of Agriculture, Agriculture Research Service, Madison, WI.

[2] 1 = United States; 2 = Europe.

[3] *Cucumis anguria* L. of African origin.

[4] Heirloom European cucumber.

Results and discussion

In previous studies, the degree of variation at 21 isozyme loci established the genetic diversity present in the U.S. cucumber collection (Meglic & Staub, 1995; companion paper, this issue) and 14 loci played a similar role for modern U.S. and European cultivars and breeding lines (Staub & Meglic, 1993). In the present study, 21 isozyme loci were assessed in 157 heirloom and modern cultivars from Europe and U.S. which were grouped according to their release date (Table 1). Four loci (*Fdp-1, Mdh-1, Mpi-1* and *Pgd-1*) were monomorphic in these accessions and thus not used in the analyses. The first three principal components explained ~70% of the total variation in the inter-character correlation matrix.

Comparisons among heirloom and modern U.S. cultivars

Cluster analysis depicted two distinct groups of cultivars; U.S. cultivars released before and in 1968 (i.e., 1846–1937 and 1937–1968) and those released after 1968 (data not presented; Meglic 1994). These groups are based on Euclidean distance such that the average maximum distance between clusters (MDC) can be measured. The MDC between cluster groupings of U.S. cultivars released before 1968 and those released after 1968 was considerable (0.45).

Table 2. Allelic frequencies at 21 enzyme coding loci in cucumber (*Cucumis sativus* L.).

Enzyme locus	Allele	Frequencies	Period when cultivars were released			
		U.S. NPGS germplasm collection	U.S. 1846–1937	U.S. 1938–1968	U.S. >1968	Europe >1968
Ak-2	1	0.87	0.53	0.46	0.47	0.60
	2	0.13	0.47	0.54	0.53	0.40
Ak-3	1	0.59	0.30	0.35	0.35	0.22
	2	0.41	0.70	0.65	0.65	0.78
Fdp-1	1	0.99	1.00	1.00	1.00	1.00
	2	0.01	0.00	0.00	0.00	0.00
Fdp-2	1	0.57	0.40	0.43	0.47	0.33
	2	0.43	0.60	0.57	0.53	0.67
Gpi	1	0.04	0.00	0.47	0.67	0.92
	2	0.96	1.00	0.53	0.33	0.08
G2dh	1	0.01	0.00	0.06	0.00	0.00
	2	0.99	1.00	0.94	1.00	1.00
Gr	1	0.92	1.00	1.00	1.00	0.97
	2	0.08	0.00	0.00	0.00	0.03
Idh	1	0.01	0.00	0.06	0.00	0.00
	2	0.99	1.00	0.94	1.00	1.00
Mdh-1	1	0.99	1.00	1.00	1.00	1.00
	2	0.01	0.00	0.00	0.00	0.00
Mdh-2	1	0.05	0.06	0.00	0.36	0.05
	2	0.95	0.94	1.00	0.64	0.95
Mdh-3	1	0.82	0.94	0.94	0.87	0.82
	2	0.18	0.06	0.06	0.13	0.18
Mpi-1	1	0.03	0.00	0.00	0.00	0.00
	2	0.97	1.00	1.00	1.00	1.00
Mpi-2	1	0.52	1.00	1.00	0.54	0.49
	2	0.48	0.00	0.00	0.46	0.51
Pgd-1	1	0.99	1.00	1.00	1.00	1.00
	2	0.01	0.00	0.00	0.00	0.00
Pgd-2	1	0.40	0.11	0.29	0.38	0.34
	2	0.60	0.89	0.71	0.62	0.66
Per	1	0.99	1.00	0.92	0.79	0.97
	2	0.01	0.00	0.08	0.21	0.03
Pep-la	1	0.80	0.95	1.00	1.00	1.00
	2	0.20	0.05	0.00	0.00	0.00
Pep-pap	1	0.99	1.00	0.94	0.98	0.61
	2	0.01	0.00	0.06	0.02	0.39
Pep-gl	1	0.64	0.68	0.81	0.93	0.68
	2	0.36	0.32	0.19	0.07	0.32
Pgm	1	0.29	0.56	0.47	0.26	0.58
	2	0.71	0.44	0.53	0.74	0.42
Skdh	1	0.02	0.06	0.00	0.00	0.00
	2	0.98	0.94	1.00	1.00	1.00

The heirloom cultivars were representative of the genetic diversity present in open pollinated cucumber populations between 1846 and 1937. Cultivars released between 1937 to 1968 pre-date the broad use of F_1 hybrids in commercial production. These cultivars typify U.S. genotypes with a superior fruit shape, fruit color, fruit yield, non-bitterness and disease resistance (e.g., 'Early Michigan') as compared to heirloom cultivars. Often, simply-inherited traits found in exotic germplasm were incorporated by backcrossing and/or simple pedigree selection. The newer U.S. and European hybrid cultivars (>1968) are uniform for production and culinary characteristics as well as adaptation to specific growing conditions. Each cucumber type is the result of selecting different morphological traits, according to market preferences.

One possible explanation for the observed broad groupings (1846–1937, 1937-1968 and >1968) is the increased emphasis placed on specific selection criteria (e.g., brine quality, disease resistance) during breeding in the U.S. For instance, modern genotypes are highly resistant to disease resistance as compared to heirloom cultivars. Some disease resistance genes are linked to isozyme loci (e.g., *Per* and *Pgm* flank *dm* which conditions resistance to downy mildew; Kennard et al., 1994; Meglic, 1994), and these linkages may have affected the frequencies of specific allozymes. This hypothesis is partially supported by the association of alleles (progressive increase) *Per (2)*'s and *Pgm (2)*'s frequencies with downy mildew resistance during the cultivar release periods examined (Table 2).

Comparisons between U.S. and European cultivars

Modern U.S. and European cultivars (>1968) differed by isozyme frequency (Table 2). The present study investigated variation at 7 loci (*Ak-3*, *Fdp-1*, *Fdp-2*, *Idh*, *Mpi-1*, *Pep-la*, and *Skdh*) not evaluated by Staub and Meglic (1993). In addition to those loci reported by Staub and Meglic (1993), variation at *Ak-3* and *Fdp-2* was useful for comparing cultivars.

Allele frequency, as well as frequency of appearance of alleles in nine isozyme loci may be a reliable predictor of survival ability in landraces of maize (Allard, 1992). Selection pressures during recurrent mating cycles can often lead to increases in the frequency of prevalent alleles and to the elimination of infrequent alleles that have selective value. An increase in the frequency of specific alleles in commercial cucumber through time may indicate that these alleles are associated with some economically desirable traits. Likewise, isozymes whoses frequencies decrease over time might indicate instances isozymes associated with undesirable attributes. In cucumber, alleles that are infrequent in landraces are rarely found in advanced germplasm (i.e., elite lines), and thus the fixed loci observed in cucumber may be important for general fitness (i.e., alleles contributing to a high level of adaptation to contemporary growing conditions).

The allelic frequencies of *Ak-3 (1) Fdp-2 (1)* and *Gr (2)* were lower in European cultivars than in U.S. cultivars. Similarly, the frequencies of *Mdh-2(1)* and *Per (2)* were very low (5% and 3%, respectively) in European cultivars and moderately low (36% and 21%, respectively) in U.S. cultivars. These alleles might be associated with traits which received differing selection pressure. For instance, *Fdp-2* is loosely linked (~24 cM) to the gene (*Ccu*) which conditions resistance to target leaf spot resistance (TLS) (Meglic, 1994). Although selection for TLS resistance is the focus of some U.S. breeding programs, it is not an important pathogen in many European production areas. In contrast, *Pep-gl (2)* was infrequent (7%) in modern U.S. cultivars but more frequent (32%) in European germplasm, in which *Fdp-1, Idh, Mpi-1, Pep-la* and *Skdh* were fixed. Likewise, *Mpi-2 (3)* and *Mpi-2 (4)* were reported to be fixed in the accessions studied by Staub and Meglic (1993).

Cluster analysis of cultivars resulted in a dendrogram with 14 nodes and 28 clustered groups (Figure 1). Cluster analysis placed two entries, *Cucumis anguria* (cluster 28; MDC = 9.2) and 'Windermoor Wonder' (cluster 27; MDC = 4.0) in two distinct nodes (nodes 1 and 2, respectively; Figure 1). *C. anguria* possesses unique alleles for *Per (2), G2dh (2), Gpi (2)* and *Idh (1)*. Likewise, 'Windermoor Wonder' possesses unique alleles for *Mdh-2(1)*. West Indian gherkin and Windermoor Wonder are the only cultivars with the *Mdh-3(2)* allele. These results agree with those reported by Staub and Meglic (1993).

Cultivars in cluster groupings 20 to 26 are all modern cultivars or lines, and based on their isozyme profiles and source are considered different from the remaining cultivars (Figure 1). Cluster groups 1, 4, 6, 8, 9, 19, and 14 collectively include 101 (~64%) of the cultivars examined. 'Gergana' and 'Seiram' (Nunhems Zaden BV), two modern European hybrids formed a cluster at node 3 (Cluster grouping = 24 & 25; MDC = 2.0). 'Seiram' is of Japanese origin and is a cold tolerant, long-fruited open pollinated variety (personal communication, G. Reuling, 1994). 'Gergana' is a vigorous, monoecious variety which bears long, dark green fruit, and was derived from a Japanese accession

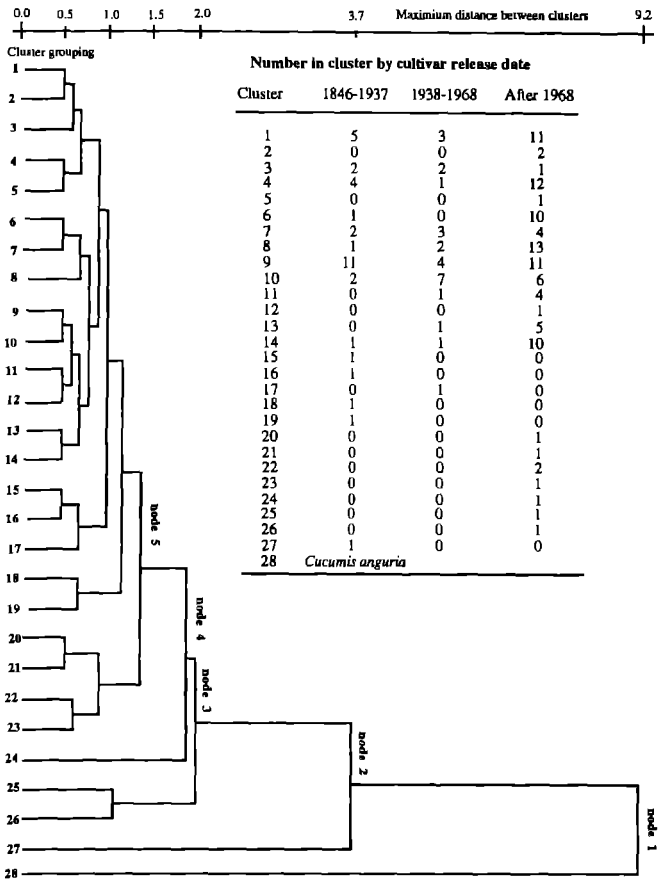

Figure 1. Cluster analysis (complete linkage method) depicting genetic affinities among 157 cucumber cultigens assayed for 21 isozyme loci.

(Japanese #101; personal communication, M. Alexandrova, 1996). Recurrent selection (3 cycles) for fruit type (cylinderical and ~28 cm in length), color and quality produced three selections that did not segregate for morphological characteristics. Seed of these selections were bulked, and the resulting bulk was named 'Gergana' (Maritsa Institute-Plovdiv, Bulgaria). 'Gergana' possesses resistance to powdery mildew and cucumber mosaic virus under outdoor plastic culture in Bulgaria.

Although of Japanese origin, 'Gergana' and 'Seiram' are apparently not directly related. They do, however, carry unique allelic composition for *Gr* ['Gergana' is heterozygous (12) and 'Seiram' is homozygous (11)]. WI 2757 which has a complex pedigree incorporating several exotic accessions is distinct from the other cultivars analyzed (Cluster grouping 24; node 4, MDC = 1.8; Peterson et al., 1986). It is the only accession heterozygous for *Pep-la*. Four modern cultivars were separated from the rest of the entries in node 5 (MDC = 1.3). This node is comprised of a U.S. processing (Fancipak) and slicing (Dasher 2), and two unreleased European glasshouse cultivars (B 880027, K 907287) of diverse parentage (Miller and Wehner, 1989; personal communication Kees Hertogh, 1994). The remaining 9 nodes (6–14) share strong biochemical affinities (MDCs from 0.9 to 0.5), and thus discriminating these cultivars is difficult.

Comparisons of heirloom and modern cultivars with the U.S. NPGS collection

The U.S. NPGS cucumber germplasm collection is composed of exotics [i.e., *C. sativus* var. *hardwickii* (R.) Alef.], landraces, and phenotypically uniform cultivars. Isozyme variation present in the U.S. NPGS cucumber collection differs from the cultivars examined in this study. In Staub and Meglic's (1993) comparison of exotic germplasm and elite cultivars, some alleles that were frequent in the U.S. collection were infrequent in the commercial cultivars examined. In

this study, allelic frequencies at certain loci (e.g., *Gr, Mdh-3, Pgd-1, Idh*) were similar throughout the five groups of cultivars examined (Table 2). Allelic frequencies at some other loci [*Ak-2(2), Ak-3(2), Gpi(1), Pep-la(1)* and *Pep-gl(1)*] were low in the U.S. collection as compared to the other cultivars examined. For instance, the frequency of *Ak-2(2)* across the U.S. NPGS collection was 13%, but its frequency in modern commercial cultivars (U.S and European) ranged between 40 to 53%. Conversely, some alleles were frequent in the U.S. NPGS collection but relatively infrequent in the modern cultivars examined. For example, the frequency of *Gpi (2)* was high in the U.S. NPGS collection (96%) and in the turn of the century cultivars (100%), but decreased to 53% in U.S. cultivars released between 1937 to 1968, and was 33% in newer U.S. cultivars. Its frequency was often lower (8%) in modern European cultivars. There were also instances (e.g., *Mpi-2*) where allelic frequencies remained unchanged (~50%) in the U.S. collection and in modern U.S. and European cultivars, but were absent from older U.S. cultivars (1846–1937 and 1937–1968). In some instances, alleles that were rare in the U.S. collection [e.g., *Fdp-1(1), Mpi-1(1), Pgd-1(2)*] were absent from any modern commercial cultivars.

This study characterized genetic variation within and among cucumber cultivars which had not previously been examined isogeographically. Cluster analysis partitioned cultivars into two distinct groups and clearly discriminated among some cultivars with unique attributes and/or pedigrees, based on their market type and source. Certain economically important traits are linked to isozymes (Kennard et al., 1994; Meglic & Staub, 1995). Thus, one way to determine the potential value of cultivars could be to evaluate them for isozymes linked to these traits. Cultivars with unique morphological attributes and broad genetic variation should be considered potential candidates for developing populations for increasing genetic variation in cucumber breeding programs.

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