Plant Syst. Evol. 226: 129–142 (2001)

Plant Systematics and Evolution

Genetic structure and differentiation of wild and domesticated populations of *Capsicum annuum* (Solanaceae) from Mexico

S. Hernández-Verdugo[1], **R. Luna-Reyes**[2], and **K. Oyama**[3]

[1]Facultad de Agronomía, Universidad Autónoma de Sinaloa, Culiacán, Sinaloa, México
[2]Instituto de Ecología, UNAM, México
[3]Instituto de Ecología, UNAM, México

Received May 5, 1999
Accepted October 30, 2000

Abstract. Genetic variation and structure of ten wild, three domesticated and one wild-cultivated populations of pepper (*Capsicum annuum*) from northwestern Mexico were studied in order to find out if the domestication process has reduced the genetic variation of the modern cultivars of this species. The analysis was based on 12 polymorphic loci from nine isozymes. Wild populations were sampled in different habitats along a latitudinal gradient of ca. 500 km. All populations had high genetic variation (i.e. wild: $A = 2.72$, $P = 90.8\%$, $He = 0.445$; wild-cultivated: $A = 2.50$, $P = 92.3\%$, $He = 0.461$; domesticated: $A = 2.60$, $P = 84.6\%$, $He = 0.408$), indicating little genetic erosion in modern cultivars of pepper. Genetic diversity estimated by Nei's method showed that most genetic variation is found within, rather than among populations. However, genetic differentiation is greater among cultivated ($G_{ST} = 0.167$) than among wild ($G_{ST} = 0.056$) populations. Wild populations had an average genetic identity (I) of 0.952, indicating little differentiation and high gene flow ($Nm = 4.21$) among these populations. Average genetic identity between wild and domesticated populations was of $I = 0.818$, revealing that the domestication process has modified the genetic composition of commercial varieties of pepper. Changes in genetic composition among commercial varieties seem to have occurred in different directions, as indicated by the average value of $I = 0.817$ among these populations. The high level of diversity found in wild populations of *C. annuum* suggests that the wild relatives of cultivated peppers are a valuable genetic resource which must be conserved.

Key words: *Capsicum annuum*, Solanaceae, population genetics, genetic differentiation, domestication.

The capability of a species for evolutionary change depends on the amount of its genetic variation and on how this variation is allocated among and within populations. The non-random distribution of genetic variation in conspecific populations is known as the genetic structure of these populations. This structure is determined by factors such as mutation rate, random genetic drift, natural selection and gene flow (Wright 1949, 1951), and by ecological factors including life history, mating system, geographic distribution and dispersal mechanisms (Hamrick et al. 1979, Loveless and Hamrick 1984, Hamrick and Godt 1990).

During their process of domestication, cultivated plant species are dispersed beyond their centers of origin and are canalized to adapt to different ecological conditions

(Harlan 1992). Likewise, populations of cultivated plants are subjected to strong selective pressures (Dogget and Majisu 1968) which result in modifications of their natural mating systems and mechanisms for dispersal (Pickersgill 1969), as well as in changes in their morphology, physiology (Harlan et al. 1973, Pickersgill et al. 1979, Ladizinsky 1985), and in their genetic structure (Doebley 1989).

All these changes cause cultivated populations to differentiate with respect to their wild progenitors and their close relatives. Changes in morphology are more perceptible in parts which are of human interest such as size, color and form of fruits (Pickersgill et al. 1979), or number and size of seeds (Harlan 1992). In the case of seed-propagated plants, the physiological characteristics which have been most modified by artificial selection are the loss of natural mechanisms for dispersal and seed dormancy (Ladizinsky 1985).

In general, the populations of the wild relatives of cultivated plants maintain high levels of generic variation (Kahler and Allard 1981, Ellstrand and Marshall 1985, Doebley 1989). The genetic variation of populations of cultivated plants, compared to that of their wild progenitors, is more frequently found among, rather than within populations (Doebley 1989). Comparison of levels of allozyme variation between wild and cultivated populations of 21 species indicated that cultivated populations have less genetic variation than their respective wild counterparts (Doebley 1989) with the exception of cultivated *Cucurbita pepo* and its putative wild relative *C. texana* (Decker and Wilson 1987).

The genus *Capsicum* (Solanaceae) originated in South America (Hunziker 1979) includes ca. 30 species, ranging from southern United States of America to northern Argentina (Eshbaugh 1980, Pickersgill 1984). The domesticated species of the genus are *C. annuum* L., *C. frutescens* L., *C. chinense* Jacq., *C. baccatum* L. and *C. pubescens* Ruiz & Pav.. *Capsicum annuum* is the cultivated species with the greatest economic importance, both worldwide and in Mexico, where it was putatively domesticated (Pickersgill 1971, 1984). This species is also the pepper with the greatest variation in size, form and color of its fruits. Some of the most important types are, among others, the pungent "serranos" and "jalapeños", and the sweet "morrones" or "bell peppers".

Studies of isozymes in the genus *Capsicum* have shown that domesticated species and their close relatives maintain low levels of genetic variation (McLeod et al. 1983, Loaiza-Figueroa et al. 1989). Nevertheless, these results were based on a small number of individuals from each accession studied; it is thus possible that the genetic variation in populations of these species was underestimated. The first step towards the conservation, use, and management of the genetic resources, existing in wild relatives of cultivated plants, is to know the genetic variation they contain and the pattern of distribution of such variation (Vida 1994).

Genetic resources from wild relatives of cultivated plant species represent a gene reservoir which may be utilized in breeding of commercial varieties, and in solutions of agricultural problems such as conferring pest and disease resistance, or increasing quality and yield (Watson 1970, Harlan 1976, Stalker 1980, Hawkes 1983, Burdon and Jarosz 1989).

Wild plants of *C. annuum* are short-lived perennial, erect or climbing herbs up to 4 m tall (D'Arcy and Eshbaugh 1974, Hernández-Verdugo et al. 1999). Generally, there is a single white flower per node; the calyx may have rudimentary indentations or not. Its fruits are small, erect, deciduous, red and pungent (D'Arcy and Eshbaugh 1974), and these are eaten and dispersed by birds (Laborde and Pozo-Campodónico 1982, Pozo-Campodónico et al. 1991, Vázquez-Dávila 1996). Wild populations of *C. annuum* can be found throughout Mexico in undisturbed sites of tropical deciduous forests, in orchards, in pasture grasslands, and along roads (Hernández-Verdugo et al. 1999) which rarely exceed 1000 m altitude (D'Arcy and Eshbaugh 1974).

A study of the resistance to the PHV geminivirus ("Pepper Huasteco Virus") of wild

populations of *C. annuum* from northwestern Mexico revealed high levels of variation, and two populations with high resistance to the virus (Hernández-Verdugo et al. in press). Plants from these populations also exhibited high levels of morphological variation in characters such as height and width of plants, leaves and of fruits, number and weight of seeds per fruit, and others. Additionally, the same populations showed high variation in their responses to germination factors, differing from seeds of cultivated populations in having dormancy mechanisms as evidenced by their inability to germinate in the dark (Hernández-Verdugo et al. 1998).

The present isozyme survey attempts to clarify the genetic structure and differentiation of wild and cultivated populations of *C. annuum*, aiming at the management and conservation of the genetic resources from wild populations of pepper. The objectives of this study are to: 1) estimate the genetic variation of wild, wild-cultivated and domesticated populations; 2) compare the levels of genetic variation present in wild populations of *C. annuum* with previous results derived from agronomic accessions of this species (McLeod et al. 1983, Loaiza-Figueroa et al. 1989); 3) clarify if the domestication process has eroded the level of genetic variation in cultivated populations of *C. annuum*; 4) describe the distribution of genetic variation within and among populations of wild, wild-cultivated and domesticated populations of *C. annuum*; and 5) estimate the amount of gene flow between wild populations of *C. annuum*.

Materials and methods

Plant material and collection sites. Samples of *Capsicum annuum* were collected from ten wild, one wild-cultivated, and three domesticated populations in northwestern Mexico. Wild populations are located in a latitudinal gradient of 500 km from 108°33′ N to 105°55′ N, at altitudes ranging from 3 to 390 m (Table 1). The closest collection sites of wild populations (ABL and ALC) were 24.4 km apart; the most distant populations (PAJ and OTA) were 476.8 km apart. The wild-cultivated population (FUE) was collected in a home garden in the town of El Fuerte. Cultivated samples belong to the pungent types "serrano" (PON) and "jalapeño" (BJU), and to a sweet, "morrón" or "bell pepper" (CBA). The average number of plants sampled per wild population was 47.2, with a range of 35–60. Forty plants were sampled in each cultivated population studied, and 12 plants were

Table 1. Collection data for the populations of *C. annuum* studied: locality, abbreviation, sample size, status (wild, wild-cultivated, domesticated), latitude (N), longitude (W), and altitude (m)

Population	Abbreviation	Sample size	Status	Lat.	Long.	Alt.
Pajaritos	PAJ	39	Wild	26°41′	108°33′	200
Yecorato	YEC	45	Wild	26°29′	108°15′	390
Tehueco	TEH	48	Wild	26°20′	108°45′	50
Texcalama	TEX	40	Wild	25°43′	108°03′	380
El Reparo	REP	60	Wild	25°31′	107°51′	200
Aguas Blancas	ABL	45	Wild	24°54′	107°19′	80
Alcoyonqui	ALC	60	Wild	24°43′	107°12′	85
Chapeteado	CHP	35	Wild	24°29′	107°26′	3
Tabalá	TAB	50	Wild	24°24′	107°05′	50
Otates	OTA	50	Wild	23°02′	105°55′	120
El Fuerte	FUE	12	Wild-cultivated	26°48′	108°37′	80
Ponce	PON	40	Domesticated	22°59′	105°51′	20
Benito Juárez	BJU	40	Domesticated	26°48′	109°00′	10
Campo Bátiz	CBA	40	Domesticated	24°48′	107°23′	60

screened from the single wild-cultivated population. In every population 9–15 leaves were collected per individual to be used for electrophoresis. Leaf samples were transported to the laboratory in liquid nitrogen, and were stored at −80 °C until electrophoresis.

Protein electrophoresis. Leaf samples of all plants screened were ground in extraction buffer, which was prepared with three parts YO buffer (Yeh and Malley 1980) and one part Veg II buffer (Cheliak and Pitel 1984). The ground material was absorbed in wicks of filter paper (Whatman No. 17) and inserted into horizontal starch (Sigma, S4501) gels which had a concentration of 11.5% for maize system C, 12.0% for maize system D (Stuber et al. 1988), and 12.5% for the PP system of Mitton et al. (1979). Nine enzymes were resolved in these three gel systems. Maize system C resolved glutamate oxaloacetate transaminase (*GOT*, E.C.2.6.1.1), peroxidase (*APX* and *CPX*, E.C.1.1.1.7), malic enzyme (*ME*, E.C.1.1.1.40), and phosphoglucose-isomerase (*PGI*, E.C.5.3.1.9). Maize system D resolved isocitrate dehydrogenase (*IDH*, E.C.1.1.1.42), malate dehydrogenase (*MDH*, E.C.1.1.1.37), and 6-phosphogluconate isomerase (6-*PGD*, E.C.1.1.1.44), and system PP acid phosphatase (*ACPH*, E.C.3. 1.3.2) and menadione reductase (*MNR*, E.C.1.6.9.2). The electrode buffer of maize system C was prepared with 0.19 M boric acid, 0.04 M lithium hydroxide, and the pH was adjusted to 8.3. The gel buffer for this system was prepared mixing one part electrode buffer with nine parts of a 0.05 M Trizma Base and 0.007 M citric acid buffer, adjusting the pH to 8.3. The electrode buffer of the maize system D was made with 0.065 M L-histidine and 0.007 M citric acid, the pH adjusted to 6.5; the gel system was prepared diluting the electrode buffer with distilled water in a proportion of 1:4. The electrode buffer of the PP system contained 0.031 M sodium hydroxide and 0.295 M boric acid with the pH adjusted to 7.5; the gel buffer had 0.015 M tris and 0.295 citric acid, pH 7.5.

Statistical analyses. The level of genetic variation in all populations studied was assessed using the program BIOSYS-1 (Swofford and Selander 1981). Estimates were computed of the average number of alleles per locus (*A*), the proportion of polymorphic loci (*P*), the average observed heterozygosity (*Ho*), and the average expected heterozygosity (*He*) under Hardy-Weinberg equilibrium. A chi-square test was made to test for statistical significance of the deviations between observed and expected gene frequencies. The fixation index (*F*) (Wright 1921) was estimated for each polymorphic locus and population; it measures the decrease in number of heterozygous plants due to non-random mating between individuals. The significance of the differences from zero of F values was tested by $X^2 = N\mathrm{F}^2(k-1)$, with $\mathrm{df} = [k(k-1)]/2$, where $N =$ sample size, and $k =$ number of alleles per locus (Li and Horvitz 1953).

Genetic diversity, defined as the frequency of heterozygous individuals that is expected under Hardy-Weinberg equilibrium, was divided within and among population levels (Nei 1973, 1987). Total (H_T), within population (H_S),and between population (D_{ST}) genetic diversity, and the genetic differentiation coefficient (G_{ST}) are related by: $H_T = H_S - D_{ST}$ and $G_{ST} = D_{ST}/H_T$.

Wright's *F*-statistics, F_{IS}, F_{IT} and F_{ST} (Wright 1951) were estimated following Weir and Cockerham's (1984) method. The relation of these *F*-statistics is given by: $1 - F_{IT} = (1 - F_{IS})(1 - F_{ST})$. F_{IS} and F_{IT} are the correlations between allele pairing in an individual, relative to the subpopulations and the total population respectively. Both indices (F_{IS} and F_{IT}) measure the reduction in the number of heterozygous individuals due to non-random matings between individuals within subpopulations and in the total population, respectively. F_{ST} measures the correlation between two alleles picked at random from each population, and it assesses the amount of population differentiation. F_{IS} and F_{IT} may have negative values, while F_{ST} is always positive (Wright 1951). Mean values of *F*-statistics and their variances were estimated by jackknifing over populations, and a summary value for each one was estimated by jackknifing over all loci. Significance of the difference from 0 of the "Jackknifed" means was assessed by *t*-tests. The 95% confidence intervals (CI) for the summary *F*-statistic values were estimated by the bootstrap procedure with 1000 iterations (Weir 1990).

Indirect estimations of the amount of gene flow between wild populations were made from G_{ST} values (Nei 1973, 1997) by the formula: $Nm = (1/G_{ST} - 1)/4$ (Wright 1951), where *Nm* is the number of migrants per generation. Nei's method was used to estimate Wright's F_{ST} values (Nei 1977), because computer simulations (Slatkin and Barton 1989) have shown that this method is less biased than that of Weir and Cockerham (1984). Average genetic

identities and distances (Nei 1972) were estimated for all pairwise-comparisons of subpopulations, and a dendrogram was made from this values by the unweigthed pair group method with arithmetic averaging (UPGMA) (Sneath and Sokal 1973).

Results

In total 12 polymorphic loci from nine enzyme systems were analyzed in all populations of *C. annuum*: *Acph-2*, *Apx-1*, *Cpx-1*, *Cpx-2*, *Got-1*, *Idh-2*, *Mdh-2*, *Mdh-4*, *Me-1*, *Mnr-1*, *6-Pgd-2,* and *Pgi-1*. The loci *Cpx-1* and *Cpx-2* were monomorphic in one cultivated population (CBA), and locus *Mdh-3* was monomorphic in all populations studied. Nine additional loci did not consistently resolve in all populations and were not analyzed.

Genetic variation. A total of 35 alleles was recorded in the 12 loci of the nine enzyme systems analyzed in the wild populations; 38 alleles in the cultivated populations; and, 32 in the wild-cultivated population. More alleles were found in cultivated populations, which was due to the exclusive alleles of these populations do not share with the other populations (Appendix).

The average number of alleles per locus (*A*) in the studied populations of *C. annuum* was 2.7, ranging from 2.5 to 2.8 in the wild, and from 2.4 to 2.8 in cultivated populations (Table 2). The average percentage of polymorphic loci (*P*) was 90.8 in wild, and 84.6 in cultivated populations, ranging, respectively, from 84.6 to 92.3, and from 76.9 to 92.3. Average observed (*Ho*) and expected heterozygosity (*He*) was 0.296 (0.234–0.336), and 0.445 (0.385–0.494) for wild; and 0.259 (0.199–0.315), and 0.408 (0.351–0.466) for cultivated populations, respectively (Table 2). In all populations, *He* exceeded *Ho*, which indicates a deficiency of heterozygous individuals. The

Table 2. Genetic variation parameters estimated for wild, wild-cultivated and domesticated populations of *C. annuum* studied: sample size (*N*), number of alleles per locus (*A*), percentage of polymorphic loci (*P*), observed heterozygosity (*Ho*), and expected heterozygosity (*He*). Standard errors (SE) are given in parentheses

Populations	*N*	*A*	*P*	*Ho*	*He*
Wild					
PAJ	36	2.8	92.3	0.309 (±0.060)	0.406 (±0.058)
YEC	33	2.7	92.3	0.286 (±0.060)	0.440 (±0.054)
TEH	33	2.7	92.3	0.257 (±0.041)	0.401 (±0.055)
TEX	23	2.5	84.6	0.234 (±0.041)	0.385 (±0.056)
REP	34	2.8	92.3	0.310 (±0.054)	0.465 (±0.059)
ABL	37	2.8	92.3	0.336 (±0.061)	0.494 (±0.051)
ALC	41	2.8	92.3	0.316 (±0.044)	0.453 (±0.045)
CHP	26	2.7	84.6	0.308 (±0.051)	0.459 (±0.056)
TAB	34	2.6	92.3	0.288 (±0.064)	0.463 (±0.057)
OTA	33	2.8	92.3	0.316 (±0.059)	0.484 (±0.052)
Average	**33.0**	**2.7**	**90.8**	**0.296**	**0.445**
Wild-cultivated					
FUE	10	2.5	92.3	0.245 (±0.074)	0.461 (±0.057)
Domesticated					
PON	24	2.8	92.3	0.315 (±0.066)	0.466 (±0.052)
BJU	33	2.6	84.6	0.262 (±0.050)	0.407 (±0.054)
CBA	33	2.4	76.9	0.199 (±0.051)	0.351 (±0.061)
Average	**30.0**	**2.6**	**84.6**	**0.259**	**0.408**

wild-cultivated population (FUE) had an average of 2.5 alleles per locus, 92.3% of the loci were polymorphic, and estimates of *H*o and *H*e were 0.245 and 0.461, respectively.

Fixation indices. The fixation index (F) measures the proportional reduction of heterozygosity in a population in relation to that expected under Hardy-Weinberg equilibrium. Values of F which do not significantly differ from zero indicate that the population is in Hardy-Weinberg equilibrium at those loci, i.e., mating among individuals occurs randomly. Values of F being significantly larger than zero indicate heterozygous deficiency, and those significantly smaller than zero indicate heterozygous excess.

Out of 119 estimates of F made for the 12 polymorphic loci recorded in the wild populations, 63 (52.9%) were positive and significantly different from zero, suggesting an excess of homozygous individuals (Table 3). However, in one locus (*Acph-2*), F was negative and significantly different from zero in population YEC, in which $He = 13.679$ and $Ho = 20$ ($F = 12.965$; $P < 0.01$). From the 34 estimates of F made from the cultivated populations, 19 (55.8%) were positive and significantly different from zero, indicating an excess of homozygous individuals in these populations. However, all negative estimates were not significantly different from zero. Out of the 12 estimates of F made from the wild-cultivated population (FUE), 5 (45.8%) were significantly positive, suggesting an excess of homozygous individuals in those loci. All negative estimates of F for this population were not significantly different from zero.

Population differentiation. The total genetic diversity was high in both the wild ($H_T = 0.500$) and cultivated ($H_T = 0.526$) populations of *C. annuum* studied (Table 4). The highest value of H_T recorded in wild populations was 0.681 for the *Cpx-2* locus, whereas the lowest was 0.291 for *Mdh-4*. In cultivated populations, the largest estimates of H_T corresponded to the *Got-1* ($H_T = 0.605$) and the *Cpx-2* ($H_T = 0.603$) loci, the smallest was for locus *6-Pgd-2* ($H_T = 0.318$).

Table 3. Fixation index (F) for each polymorphic locus estimated for the populations of *C. annuum* studied. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

Locus	Populations													
	PAJ	YEC	TEH	TEX	REP	ABL	ALC	CHP	TAB	OTA	FUE	PON	BJA	CBA
Acph-2	−0.049	−0.490**	−0.130	−0.097	−0.040	−0.354	0.085	0.157	−0.300	0.136	0.432	−0.103	0.676***	0.760***
Apx-1	−0.180	0.262	−0.057	–	−0.111	0.000	0.595**	−0.050	0.607**	0.067	1.000***	−0.255	−0.288	1.000***
Cpx-1	−0.086	−0.190	0.683***	0.537*	0.496**	−0.028	0.091	0.073	0.203	0.190	−0.100	0.822***	1.000***	–
Cpx-2	−0.043	0.122	0.384*	0.291*	0.514***	0.262	0.606***	0.754***	0.220	0.135	1.000***	−0.221	−0.040	–
Got-1	−0.048	0.631**	0.118	0.356	0.250	0.280	0.026	−0.097	0.666***	0.300	−0.416	−0.111	0.069	−0.025
Idh-2	0.350*	0.878***	0.272*	−0.159	0.697***	0.671***	0.221	0.624**	0.758***	0.563***	−0.333	0.669***	0.067	−0.185
Mdh-2	0.523***	0.284*	0.232*	0.175	−0.084	0.269	0.225	0.512**	0.078	0.506***	0.445	0.421*	0.388**	0.161
Mdh-4	0.690***	0.544***	−0.095	0.083	0.465***	0.448***	0.252	0.090***	0.844***	0.921***	0.010	0.262	0.135	0.432**
Me-1	0.536*	0.677***	0.538***	0.717***	0.672***	0.403**	0.634**	0.384	0.387**	0.410**	0.525	0.674***	−0.041	0.418**
Mnr-1	0.599***	0.230*	0.693***	0.387*	0.498***	0.397**	0.388**	0.644***	0.472**	−0.024	1.000***	0.492**	0.584***	0.687**
6-Pgd-2	0.372*	0.447**	0.423**	0.717*	−0.059	0.924***	−0.235	0.238	0.768**	1.000***	1.000*	0.628***	0.469**	0.071
Pgi-1	0.131	0.549***	0.344**	0.651***	0.302	0.524***	0.500***	0.155	0.433*	0.240	0.645*	0.621***	0.474***	0.761***

Table 4. Total (H_T), within (H_S) and between (D_{ST}) population genetic diversity, and the genetic differentiation coefficient (G_{ST}) for wild and cultivated populations of *C. annuum*

Locus	Wild				Cultivated			
	H_T	H_S	D_{ST}	G_{ST}	H_T	H_S	D_{ST}	G_{ST}
Acph-2	0.609	0.592	0.017	0.028	0.561	0.533	0.028	0.050
Apx-1	0.342	0.303	0.034	0.114	0.555	0.339	0.216	0.389
Cpx-1	0.429	0.403	0.026	0.061	0.469	0.323	0.146	0.311
Cpx-2	0.681	0.656	0.025	0.037	0.603	0.241	0.362	0.600
Got-1	0.534	0.520	0.014	0.026	0.605	0.551	0.054	0.089
Idh-2	0.551	0.510	0.041	0.074	0.582	0.356	0.226	0.388
Mdh-2	0.520	0.500	0.020	0.040	0.487	0.474	0.023	0.027
Mdh-4	0.291	0.277	0.014	0.048	0.585	0.555	0.030	0.051
Me-1	0.529	0.483	0.046	0.087	0.508	0.496	0.012	0.024
Mnr-1	0.516	0.496	0.020	0.039	0.508	0.495	0.013	0.026
6-Pgd-2	0.401	0.373	0.028	0.070	0.318	0.308	0.010	0.031
Pgi	0.607	0.576	0.031	0.051	0.540	0.532	0.008	0.015
Mean	**0.500**	**0.474**	**0.027**	**0.056**	**0.526**	**0.434**	**0.093**	**0.167**

Most genetic diversity was found within populations, both in the wild ($H_S = 0.474$) and in the cultivated ($H_S = 0.434$) populations. In the wild populations, the largest value of H_S was recorded for the locus *Cpx-2* ($H_S = 0.656$), and the smallest in *Mdh-4* ($H_S = 0.227$). In contrast, in the cultivated population the smallest value of H_S was recorded in the locus *Cpx-2* ($H_S = 0.241$), and the largest in the locus *Mdh-4* ($H_S = 0.555$).

Between population diversity (D_{ST}) was smaller among wild ($D_{ST} = 0.027$), than among cultivated ($D_{ST} = 0.093$) populations. In wild populations, the estimates of genetic diversity within populations (H_S) were higher for all loci than for genetic diversity among populations (D_{ST}), while in cultivated populations the locus *Cpx-2* had a value of D_{ST} (0.362) larger than H_S (0.241).

The estimated coefficient of genetic differentiation was also smaller in wild ($G_{ST} = 0.056$) than in cultivated populations ($G_{ST} = 0.167$). Among wild populations, about 6% of the genetic variation was found between populations, and the remaining 94% within populations. In cultivated populations 17% of the genetic variation was observed among, and 83% within populations Estimates of Wright's F_{ST} agree with Nei's measurements of total (D_{ST}) and relative (G_{ST}) genetic differentiation, suggesting that most genetic variation of the populations of *C. annuum* studied is allocated within, rather than between populations (Table 4).

Estimates of F_{ST} were small, but for most loci (except *Got-1*) significantly different from zero ($P > 0.05$) (Table 5). The summary value for all loci of F_{ST} was 0.036, indicating that 3.6% of the total variance in allelic frequencies is due to genetic differences among populations. Estimates of F_{IS} were significantly different from zero in 11 loci, revealing a deficiency in heterozygous individuals, whereas that for the loci *Acph-2* did not significantly differ from zero. The average of loci values of F_{ST} and F_{IS} estimated was highly significant ($P < 0.001$), and their corresponding CI values did not overlap with zero. On average, cultivated populations registered higher estimates of F_{ST} than wild populations. However, F_{ST} values for cultivated populations were significant only for loci *Idh-2* and *Mdh-4*. The mean F_{ST} estimate for all polymorphic loci for the cultivated populations was 0.210, i.e., 21% of the total variance was due to genetic differences between populations. Four of the

Table 5. Wright's *F*-statistics (means ± SE) of wild and domesticated *C. annuum* populations. Single locus values were obtained by jackknifing over populations and summary values jackknifing over loci. Significance levels were determined by t-test. Confidence intervals were calculated by bootstrap. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

Locus	Wild			Cultivated		
	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}
Acph-2	−0.025 ± 0.066**	−0.011 ± 0.060	0.013 ± 0.012**	0.534 ± 0.233	0.549 ± 0.211*	0.045 ± 0.065
Apx-1	0.174 ± 0.122***	0.249 ± 0.104***	0.089 ± 0.040***	−0.038 ± 0.323	0.598 ± 0.629	0.500 ± 0.391
Cpx-1	0.226 ± 0.103***	0.267 ± 0.104***	0.053 ± 0.032***	0.904 ± 0.098**	0.928 ± 0.056**	0.306 ± 0.345
Cpx-2	0.356 ± 0.071***	0.369 ± 0.069***	0.020 ± 0.018**	−0.291 ± 0.125	0.476 ± 0.439	0.555 ± 0.365
Got-1	0.193 ± 0.079***	0.193 ± 0.080***	0.001 ± 0.007	0.014 ± 0.040	0.030 ± 0.105	0.018 ± 0.116
Idh-2	0.555 ± 0.084***	0.581 ± 0.081***	0.059 ± 0.022***	0.283 ± 0.278	0.752 ± 0.207*	0.712 ± 0.352*
Mdh-2	0.285 ± 0.067***	0.301 ± 0.064***	0.023 ± 0.010***	0.341 ± 0.077*	0.349 ± 0.083*	0.012 ± 0.037
Mdh-4	0.430 ± 0.104***	0.445 ± 0.094***	0.030 ± 0.025**	0.322 ± 0.128	0.424 ± 0.114*	0.156 ± 0.086*
Me-1	0.533 ± 0.045***	0.569 ± 0.039***	0.079 ± 0.031***	0.345 ± 0.184	0.345 ± 0.177	0.004 ± 0.029
Mnr-1	0.402 ± 0.071***	0.415 ± 0.076***	0.020 ± 0.022*	0.629 ± 0.055**	0.628 ± 0.044**	0.000 ± 0.027
6-Pgd-2	0.562 ± 0.114***	0.575 ± 0.106***	0.032 ± 0.028**	0.298 ± 0.188	0.318 ± 0.195	0.023 ± 0.023
Pgi	0.402 ± 0.051***	0.421 ± 0.044***	0.033 ± 0.018***	0.603 ± 0.091*	0.605 ± 0.098**	0.014 ± 0.022
Summary values	**0.335 ± 0.055*****	**0.359 ± 0.056*****	**0.036 ± 0.008*****	**0.353 ± 0.081***	**0.490 ± 0.062****	**0.210 ± 0.704***
95% CI	0.237 to 0.434	0.259 to 0.457	0.023 to 0.052	0.213 to 0.513	0.373 to 0.610	0.0705 to 0.341

loci for which estimates of F_{IS} were recorded in cultivated populations were significantly higher than zero (*Cpx-1*, *Mdh-2*, *Mnr-1* and *Pgi*), indicating and excess of homozygous individuals, whereas for loci *Apx-1* and *Cpx-2* a slight, but not significant, excess of heterozygous individuals was measured. The average for all polymorphic loci summary estimates of F_{ST} and F_{IS} were significant ($P < 0.05$), having CI which did not overlap with zero. These results suggest that the wild populations of *C. annuum* studied have higher levels of homozygous excess and of genetic differentiation than the screened cultivated populations.

Wild, wild-cultivated, and cultivated populations are clearly resolved in the UPGMA dendrogram (Fig. 1). Wild populations display high values of genetic identity (average $I = 0.952$, ranging from 0.917 to 0.983), splitting from cultivated populations at an average level of $I = 0.818$, and from the wild-cultivated population (FUE), at an average level of $I = 0.921$. In contrast, cultivated populations had low levels of similarity among them (average $I = 0.817$, ranging from 0.709 to 0.833), and did not cluster together but nest independently from each other. Indirect estimates of gene flow (*Nm*) calculated from G_{ST} (Nei 1973), was 4.21 for the wild populations, suggesting high levels of allele exchange among

Fig. 1. Nei's (1972) genetic identity UPGMA dendrogram for the populations of *C. annum* studied

these. No correlation was found between genetic identities and geographical distances ($r = 0.126$; $P = 0.411$).

Discussion

The studied wild and domesticated populations of *C. annuum* from northwest Mexico maintain high levels of genetic variation, a finding that contrasts with previous reports for this and other species of *Capsicum* (McLeod et al. 1983. Loaiza-Figueroa et al. 1989).

Observed estimates of polymorphism in wild ($P = 90.8$) and cultivated ($P = 84.6$) populations were higher than those previously known for wild ($P = 30.7$) and cultivated ($P = 26.9$) populations of *C. annuum* (McLeod et al. 1983); and were also higher than the values reported for other cultivated plant species and for their wild counterparts (wild, $P = 32.0$; cultivated, $P = 25.5$) (Doebley 1989). The estimates of $A = 2.7$ for wild, and $A = 2.6$ for cultivated populations of *C. annuum*, exceed previously reported values for this same species (wild, $A = 1.5$; cultivated, $A = 1.4$) (McLeod et al. 1983). They are also slightly higher than the those reported for other cultivated ($A = 2.5$) plant species and their closest wild relatives ($A = 2.2$) (Doebley 1989).

Average expected heterozygosity reported here for wild ($He = 0.445$) and cultivated ($He = 0.408$) populations of *C. annuum* is much higher than that previously reported for wild ($He = 0.012$) and cultivated ($He = 0.003$) populations of this same species (McLeod et al. 1983) and also higher than the reported average estimates for 28 species of cultivated ($He = 0.117$) and their closest wild-relative ($He = 0.093$) plant populations (Doebley 1989). Similarly, the expected heterozygosity under Hardy-Weinberg equilibrium within the wild ($H_S = 0.474$), and cultivated ($H_S = 0.434$) populations of *C. annuum* studied here, were larger than the reported average estimates for the five species of cultivated peppers of $H_S = 0.012$ for cultivated, and $H_S = 0.025$ for their closest wild-relatives (Loaiza-Figueroa et al. 1989).

The low level of genetic diversity found in wild and cultivated populations of *C. annuum* by McLeod et al. (1983), and by Loaiza-Figueroa et al. (1989) may have been caused by a biased sampling. These authors studied plants from accessions derived from one or a few mother-plants, occasionally even from a single fruit, which will result in an underestimation of the genetic diversity represented in a species. Additionally, the analysis of inbred plants, which are derived from matings among related individuals, will increase the proportion of homozygous individuals at the expense of the number of heterozygous plants.

The level of genetic diversity of a wild plant species has been related with its life form, geographic range, mating system, seed-dispersal mechanisms, and with other ecological factors (Hamrick et al. 1979, Loveless and Hamrick 1984, Hamrick and Godt 1990). It has been established that perennial, herbaceous plant species which have a broad geographic range, a mixed mating system are pollinated by wind, and have seeds which are ingested and dispersed by animals, have high levels of allozyme variation (Hamrick and Godt 1990). *C. annuum* is a herbaceous, perennial plant species, which has a broad geographic distribution, is cross-pollinated (Pickersgill 1969), and has fruits which are dispersed by birds (Laborde and Pozo-Capodónico 1982, Pozo-Campodónico et al. 1991, Vázquez-Dávila 1996). It is therefore possible that this combination of characteristics may be responsible for the high levels of genetic variation observed in the wild populations of the species studied here.

As referred to above, most genetic variation observed in the wild and cultivated populations of *C. annuum* studied was allocated within populations. However, estimated genetic differentiation was larger among cultivated than among wild populations. In cultivated populations, 16.7% of the total genetic variation detected was allocated between populations ($G_{ST} = 0.167$), while in wild populations, this proportion was only 5.6%

Table 6. Pairwise values of Nei's (1972) genetic identity for wild (1–10), wild-cultivated (11), and domesticated (12–14) populations of *C. annuum*

Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 PAJ	–	0.943	0.951	0.941	0.963	0.948	0.971	0.925	0.947	0.945	0.948	0.821	0.809	0.759
2 YEC		–	0.953	0.932	0.966	0.943	0.950	0.944	0.965	0.969	0.936	0.838	0.817	0.767
3 TEH			–	0.972	0.954	0.925	0.960	0.953	0.943	0.924	0.953	0.867	0.811	0.759
4 TEX				–	0.944	0.937	0.962	0.960	0.932	0.917	0.909	0.850	0.837	0.757
5 REP					–	0.969	0.975	0.941	0.982	0.960	0.905	0.884	0.839	0.763
6 ABL						–	0.977	0.940	0.983	0.971	0.906	0.855	0.859	0.772
7 ALC							–	0.950	0.968	0.955	0.934	0.869	0.838	0.801
8 CHP								–	0.930	0.946	0.925	0.857	0.810	0.750
9 TAB									–	0.969	0.897	0.868	0.849	0.768
10 OTA										–	0.926	0.826	0.824	0.757
11 FUE											–	0.795	0.791	0.767
12 PON												–	0.833	0.823
13 BJU													–	0.709
14 CBA														–

($G_{ST} = 0.056$). This means that, despite similar levels of genetic variation in wild and in cultivated populations of *C. annuum*, the domestication process had an effect on the allocation of such variation among the different types of cultivated peppers.

Observed levels of genetic differentiation in wild ($G_{ST} = 0.056$) and cultivated ($G_{ST} = 0.167$) populations of *C. annuum* are lower than the reported average for other 406 plant species (Hamrick and Godt 1990) These estimates are also lower than the average values reported for cultivated plant species ($G_{ST} = 0.370$) and for their closest wild relatives ($G_{ST} = 0.495$) (Doebley 1989). The estimates of G_{ST} presented here are also much smaller than the values previously reported for the five cultivated species of *Capsicum* ($G_{ST} = 0.909$) and for the wild relatives of these species ($G_{ST} = 0.903$) (Loaiza-Figueroa et al. 1989). The high level of genetic differentiation found by Loaiza-Figueroa et al. (1989) may be due to the fact that these authors pooled together under "wild" and "cultivated" individuals of all five cultivated species of *Capsicum* and of their wild relatives. By this procedure, total diversity estimates appear to be greater (wild, $H_T = 0.282$; cultivated, $H_T = 0.176$); likewise, the analysis of plants from a single mother-plant underestimates the genetic variation found within populations (wild, $H_S = 0.025$; cultivated, $H_S = 0.012$). Given the relations: $D_{ST} = H_T - H_S$, and, $G_{ST} = D_{ST}/H_T$, an increase in total genetic diversity (H_T), along with a decrease in within-population genetic diversity (H_S), will determine an increase in the total D_{ST} and in the relative G_{ST} genetic differentiation between populations.

The high estimated average Nei's (1972) genetic identity of $I = 0.952$ for wild samples reinforces the result that a relatively low level of differentiation exists among these populations. Theoretical studies have established that, for neutral alleles, small amounts of gene flow ($Nm > 1$) are enough to restrain population differentiation (Wright 1943, 1951; Slatkin and Maruyama 1975; Slatkin and Barton 1989).

The estimated level of gene flow in wild populations of 4.21 average migrants per generation ($Nm = 4.21$), would be large enough to hinder population differentiation. The estimated average $I = 0.818$ between wild and cultivated populations is evidence for changes produced by the domestication process in the genetic composition of modern pepper cultivars. The average value obtained from domesticated populations of $I = 0.817$(0.709–0.833) indicates

Appendix. Allelic frequencies for the twelve polymorphic loci resolved in populations of *C. annuum*. Locus *Mdh-3* was monomorphic in all populations. Sample size is given in parentheses

Alleles	Populations													
	PAJ	YEC	TEH	TEX	REP	ABL	ALC	CHP	TAB	OTA	FUE	PON	BJU	CBA
Acph-2	(38)	(27)	(34)	(26)	(28)	(26)	(38)	(31)	(27)	(26)	(9)	(27)	(35)	(39)
1	0.487	0.593	0.485	0.327	0.464	0.327	0.395	0.425	0.333	0.462	0.500	0.056	0.129	0.038
2	0.303	0.389	0.426	0.615	0.375	0.481	0.421	0.403	0.519	0.365	0.389	0.389	0.629	0.513
3	0.211	0.019	0.088	0.058	0.161	0.192	0.184	0.145	0.148	0.173	0.111	0.556	0.243	0.449
Apx-1	(36)	(24)	(37)	(15)	(24)	(25)	(31)	(21)	(22)	(24)	(11)	(27)	(38)	(18)
1	0.153	0.271	0.054	0.000	0.250	0.400	0.274	0.048	0.364	0.375	0.091	0.204	0.224	0.000
2	0.847	0.729	0.946	1.000	0.750	0.600	0.726	0.952	0.636	0.625	0.909	0.796	0.776	0.222
3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.778
Cpx-1	(38)	(39)	(38)	(22)	(31)	(37)	(49)	(31)	(36)	(35)	(11)	(24)	(20)	(15)
1	0.079	0.346	0.474	0.432	0.339	0.243	0.214	0.419	0.347	0.229	0.091	0.625	0.500	0.000
2	0.921	0.654	0.526	0.568	0.661	0.757	0.786	0.581	0.653	0.771	0.909	0.375	0.500	1.000
Cpx-2	(20)	(33)	(34)	(22)	(35)	(34)	(41)	(26)	(30)	(28)	(11)	(24)	(13)	(15)
1	0.400	0.545	0.588	0.500	0.386	0.309	0.523	0.538	0.350	0.375	0.636	0.417	0.000	1.000
2	0.325	0.197	0.088	0.295	0.300	0.412	0.293	0.250	0.250	0.321	0.273	0.229	0.962	0.000
3	0.250	0.197	0.059	0.091	0.214	0.235	0.134	0.115	0.267	0.214	0.091	0.000	0.000	0.000
4	0.025	0.061	0.265	0.114	0.100	0.044	0.049	0.096	0.133	0.089	0.000	0.354	0.038	0.000
Got-1	(39)	(16)	(38)	(15)	(21)	(27)	(46)	(31)	(24)	(17)	(9)	(15)	(32)	(39)
1	0.256	0.313	0.197	0.400	0.28	0.204	0.196	0.258	0.146	0.176	0.222	0.067	0.219	0.244
2	0.590	0.625	0.658	0.567	0.476	0.593	0.652	0.677	0.667	0.735	0.611	0.367	0.625	0.577
3	0.154	0.063	0.145	0.033	0.286	0.204	0.152	0.065	0.188	0.088	0.167	0.567	0.156	0.179
Idh-2	(38)	(37)	(36)	(26)	(39)	(43)	(47)	(20)	(38)	(39)	(6)	(22)	(38)	(32)
1	0.039	0.324	0.139	0.019	0.013	0.081	0.117	0.125	0.053	0.103	0.500	0.023	0.026	0.000
2	0.737	0.365	0.625	0.846	0.538	0.512	0.670	0.625	0.421	0.462	0.500	0.182	0.000	0.000
3	0.224	0.311	0.236	0.135	0.449	0.407	0.213	0.250	0.526	0.436	0.000	0.091	0.000	0.000
4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.636	0.118	0.844
5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.855	0.156
Mdh-2	(39)	(40)	(42)	(26)	(40)	(43)	(51)	(31)	(41)	(42)	(11)	(27)	(40)	(39)
1	0.154	0.063	0.083	0.058	0.087	0.174	0.049	0.194	0.073	0.107	0.045	0.130	0.112	0.103
2	0.538	0.762	0.750	0.808	0.563	0.523	0.559	0.548	0.598	0.679	0.636	0.556	0.712	0.756
3	0.308	0.175	0.167	0.135	0.350	0.302	0.392	0.258	0.329	0.214	0.318	0.315	0.175	0.141
Mdh-4	(35)	(41)	(23)	(22)	(41)	(43)	(46)	(32)	(42)	(42)	(10)	(11)	(40)	(39)
1	0.029	0.122	0.000	0.182	0.134	0.151	0.130	0.297	0.083	0.155	0.100	0.318	0.112	0.436
2	0.900	0.878	0.913	0.818	0.841	0.826	0.772	0.625	0.917	0.821	0.650	0.500	0.700	0.462
3	0.071	0.000	0.087	0.000	0.024	0.023	0.098	0.078	0.000	0.024	0.250	0.182	0.188	0.103
Me-1	(38)	(39)	(34)	(27)	(37)	(42)	(40)	(26)	(40)	(40)	(11)	(27)	(28)	(39)
1	0.276	0.436	0.132	0.093	0.284	0.155	0.18	0.288	0.225	0.550	0.409	0.204	0.107	0.128
2	0.684	0.500	0.853	0.759	0.649	0.524	0.688	0.692	0.525	0.375	0.500	0.704	0.589	0.679
3	0.039	0.064	0.015	0.148	0.068	0.321	0.175	0.019	0.250	0.075	0.091	0.093	0.304	0.192
Mnr-1	(38)	(41)	(19)	(27)	(45)	(50)	(40)	(24)	(47)	(46)	(11)	(25)	(24)	(39)
1	0.487	0.293	0.342	0.204	0.233	0.130	0.188	0.104	0.223	0.228	0.455	0.120	0.208	0.103
2	0.487	0.634	0.605	0.685	0.578	0.700	0.675	0.792	0.638	0.630	0.364	0.760	0.542	0.667
3	0.026	0.073	0.053	0.111	0.189	0.170	0.138	0.104	0.138	0.141	0.182	0.120	0.250	0.231

Appendix (continued)

6-Pgd-2	(35)	(17)	(25)	(17)	(21)	(28)	(10)	(16)	(18)	(16)	(9)	(25)	(34)	(37)
1	0.200	0.088	0.180	0.294	0.024	0.304	0.150	0.438	0.139	0.313	0.444	0.020	0.191	0.081
2	0.771	0.882	0.680	0.706	0.929	0.661	0.750	0.562	0.861	0.625	0.556	0.880	0.794	0.770
3	0.029	0.029	0.140	0.000	0.048	0.036	0.100	0.000	0.000	0.063	0.000	0.100	0.015	0.149
Pgi-1	(39)	(29)	(32)	(26)	(32)	(34)	(38)	(22)	(33)	(28)	(11)	(27)	(40)	(38)
1	0.103	0.362	0.156	0.096	0.203	0.191	0.053	0.432	0.242	0.286	0.273	0.17	0.125	0.066
2	0.744	0.483	0.641	0.577	0.484	0.500	0.579	0.341	0.561	0.411	0.636	0.556	0.563	0.711
3	0.154	0.155	0.203	0.327	0.313	0.309	0.368	0.227	0.197	0.304	0.091	0.278	0.313	0.224

that these changes were brought about by modern breeding and have occurred in different directions.

The high genetic variation found in populations of *C. annuum* from northwestern Mexico is very similar to that previously observed in five of the populations studied here using 22 isozyme loci (Hernández-Verdugo et al. 1998). The populations analysed here have also been shown to have high levels of diversity, both in morphology and in the physiology of seed germination (Hernández-Verdugo et al. 1998, in press). In addition, two of the wild populations included in the present analysis were found to be resistant to the geminivirus PHV, a pathogen for which none of the available commercial varieties has resistance (Hernández-Verdugo et al., in press). In conclusion, the wild relatives of cultivated *C. annuum* are a valuable genetic resource which needs to be conserved.

We thank A. Casas and S. Zárate for their constructive comments on a preliminary draft, N. Pérez-Nasser and E. Pedraza-Ortega for their assistance in the laboratory, and V. Zarco-Espinosa, A. González-Rodríguez, P. Cuevas Reyes, H. Luna and G. Bojórquez for their help in the field work. This project was supported by the grant CONACYT 31866-B to SHV.

References

Burdon J. J., Jarosz A. M. (1989) Wild relatives as source of disease resistance. In: Brown A. D. H., Frankel O. H., Marshall D. R., Williams J. T. (eds.) The use of the plant genetic resources. Cambridge University Press, Cambridge, pp. 280–296.

Cheliak W. M., Pitel J. A. (1984) Techniques for starch gel electrophoresis of enzymes from forest tree species. Information Report PI-X-42. Petawa National Forestry Institute, Berkeley.

D'Arcy W. G., Eshbaugh W. H. (1974) New world peppers (*Capsicum*-Solanaceae) north of Colombia. Baileya 19: 93–103.

Decker D. S., Wilson H. D. (1987) Allozyme variation in the *Cucurbita pepo* complex: *C. pepo* var. *ovifera* vs *C. texana*. Syst. Bot. 12: 263–273.

Doebley J. (1989) Isozymic evidence and evolution of crop plants. In: Soltis E. D., Soltis P. M. (eds.) Isozymes in plant biology. Oregon Dioscorides, Portland, pp. 165–191.

Doggett H., Majisu B. N. (1968) Disruptive selection in crop development. Heredity 23: 1–23.

Ellstrand N. C., Marshall D. L. (1985) The impact of domestication on distribution of allozyme variation within and among cultivars of radish, *Raphanus sativus* L. Theor. Appl. Genet. 69: 393–398.

Eshbaugh W. H. (1980) The taxonomy of the genus *Capsicum* (Solanaceae). Phytologia 47: 153–156.

Hamrick J. L., Godt M. J. W. (1990) Allozyme diversity in plant species. In: Brown A. H. D., Clegg M. T., Kahler A. L., Weir B. S. (eds.) Plant population genetics, breeding, and genetic resources. Sinauer, Sunderland, MA, pp. 43–63.

Hamrick J. L., Godt M. J. W., Linhart Y. B., Mitton J. B. (1979) Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. Ann. Rev. Ecol. Syst. 10: 173–200.

Harlan R. J. (1976) Genetic resources in the wild relatives of crops. Crop Sci. 16: 329–336.

Harlan R. J. (1992) Crops and man. Second edition American Society of Agronomy, Inc., Crop Science Society of America, Inc., Madison, Wisconsin, USA.

Harlan R. J., de Wet J. M. J., Stuart Davis M. (1973) Comparative evolution in cereals. Evolution 27: 311–325.

Hawkes, J. G. (1983) The diversity of crop plants. Harvard University Press, Cambridge.

Hernández-Verdugo S., Guevara-Gónzalez R. G., Rivera-Bustamante R. F., Vázquez-Yanes C., Oyama K. (1998) Los parientes silvestres del chile (*Capsicum* spp.) como recursos genéticos. Bol. Soc. Bot. México 62: 171–181.

Hernández-Verdugo S., Guevara-Gónzalez R. G., Rivera-Bustamante R. F., Vázquez-Yanes C., Oyama K., Dávila P., Oyama K. (1999) Síntesis del conocimiento taxonómico, origen y domesticación del género *Capsicum*. Bol. Soc. Bot. México 64: 65–84.

Hernández-Verdugo S., Guevara-González R. G., Rivera-Bustamante S., Oyama K. (2001) Screening wild plants of *Capsicum annuum* for resistance to Pepper Huasteco Virus: presence of viral DNA and differentiation among populations. Euphytica (in press).

Hernández-Verdugo S., Oyama K., Vázquez-Yanes C. (2001) Differentiation in seed germination among populations of *Capsicum annuum* along a latitudinal gradient in Mexico. Pl. Ecol. (in press).

Hunziker A. T. (1979) South American Solanaceae: a synoptic survey. In: Hawkes J. K., Lester R. N., Skelding A. D. (eds.) Biology and taxonomy of Solanaceae. Academic Press, New York, pp. 49–85.

Kahler A. L., Allard R. W. (1981) Worldwide patterns of genetic variation among four esterase loci in barley (*Hordeum vulgare* L.). Theor. Appl. Genet. 59: 101–111.

Laborde C. J. A., Pozo-Campodónico O. (1982) Presente y pasado del chile en México. Publicación Especial Num. 85. SARH-INIA. Mexico.

Ladizinsky G. (1985) Founder effect in crop-plant evolution. Econ. Bot. 39: 191–199.

Li C. C., Horvitz D. C. (1953) Some methods of estimating the inbreeding coefficient. Am. J. Hum. Gen. 5: 107–117.

Loaiza-Figueroa F., Ritland K., Laborde Cancino J. A., Tanksley S. D. (1989) Patterns of genetic variation of genus *Capsicum* (Solanaceae) in Mexico. Plant Syst. Evol. 165: 159–188.

Loveless M. D., Hamrick J. L. (1984) Ecological determinants of genetic structure in plant populations. Ann. Rev. Ecol. Syst. 15: 65–95.

McLeod M. J., Guttman S. I., Eshbaugh W. H., Rayle R. E. (1983) An electrophoretic study of evolution in *Capsicium* (Solanaceae). Evolution 37: 562–574.

Mitton J. B., Linhart Y. B., Sturgeon K. B., Hamrick J. L. (1979) Allozyme polymorphism detected in mature tissue of ponderosa pine. J. Hered. 70: 86–89.

Nei M. (1972) Genetic distance between populations. Amer. Nat. 106: 283–292.

Nei M. (1973) Analysis of gene diversity in subdivided populations. Proc. Natl. Acad. Sc. U.S.A. 70: 3321–3323.

Nei M. (1997) F-statistics and analysis of gene diversity in subdivided populations. Ann. Human Genet. 41: 225–233.

Nei M. (1987) Molecular evolutionary genetics. Columbia University Press, New York.

Pickersgill B. (1969) The domestication of peppers. In: Ucko P. J., Dimbley G. W. (eds.) The domestication and exploration of plants and animals. Duckwor, London, pp. 443–450.

Pickersgill B. (1971) Relationships between weedy and cultivated forms in some species of peppers (genus *Capsicum*). Evolution 25: 683–691.

Pickersgill B. (1984) Migration of peppers, *Capsicum* spp. in the Americas. In: Stone D. (ed.) Papers of the Peabody Museum of Archeology and Ethnology, vol. 6. Harvard University Press, pp. 105–123.

Pickersgill B., Heiser C. B., Mcneill J. (1979) Numerical taxonomy studies on variation and domestication in some species of *Capsicum*. In: Hawkes J. G., Lester R. N., Skelding A. D. (eds.) The biology and taxonomy of Solanaceae. Academic Press, New York, pp. 679–700.

Pozo-Camodónico O., Montes H. S., Redondo J. E. (1991) Chile (*Capsicum* spp.) In: Avances en el estudio de los recursos fitogenéticos de México, Sociedad Mexicana de Fitogenética, A. C. Mexico City, pp. 217–238.

Slatkin M., Barton N. H. (1989) A comparison of three indirect methods for estimating average levels of gene flow. Evolution 43: 1349–1369.

Slatkin M., Barton N. H., Maruyama T. (1975) The influence of gene flow on genetic distance. Am. Nat. 109: 597–601.

Sneath P. H., Sokal R. R. (1973) Numerical taxonomy, the principles and practice of numerical classification. Freeman, San Francisco.

Stalker H. T. (1980) Utilization of the wild species for crop improvement. Adv. Agron. 33: 717–724.

Stuber C. W., Wendel J. M., Goodman M. M. (1988) Techniques and scoring procedures for starch gel electrophoresis of enzymes for maize (*Zea mays*). Technical Bulletin 286. North Caroline State University, NC.

Swofford D. L., Selander R. K. (1981) Biosys-1 (release 1.7): a computer program for the analysis of allelic variation in population genetics and biochemical systematics. User's manual. Illinois Natural History Survey, Illinois.

Vázquez-Dávila M. A. (1996) El amash y el pistoqué: un ejemplo de la etnoecología de los chontales de Tabasco, México. Etnoecológica 3: 59–63.

Vida G. (1994) Global issues of genetic diversity. In: Loeschcka V., Tomiuk J., Jain S. K. (eds.) Conservation genetics. Birkhäuser Verlag, Basel, pp. 9–19.

Watson I. A. (1970) The utilization of wild species in the breeding of cultivated crops resistant to plant pathogens. In: Frankel O. H., Bennet E. (eds.) Genetic resources in plants – Their exploration and conservation. Blackwell Scientific Publications, Oxford and Edinbourgh, pp. 441–457.

Weir B. S. (1990) Genetic data analysis. Sinauer Associates, Sunderland, MA.

Weir B. S., Cockerham C. C. (1984) Estimating F-statistics for the analysis of population structure. Evolution 38: 1358–1370.

Wright (1921) Systems of mating. Genetics 6: 111–178.

Wright (1943) Isolation by-distance. Genetics 28: 114–138.

Wright (1949) Population structure in evolution. Proc. Am. Phil. Soc. 93: 471–478.

Wright (1951) The genetic structure of populations. Ann. Eugen. 15: 322–354.

Yeh F. Ch. H., Malley D. O. (1980) Enzyme variations in natural populations of Douglas-fir, *Pseudotsuga menziessi* (Mirb.) Franco, from British Columbia. 1. Genetic variation patterns in coastal populations. Silvae Genetica 29: 83–92.

Addresses of the authors: S. Hernández-Verdugo, Facultad de Agronomía, Universidad Autónoma de Sinaloa, Culiacán, Sinaloa, México. R. Luna-Reyes, Instituto de Ecología, UNAM, Apartado Postal 70-275, México, 04510, D. F. México. K. Oyama, Instituto de Ecología, UNAM, Apartado Postal 70-275, México, 04510, D. F., México (e-mail: akoyama@ate.unam.mx).