Copyright © 1988 by the Genetics Society of America

Comparative Assessment of Genetic Diversity in Wild and Primitive Cultivated Barley in a Center of Diversity

Sakti Jana and Lukasz N. Pietrzak

Department of Crop Science and Plant Ecology, University of Saskatchewan, Saskatoon, Saskatchewan S7N OWO, Canada

Manuscript received September 2, 1987
Revised copy accepted April 27, 1988

ABSTRACT

Wild barley (*Hordeum spontaneum* K.) and indigenous primitive varieties of cultivated barley (*Hordeum vulgare* L.), collected from 43 locations in four eastern Mediterranean countries, Jordan, Syria, Turkey and Greece, were electrophoretically assayed for genetic diversity at 16 isozyme loci. Contrary to a common impression, cultivated barley populations were found to maintain a level of diversity similar to that in its wild progenitor species. Apportionment of overall diversity in the region showed that in cultivated barley within-populations diversity was of higher magnitude than the between-populations component. Neighboring populations of wild and cultivated barleys showed high degree of genetic identity. Groups of 3 or 4 isozyme loci were analyzed to detect associations among loci. Multilocus associations of varying order were detected for all three groups chosen for the analysis. Some of the association terms differed between the two species in the region. Although there was no clear evidence for decrease in diversity attributable to the domestication of barley in the region, there was an indication of different multilocus organizations in the two closely related species.

WILD barley, *Hordeum spontaneum* Koch., is the immediate evolutionary progenitor of cultivated barley, *Hordeum vulgare* L. (ZOHARY 1969; HARLAN 1979). The Near East Fertile Crescent in Southwest Asia is known to be the center of distribution of both the species and a region of great genetic diversity (HARLAN and ZOHARY 1966; ZOHARY 1969). In a series of papers since 1978, E. NEVO and his associates repeatedly emphasized the richness of wild barley in the region as a vast untapped reservoir of genetic diversity [see NEVO, BEILES and ZOHARY (1986) for a recent review]. In their comparative assessments of genetic diversity in wild and cultivated barleys in parts of the Fertile Crescent, BROWN and MUNDAY (1982) and NEVO, BEILES and ZOHARY (1986) found greater genetic diversity in wild barley than in primitive cultivars or landraces of cultivated barley.

This richness of genetic diversity in wild barley and its occurrence in a wide range of habitats including many extremely unfavorable conditions such as biotic and physical stresses in the region suggest that the genetic resources in wild barley in the Near East Fertile Crescent can be exploited for the improvement of cultivated barley. Breeding research by BROWN and MUNDAY (1983) and FREY *et al.* (1984) indicated that transgressive segregation from wild × cultigen crosses can be exploited for improving grain yield of cultivated barley. An essential first step toward a fuller utilization of the wild genetic resources in plant improvement is their reliable characterization for a wide range of characters (BROWN and MARSHALL 1986). We have undertaken the characterization of both wild and primitive domesticated barley still in cultivation in the Near East Fertile Crescent. The purpose of the present paper is to use our biochemical-characterization data to assess genetic diversity in these two closely related species. We hope that this survey would reveal useful information on their relative values in broadening the genetic base of modern cultivated barley.

MATERIALS AND METHODS

Recent collections of wild and cultivated barleys: Diploid wild barley (*H. spontaneum* K.) and cultivated barley (*H. vulgare* L.) were collected from 43 sites distributed over a wide range of habitats from eastern Turkey to the Greek Island of Crete in the Mediterranean Sea. Despite conscious attempts to collect both wild and cultivated barley from the same sites to avoid the confounding effect of environments on diversity estimates, only 23 sites were found from which sufficient numbers ($n \geq 25$) of wild plants could be sampled. In these common sites, wild barley was found to grow either in mixed stand with cultivated barley on the edges of cultivated barley fields, or on roadsides bordering barley fields. Additional 12 wild barley collection sites, although located in barley growing districts, did not have a cultivated barley field in the immediate vicinity ($\leq$1 km). Similarly, no wild barley population was located in the immediate neighborhood of 8 cultivated barley collection sites. All the 35 wild barley sites represented disturbed habitats to varying degrees, caused by the cultivation of lands under horticultural or field crops, or repeated grazing. Only one random wild barley plant was collected within a radius of 3 m. This strategy was followed to avoid duplicate sampling from the same family as much as possible. Cultivated barley plants were collected at random from each site to represent the entire standing crop in a field. According to the information available from local peasant farmers, cultivated barley in all

cases represented old indigenous varieties grown on family farms for at least four decades, perhaps many more. Only one mature spike was collected from each wild or cultivated plant. In this way, individually harvested seeds from 975 wild and 846 cultivated barley plants representing 43 populations were available for the studies.

Because of the difference in population size, a varying number of plants of either species was collected from each site. Twenty-five or more plants of each species were available from the 23 common sites, providing 663 wild and 609 cultivated barley plants for the comparison of diversity between wild and cultivated barleys collected from several common environments.

Cultivated barley accessions from a world collection: D. H. SMITH, JR., Curator of the National Small Grains Collection, U.S. Department of Agriculture (USDA), Crop Research Division, Beltsville, Maryland, kindly supplied seeds of a random sample of 998 accessions from about 19,000 accessions of cultivated barley in 1983 from the American World Collection of Spring Barley (USDA).

Electrophoretic assay: Each plant from both wild and cultivated barley collections (described above under *Recent collections of wild and cultivated barley*) was assayed for 16 electrophoretically discernible enzyme zones following the methods described by KAHLER and ALLARD (1970) and KAHLER, HEATH-PAGLIUSO and ALLARD (1981) with the following minor modifications. Depending on the enzymes, the electrophoresis was carried out in either discontinuous or continuous system. The gel buffer for the discontinuous system was made of 0.019 M Tris and 0.005 M citric acid with the pH adjusted at 7.1. The electrode buffer was made of 0.06 M NaOH and 0.23 M boric acid with the pH of 8.1. For the continuous system, the gel buffer consisted of 0.007 M histidine with the pH adjusted to 7.5 with NaOH. The electrode buffer for histidine gels was made of 0.15 M Tris and 0.047 M citric acid with the pH of 7.5. Plumule extracts from individual plants were assayed for the following enzymes: esterases (EC 3.1.1.?), acid phosphatase (EC 3.1.3.2), phosphoglucoisomerase (EC 5.3.1.9), lipoamide oxidoreductase (EC 1.11.4.3), peroxidase (EC 1.11.1.7), phosphoglucomutase (EC 2.7.5.1), 6-phosphogluconate dehydrogenase (EC 1.1.1.44), and shikimate dehydrogenase (EC 1.11.4.3). The alphanumeric symbols in parentheses follow the international nomenclature (International Union of Biochemistry 1984).

For convenience, the following abbreviations will be used for the respective isozymes: *Est-1, Est-2, Est-4, Est-5, Acp-3, Pgi-1, Pgi-2, Ndh-1, Prx-1, Prx-2, Pgm, Pgd-1, Pgd-2, Pgd-3, Sdh-1* and *Sdh-2*. Each of these zones is known to be controlled by a separate gene locus (KAHLER and ALLARD 1970; FELDER 1976; KAHLER, HEATH-PAGLIUSO and ALLARD 1981; BROWN 1983; LINDE-LAURSEN, NIELSEN and JOHANSEN 1987). These abbreviations correspond to the locus designations of BROWN (1983) and/or LINDE-LAURSEN, NIELSEN and JOHANSEN (1987) for *Est-1, Est-2, Est-4, Est-5, Acp-3, Ndh-1, Prx-1, Prx-2* and *Pgm*. Our *Pgi-1* and *Pgi-2* are consistent with the international nomenclature for phosphoglucoisomerase (EC 5.3.1.9) and correspond respectively to *Gpi-1* and *Gpi-2* designations of LINDE-LAURSEN, NIELSEN and JOHANSEN (1987). Shikimate dehydrogenase (EC 1.11.4.3) in our preparations was expressed by two zones, one double-banded slow zone with mobility 1.2–2.0 cm and another faster zone with mobility 2.8–3.4 cm. We used the locus designations *Sdh-1* and *Sdh-2* for the slow and fast zones, respectively. For 6-phosphogluconate dehydrogenase (EC 1.1.1.44), we used the abbreviations *Pgd-1, Pgd-2* and *Pgd-3* for three distinct bands with mobility ranges, 1.8–3.4 cm, 3.8–4 cm and 4.5–4.9 cm, respectively. Our electrophoretic analyses excluded the possibility of acconitate hydratase (*Aco-1* and *Aco-2*) and isocitric dehydrogenase (*Idh-1*) misclassified as *Pgd-2* and *Pgd-3*, respectively. A standard barley variety (Atlas) of known banding pattern was inserted in each gel to assist in establishing migrational distances (in cm from origin) of the isozymes.

The electrophoretic assay of 998 USDA accessions (described under *Cultivated barley accessions from a world collection*) was carried out for the purpose of comparing isozyme diversity in wild and cultivated barleys in the survey region with that of the barley accessions preserved in the world collection. However, this assay was limited to the following nine isozymes only: *Est-1, Est-2, Est-4, Est-5, Acp-3, Pgi-1, Pgm, Pgd-1* and *Pgd-2*.

Measurements of diversity: Several statistics are in use to measure genetic diversity in plant populations (BROWN and WEIR 1983). Of these, two indices that have been commonly used to measure diversity in wild and cultivar barleys are: (1) NEI's (1973) heterozygosity index (*e.g.*, NEVO, BROWN and ZOHARY 1979; NEVO *et al.* 1979, 1986), and (2) SHANNON's information index (*e.g.*, TOLBERT *et al.* 1979; SAGHAI-MAROOF *et al.* 1984). Many of the attributes of these two measures have been previously discussed (*e.g.*, BROWN and WEIR 1983; ZHANG and ALLARD 1986).

NEI (1973) adapted MARSHALL and ALLARD's (1970) measure of allelic diversity to describe expected heterozygosity (the panmictic heterozygosity) in subdivided populations. The heterozygosity ($H_{e\cdot j}$) for n alleles at the jth locus is given by:

$$H_{e\cdot j} = \sum_i p_{ij}(1 - p_{ij}) = 1 - \sum_i p_{ij}^2, \quad \text{for } i = 1, 2, \ldots, n,$$

where p_{ij} is the relative frequency of the ith allele at the jth locus. The average per locus diversity ($\bar{H}_e$) over k loci in a population is given by

$$\bar{H}_e = \sum_j H_{e\cdot j}/k, \quad \text{for } j = 1, 2, \ldots, k.$$

ZHANG and ALLARD (1986) derived an unbiased estimate of the variance of $\bar{H}_e$;

$$V_{\bar{H}_e} = \frac{1}{k(k-1)} \sum_j (H_{e\cdot j} - \bar{H}_e)^2, \quad \text{for } j = 1, 2, \ldots, k.$$

SHANNON's information index ($h_{s\cdot j}$) has been defined as (BOWMAN et al. 1971):

$$h_{s\cdot j} = -\sum p_i \ln p_i, \quad \text{for } i = 1, 2, \ldots, n,$$

where p_i is the relative frequency of the ith genotype at the jth locus. The mean diversity over k loci is estimated as,

$$H = \sum_j \hat{h}_{s\cdot j}/k, \quad \text{for } j = 1, 2, \ldots, k.$$

Although the approximate variance of SHANNON's index ($\hat{h}_{s\cdot j}$) has been described (HUTCHESON 1970), the variance of the mean diversity index (H) has not been characterized. However, considering the 16 isozyme loci used in our study as a random sample of loci from the barley genome, the empirical variance computed from the 16 $h_{s\cdot j}$ values for each population can be regarded as an estimate of the variance of H (BROWN and WEIR 1983).

Measurements of genetic similarity: NEI (1972) defined an identify index (I_j) to measure genetic similarity at the jth

locus between two populations say C and W (normalized identity):

$$I_j = \sum_i p_{ji\cdot c}\, p_{ji\cdot w} \Big/ \left[\left(\sum_i p_{ji\cdot c}^2\right)\left(\sum_i p_{ji\cdot w}^2\right)\right]^{1/2}, \quad \text{for } i = 1, 2, \ldots, n,$$

where $p_{ji\cdot c}$ and $p_{ji\cdot w}$ are the relative frequencies of the ith allele at the jth locus in population C and population W, respectively. The maximum value of I_j is unity when C and W have the same alleles in identical frequencies and the minimum value of I_j is zero when the two populations have no common alleles at the jth locus.

Let the arithmetic means of the three quantities

$$\sum_{ipji\cdot c\cdot pji\cdot w\cdot}, \quad \sum_{ipji\cdot c}^{2} \quad \text{and} \quad \sum_{ipji\cdot w}^{2}$$

over k loci be J_{cw}, J_c and J_w, respectively. The normalized genetic identity (I_N) between C and W over k loci is defined as

$$I_N = J_{cw}/(J_c J_w)^{1/2}.$$

The genetic difference (D_N) between C and W is defined as

$$D_N = -\ln I_N.$$

The minimum value of D_N is zero when C and W have the same alleles in identical frequencies at each of k loci considered.

We calculated the statistics I_N and D_N to measure genetic similarity and dissimilarity between neighboring cultivated (C) and wild (W) barley populations with respect to the 16 isozyme loci.

Analysis of associations among loci: Tests for associations of isozyme loci were performed by constructing log-linear models which were tested using the likelihood ratio tests as described by FIENBERG (1980) and SOKAL and ROHLF (1981). The BMDP-4F program was used for the computer-based analysis of data.

Because of limitation of sample size in individual collection sites, the association analyses were carried out only for three or four isozyme loci at a time. For three-locus associations, the G^2-statistics were calculated for all nine possible log-linear models.

For four-locus association studies, because of the complexity arising from a large number (113) of log-linear models, a preliminary selection of association terms was performed and a basic log-linear model consisting only of significant interaction terms was constructed. Additional log-linear models were formed using a stepwise selection procedure. The G^2-statistics were then calculated for the respective log-linear models and tested for significance. On the basis of the G^2 values and their respective probabilities, the best three or four models were chosen. Then, the expected frequencies, standardized residuals, estimates of parameters (u's) in the chosen log-linear models, and the ratios of individual parameters and their respective standard errors (absolute standardized u's) were compared. The simplest model which fitted the data most satisfactorily was considered the "best-fitting model" for a given combination of loci under consideration. This model was then interpreted for multilocus associations.

RESULTS

Seventy-seven genotypes were observed at the 16 loci, of which 60 were common to both wild and cultivated barleys (Table 1). Altogether, 799 combinations of these genotypes were discerned over the 16 loci. Wild barley showed 412 combinations in 975 plants from 35 sites and cultivated barley showed 426 combinations in 856 plants from 31 sites. The 10 most frequent combinations in wild barley constituted 16.4% of the plants and were different from those in cultivated barley constituting 21.6% of the plants. On the other hand, 62.4% of the combinations in wild barley and 77.2% of the combinations in cultivated barley were represented by only one plant. These singleton genotypes comprised 26.4% of the wild barley and 38.4% of the cultivated barley plants. Thus, in respect of overall combinations, there was no evidence for greater genetic diversity in wild barley than in cultivated landraces in the region.

TABLE 1

Number of genotypes at individual loci in wild and cultivated barleys and the most frequent genotype

Locus	No. of genotypes				Most frequent genotype in[a]	
	Wild	Cultivated	Common	Total	Wild	Cultivated
Est-1	4	5	4	5	33 (1.8)	33
Est-2	9	9	8	10	22 (2.7)	22
Est-4	8	9	8	9	44 (3.9)	44
Est-5	9	7	7	9	11 (6.4)	11
Acp-3	6	6	5	7	22 (2.3)	11 (1.8)
Pgi-1	5	4	4	5	22 (2.0)	22
Pgi-2	3	3	3	3	11 (4.2)	11
Ndh	3	2	2	3	11 (7.0)	11
Prx-1	2	3	2	3	11 (−1.5)	11
Prx-2	5	4	4	5	11 (−2.0)	11
Pgm	4	3	3	4	11 (5.0)	11
Pgd-1	2	2	1	3	22 (2.3)	22
Pgd-2	2	3	2	3	66 (null)	66
Pgd-3	1	1	1	1	11 (4.5)	11
Sdh-1	2	3	2	3	11 (1.5)	11
Sdh-2	4	4	4	4	11 (3.2)	11
Total	69	68	60	77		

[a] The migration distance (in cm from the origin) of the most frequent genotype is given in parentheses.

Table 1 gives the most frequent genotype at each of the 16 loci. These genotypes were observed over the entire ensemble of plants of each species, as well as in samples from most (>90%) of the populations. Thus, on the overall basis, the two species shared a large number of common loci. This was also true for all isozymes except *Acp-3*, when individual collection sites were considered. At this locus, the genotype coded as 22 was most common in 90% of the wild barley populations with genotype 11 as the second most frequent type, whereas the latter was most frequent in most of the cultivated barley populations.

Genotypic frequencies at individual loci varied considerably from site to site (not given here for brevity). This variation produced a great range of diversity indices for individual loci (omitted for brevity). On

TABLE 2

Isozyme diversity (*H*) in wild and cultivated barley in Jordan, Turkey and the Eastern Mediterranean region

	Jordan		Turkey		Region	
Isozyme	Wild	Cultivated	Wild	Cultivated	Wild	Cultivated
Est-1	0.683	0.845	1.057	1.183	0.955	1.013
Est-2	1.655	1.254	1.625	0.334	1.744	0.838
Est-4	1.317	1.512	1.281	0.949	1.635	1.440
Est-5	1.288	1.168	1.470	1.085	1.508	1.165
Acp-3	0.876	1.312	1.144	0.977	1.227	1.262
Pgi-1	0.677	0.120	0.168	0.310	0.421	0.151
Pgi-2	0.164	0.073	0.020	0.000	0.152	0.037
Ndh	0.635	0.476	0.516	0.213	0.643	0.384
Prx-1	0.111	0.642	0.098	0.056	0.078	0.460
Prx-2	0.576	0.201	0.459	0.375	0.646	0.306
Pgm	0.336	0.527	0.346	0.323	0.431	0.393
Pgd-1	0.077	0.142	0.051	0.623	0.244	0.534
Pgd-2	0.041	0.144	0.021	0.296	0.120	0.213
Pgd-3	0.000	0.000	0.000	0.000	0.040	0.000
Sdh-1	0.014	0.028	0.078	0.031	0.073	0.036
Sdh-2	0.558	0.598	0.530	0.498	0.688	0.635
Mean	0.563	0.565	0.555	0.453	0.663	0.554

the regional basis, *Est-4* was the most diverse (H = 1.635 and 1.440) locus, and *Pgd-3* was nearly monomorphic in wild barley and monomorphic in cultivated barley (Table 2).

The mean average diversity (H) and heterozygosity ($\bar{H}_e$) over 16 isozyme loci per population showed considerable variation among sites (Table 3). The correlation between the two estimates of diversity, H and $\bar{H}e$, was nearly perfect for both wild (r = 0.986) and cultivated (r = 0.991) species. Although either statistics could be used to provide a comparative assessment of genetic diversity in the two species, we have presented both the statistics for the purpose of comparison with the previously published reports. The mean diversity varied from 0.01 at site 40 to 0.50 at site 5 in wild barley, and from 0.02 at site 38 to 0.55 at site 2 in cultivated barley. Thus these were highly polymorphic to nearly monomorphic populations of both species in the region. Considering the entire region, both within- and between-populations components of genetic diversity were important. However, the within-populations component was more important in cultivated barley (55% of overall diversity) than in wild barley (43% of overall diversity). This comparatively large contribution of within-populations component to the overall genetic diversity in cultivated barley was suggested also by the average heterozygosity indices, 61% for cultivated and 52% for wild barley in the region. Thus there was an indication of greater local differentiation in wild barley than in cultivated barley.

The average within-populations diversities (H's) and multilocus heterozygosity indices (H_e's) in the cultivated species were slightly higher than in the wild species in the region (Table 4). It is noteworthy that the landraces collected from a considerably smaller geographic region in Jordan showed larger average diversity than those from Turkey, which is widely recognized for its richness in genetic diversity in many species including *Hordeum*. The cultivated barley populations from Jordan were also characterized by substantially greater proportion of the within-populations component of diversity (65%) than those from Turkey (44%). Thus the landraces of barley from Jordan harbor a greater amount of genetic diversity than those from Turkey and much of the diversity is due to the variability within, rather than between landrace populations of different peasant farmers. There was no correlation between either diversity indices (r = −0.061) or heterozygosity indices (r = −0.147) of the sympatrically distributed populations of the two species. Also there was no statistically detectable (P > 0.05) difference between the two species for average diversity over collection sites in each country, or in the region.

Out of the 43 populations surveyed, 23 populations of each species were collected from sites where both species occurred together. Because environmental differences between collection sites might in part account for the differences in levels of diversity between the two species, diversity indices of populations sampled from these common sites are expected to provide a more accurate comparative assessment of diversity in the two species. At 14 of the 23 common sites, cultivated barley was more diverse, whereas wild barley was more diverse at the remaining 9 sites (Table 3). Measured over the 23 common collection sites, the average within-populations genetic diversity in cultivated barley (H = 0.307) was slightly higher than in wild barley (H = 0.278). Thus a comparison of genetic diversity using only the sympatrically distributed populations showed the same trend as the results of the more comprehensive survey.

Genetic identity indices between wild and cultivated barley populations show a high degree of genetic similarity ($I_N \geq 0.75$) at 20 of the 23 common collection sites (Table 5). At the three remaining sites, the relatively low level of genetic similarity ($0.68 < I_N < 0.75$) was mainly due to the differences in genotype frequencies at one or more of the three loci, *Est-2*, *Est-4* and *Acp-3*. Overall genetic identity index for each country, as well as for the entire region ignoring individual sites and using the entire ensemble of plants of each species for estimating genotype frequencies, confirm the similarity of genetic structure of the two closely related species (Table 5).

A point of obvious interest in relation to the conservation of genetic diversity in cultivated barley is whether the levels of diversity in wild and primitive barleys in the survey region are comparable to the

TABLE 3

Estimates of mean diversity indices (H) and mean heterozygosity indices ($\bar{H}_e$) in wild and cultivated barley in the eastern Mediterranean region

Collection site No.	Country	Mean diversity index (H)				Mean heterozygosity index ($\bar{H}_e$)			
		Wild	SE[a]	Cultivated	SE	Wild	SE	Cultivated	SE
1	Jordan	0.38	0.11	0.40	0.13	0.20	0.06	0.21	0.06
2		0.14	0.50	0.55	0.13	0.07	0.02	0.31	0.07
3		0.43	0.12	0.51	0.11	0.24	0.07	0.30	0.07
4		0.21	0.08	0.15	0.05	0.14	0.05	0.09	0.03
5		0.50	0.12	0.22	0.08	0.30	0.06	0.16	0.06
6		0.42	0.12	0.38	0.11	0.26	0.07	0.221	0.06
7		0.15	0.06	0.22	0.08	0.09	0.10	0.14	0.05
8		0.42	0.11	0.28	0.08	0.26	0.07	0.15	0.04
9		0.09	0.05	0.46	0.09	0.06	0.03	0.30	0.06
10		0.32	0.10	0.41	0.09	0.17	0.05	0.26	0.06
11				0.41	0.11			0.25	0.06
12		0.36	0.09	0.41	0.09	0.21	0.06	0.24	0.05
13				0.34	0.09			0.21	0.05
14		0.33	0.09			0.19	0.06		
15				0.47	0.11			0.28	0.06
16		0.10	0.05	0.41	0.09	0.07	0.03	0.27	0.06
17		0.31	0.09			0.18	0.06		
18	Turkey	0.42	0.09	0.33	0.08	0.25	0.05	0.20	0.05
19		0.38	0.09	0.18	0.07	0.22	0.05	0.10	0.04
20				0.34	0.10			0.22	0.06
21		0.37	0.07	0.38	0.11	0.22	0.06	0.24	0.07
22		0.28	0.10			0.16	0.06		
23		0.21	0.06	0.22	0.10	0.13	0.04	0.13	0.06
24		0.40	0.11	0.07	0.04	0.23	0.06	0.04	0.03
25				0.24	0.09			0.14	0.05
26		0.35	0.12	0.18	0.08	0.20	0.07	0.11	0.05
27		0.12	0.05			0.08	0.04		
28		0.10	0.05			0.07	0.04		
29		0.09	0.05			0.05	0.03		
30		0.19	0.09			0.10	0.05		
31		0.15	0.07			0.10	0.05		
32		0.16	0.07			0.10	0.04		
33		0.16	0.07			0.11	0.05		
34	Syria			0.25	0.09			0.16	0.06
35		0.34	0.13	0.36	0.11	0.18	0.07	0.21	0.06
36		0.18	0.08			0.10	0.05		
37		0.32	0.10			0.21	0.06		
38	Greece	0.23	0.09	0.02	0.01	0.15	0.06	0.01	0.00
39		0.23	0.09	0.27	0.10	0.13	0.05	0.17	0.06
40		0.01	0.01	0.27	0.09	0.01	0.01	0.16	0.05
41		0.21	0.08	0.35	0.09	0.13	0.05	0.22	0.06
42				0.30	0.07			0.13	0.05
43				0.20	0.07			0.19	0.05

[a] Standard error.

diversity in existing worldwide collections of barley germplasm preserved in gene banks. Because of the dearth of a comprehensive collection of wild barley, only a random sample of cultivated spring barley accessions from the American World Collection (USDA) was used for the comparative study. This study showed that isozyme diversity in wild barley was slightly higher (7%) than the USDA accessions, which in turn had about 9% higher diversity than landraces (Table 6). These results are in agreement with the results presented earlier in Table 4, that the overall genetic diversity in wild barley (H = 0.61) is slightly higher (9%) than in barley landraces (H = 0.56) in the region. However, because the differences were small, and the nine loci were chosen in a nonrandom fashion, these results must be treated with caution.

Log-linear analysis of multiple traits: Because of the closeness of diversity levels of barley landraces and wild barley in the region, we asked the questions, (1) whether the isozyme markers showing high levels of diversity are independently distributed in populations, and (2) if associated, whether these associations differ significantly between the two species. We considered log-linear analyses of the isozyme data as an

TABLE 4

Average (H) and overall isozyme diversity in four countries in the eastern Mediterranean region

Country	Species	No. of sites	No. of plants	Diversity index: Average $(H)^a$	SE[b]	Overall	SE	Heterozygosity index (H_e): Average $(\bar{H}_e)^a$	SE[b]	Overall	SE
Jordan	Wild	14	458	0.29	0.04	0.57	0.13	0.17	0.02	0.28	0.06
	Cultivated	15	390	0.37	0.03	0.57	0.13	0.23	0.02	0.30	0.06
Turkey	Wild	14	326	0.24	0.03	0.55	0.14	0.14	0.02	0.25	0.07
	Cultivated	8	200	0.24	0.04	0.45	0.10	0.15	0.02	0.25	0.05
Syria	Wild	3	58	0.28	0.05	0.47	0.15	0.16	0.03	0.25	0.07
	Cultivated	2	50	0.30	0.05	0.39	0.11	0.18	0.02	0.22	0.06
Greece	Wild	4	133	0.17	0.05	0.46	0.12	0.10	0.03	0.27	0.07
	Cultivated	6	216	0.24	0.05	0.40	0.11	0.15	0.07	0.23	0.06
Region[c]	Wild	35	975	0.26	0.02	0.61	0.15	0.15	0.01	0.29	0.07
	Cultivated	31	856	0.31	0.02	0.56	0.11	0.18	0.01	0.29	0.06

[a] Differences between wild and cultivated barleys of the respective countries and the region are not significant ($P = 0.05$) by t-tests.
[b] Standard error (SE) calculated empirically from individual site H or H_e.
[c] Includes all four countries.

TABLE 5

Estimates of genetic identity indices (I_N) and genetic distance (D_N) between wild and cultivated barley populations in 23 common sites

Country	Site number	Genetic identity index (I_N)	Genetic distance (D_N)
Jordan	1	0.964	0.036
	2	0.784	0.243
	3	0.901	0.104
	4	0.898	0.107
	5	0.932	0.070
	6	0.872	0.137
	7	0.883	0.124
	8	0.860	0.151
	9	0.847	0.166
	10	0.878	0.130
	12	0.927	0.075
	16	0.785	0.242
Turkey	18	0.798	0.225
	19	0.923	0.081
	21	0.877	0.131
	22	0.719	0.330
	23	0.742	0.299
	24	0.905	0.100
Syria	35	0.937	0.065
Greece	38	0.822	0.195
	39	0.822	0.196
	40	0.684	0.380
	41	0.817	0.202
Region		0.972	0.028

TABLE 6

Overall diversity (H) for nine isozyme loci in wild and cultivated barleys from four countries in the eastern Mediterranean and some USDA accessions of cultivated barley

Isozyme	Eastern Mediterranean: Wild	Eastern Mediterranean: Cultivated	USDA cultivated
Est-1	0.955	1.013	1.104
Est-2	1.744	0.838	0.704
Est-4	1.635	1.440	1.060
Est-5	1.508	1.165	1.400
Acp-3	1.227	1.262	1.240
Pgi-1	0.421	0.151	0.262
Pgm	0.431	0.393	1.020
Pgd-1	0.244	0.534	0.685
Pgd-2	0.120	0.213	0.256
Mean	0.921	0.779	0.859
No. of plants or accessions	975	856	998

appropriate procedure for elucidating the questions for the following reasons: (1) This discrete multivariate technique allowed us to reduce the complexity of multilocus, analysis by allowing identification and elimination of association terms from the model that have inconsequential effects; (2) it allowed us to determine the complete multilocus structure involving more than two loci; and (3) the technique provided both qualitative and quantitative evaluations of two or more loci involved in the development of multilocus genetic structures.

Because the number of phenotypic combinations involving all 16 loci was exceedingly large, the sample sizes did not permit a log-linear analysis involving all 16 loci simultaneously. For this reason, the number of isozyme markers for the analysis were first reduced to 10 following the simplification procedure of CLEGG, ALLARD and KAHLER (1972). These 10 isozyme markers were then grouped into three smaller groups of four, three and three loci as shown below:

Group 1: *Est*-1, *Est*-2, *Est*-4 and *Est*-5, coded as *A*, *B*, *C* and *D*, respectively.
Group 2: *Acp*-3, *Pgd*-1 and *Pgd*-2, coded *P*, *G* and *H*, respectively.
Group 3: *Pgi*-1, *Pgd*-3 and *Sdh*-1, coded as *I*, *M* and *S*, respectively.

While limiting the number of loci per group to three or four, the choice of isozyme markers within a group was somewhat arbitrary. Group 1 comprised of all four esterases which were highly polymorphic (Table 2). Group 2 consisted of one highly polymorphic (*Acp-3*) and two moderately polymorphic (*Pgd-1* and *Pgd-2*) loci. Group 3 consisted of the three loci with very low diversity.

For the isozyme loci with more than two genotypes, further simplification was accomplished by reducing them to the diallelic state using the procedure outlined by WEIR, ALLARD and KAHLER (1972). The most frequent genotype was designated as morph 1 (usually with a frequency of 0.5 or more) and all the remaining genotypes at the same locus were together designated as morph 2. For example, for a group with three isozyme loci, the number of genotypic combinations were reduced to eight, and for a group of four loci, reduced to 16 combinations. Observed frequencies of these genotypic combinations in a group were used to perform the log-linear analysis of association among loci.

Group 1. At first, the observed frequencies of the 16 phenotypes in the entire region ignoring sites were used for the association analysis. Application of the marginal and partial association methods to this overall frequency data of cultivated barley led to the identification of six two-locus terms and one three-locus term with significant associations ($P = 0.05$) and high G^2. These interaction terms, [*AB*], [*AC*], [*AD*], [*BC*], [*BD*], [*CD*] and [*ABC*] were then used to construct the final set of log-linear models. We used the stepwise procedure to construct three models that fitted the data most closely. Goodness-of-fit of each of these models was further verified by examining the expected frequencies and their standardized residuals. The following log-linear model was selected as the best model for cultivated barley from the region.

$$\ln \hat{f}_{i\cdot j\cdot k\cdot l} = u + u_i^A + u_j^B + u_k^C + u_l^D + u_{i\cdot j}^{AB} + u_{i\cdot k}^{AC} + u_{i\cdot l}^{AD} + u_{j\cdot k}^{BC} + u_{j\cdot l}^{BD} + u_{k\cdot l}^{CD} + u_{i\cdot j\cdot k}^{ABC}$$

where u is the grand mean of the logarithm of expected frequencies,

$u_i^A, \ldots, u_l^D$ are the individual effects of respective loci,

$u_{i\cdot j}^{AB}, \ldots, u_{k\cdot l}^{CD}$ are the respective two-locus association effects and

$u_{i\cdot j\cdot k}^{ABC}$ is the effect of the three-locus association, *Est-1–Est-2–Est-4*.

The simplest log-linear model that was found to be best fit for wild barley from the entire region is as follows:

$$\ln \hat{f}_{i\cdot j\cdot k\cdot l} = u + u_i^A + u_j^B + u_k^C + u_l^D + u_{i\cdot j}^{AB} + u_{i\cdot k}^{AC} + u_{i\cdot l}^{AD} + u_{j\cdot k}^{BC} + u_{j\cdot l}^{BD} + u_{k\cdot l}^{CD} + u_{i\cdot k\cdot l}^{ACD} + u_{j\cdot k\cdot l}^{BCD}$$

where the two new terms, $u_{i\cdot k\cdot l}^{ACD}$ and $u_{j\cdot k\cdot l}^{BCD}$ represent three-locus associations, *Est-1–Est-4–Est-5* and *Est-2–Est-4–Est-5*, respectively.

Group 2. For the second group consisting of *Acp-3* (*P*), *Pgd-1* (*G*) and *Pgd-2* (*H*), the model for cultivated barley showed slightly greater two-locus organization, [*PG*] and [*PH*], than wild barley [*GH*]:

$$\ln \hat{f}_{i\cdot j\cdot k\cdot l} = u + u_i^P + u_j^G + u_k^H + u_{j\cdot k}^{GH}: \quad \text{Wild}$$

$$\ln \hat{f}_{i\cdot j\cdot k\cdot l} = u + u_i^P + u_j^G + u_k^H + u_{i\cdot j}^{PG} + u_{i\cdot k}^{PH}: \quad \text{Cultivated.}$$

Thus in both species, only two-locus asssociations were required to explain the observed genotypic frequencies.

Group 3. This group consisted of three isozymes, *Pgi-1* (*I*), *Pgd-3* (*M*) and *Sdh-1* (*S*), each of which showed little or no diversity in each population and over all populations in the region. The following saturated log-linear model was found to be satisfactory for both species:

$$\ln \hat{f}_{i\cdot j\cdot k} = u + u_i^I + u_j^M + u_k^S + u_{i\cdot j}^{IM} + u_{i\cdot k}^{IS} + u_{j\cdot k}^{MS} + u_{i\cdot j\cdot k}^{IMS}.$$

The frequency of the genotypic combination designated as 11 11 11 was greatly in excess in all populations, wild and cultivated, and overall in the region.

DISCUSSION

Earlier population studies have revealed that wild barley in a major part (Iran, Turkey and Israel) of the Near East Fertile Crescent is a rich source of genetic diversity (BROWN *et al.* 1978; NEVO, BROWN and ZOHARY 1979; NEVO, BEILES and ZOHARY 1986; NEVO *et al.* 1986). The results of our survey confirm these findings and extend further to provide a comparative assessment of diversity in wild barley from four eastern Mediterranean countries (Jordan, Syria, Turkey and Greece) *vis-à-vis* cultivated landrace populations of barley currently grown by peasant farmers in the region. In a direct comparison of diversity for 19 allozyme loci between 25 landrace populations of cultivated barley from Iran and 28 wild barley populations from Israel, BROWN and MUNDAY (1982) showed that Iranian landraces possessed only 73% of the genetic diversity observed in the latter. Using two genetically diverse composite cross populations of cultivated barley in their survey, BROWN and MUNDAY (1982) found the following ranking in terms of allozyme diversity: wild barley > landraces > composite crosses. In our studies on electrophoretically discernible genetic diversity of wild barley and primitive indigenous varieties of cultivated barley from the same region excluding Iran and Israel did not reveal a marked excess of diversity in wild barley. In comparison with the global diversity represented by 998 random USDA accessions, both wild and cultivated barleys of the eastern Mediterranean region appeared

to be rich sources of genetic diversity. BROWN *et al.* (1978) observed outcrossing rates of about 1.6% in 28 Israel populations of *H. spontaneum.* The average natural outcrossing rate (0.9%) in both wild and cultivated barley populations in our studies were even lower (our unpublished data).

Although predominantly self-fertilizing, wild and cultivated barleys in the Near East Fertile Crescent occasionally intermate and produce fully viable offspring which segregate for several morphologically distinguishable characters. Because of their interfertility and genetic affinity, they are sometimes considered as the members of the same highly polymorphic species (HARLAN 1979; VON BOTHMER and JACOBSEN 1985). HARLAN (1979) suggested that, *H. spontaneum* could be a wild derivative from an extinct common ancestor of the wild and cultivated forms. The estimates of genetic identity indices in our studies confirmed that the two species are genetically related. If these results are a true reflection of the situation with regard to economically important traits, then the primitive cultivated barley should be more attractive genetic resources than wild barley in the region because of their closer affinity with the modern cultivars of barley that are well-adapted to improved agricultural practices. These primitive cultivars of barley deserve additional attention also because of the accelerated rate of their extinction at this major center of diversity due to the modernization of farming systems.

Contrary to the usual impression, both wild and cultivated barleys in Jordan appeared to be a richer source of genetic diversity than Turkey. This higher level of diversity in Jordan was particularly unexpected because the survey area in Turkey encompassed a much wider range of ecogeographic conditions. Relatively advanced agriculture in Turkey is unlikely a *prima facie* cause because both wild and cultivated barleys in Turkey were deficient. Environmental factors might have contributed toward the differential diversity. For example, the long-term average annual rainfall in the survey area in Jordan (300 mm) was about 100 mm less than in Turkey. The rate of loss of genetic diversity in mass-propagated heterogeneous populations of barley (composite crosses) has been found to be slower under moisture-limiting dryland conditions than under more favorable irrigated conditions (ACHARYA and JANA 1981). Drier conditions in Jordan probably produced less severe intergenotype competition leading to a slower rate of depletion of genetic diversity in both wild and cultivated barleys. However, because of the purely empirical nature of the assessment, this conclusion must be considered tentative. Further studies involving statistically verifiable association between genetic diversity and several environmental variables in the survey region would provide precise and valuable information on dynamics of genetic conservation.

Extensive studies in the past on the pattern of distribution of allozyme variation in wild barley in parts of the Fertile Crescent (Israel, Turkey and Iran) revealed that both within- and between-populations variations were important (NEVO *et al.* 1979; NEVO, BEILES and ZOHARY 1986). Approximately 47% of the variation was ascribable to the differences among populations. In similar studies in Iranian and Ethiopian landraces of barley, BROWN and MUNDAY (1982) and BEKELE (1983a–c), respectively, found 49% and 55% of the variation was due to the between-populations component. Thus there was evidence for considerable local differentiation in both wild and primitive cultivated barley populations in these major centers of diversity in *Hordeum.* Our present results are quantitatively somewhat different from those of the earlier studies in that greater local differentiation was evident among wild barley populations (61% between-populations) than among cultivated landrace populations (45% between-populations) in the region. This smaller local differentiation most probably resulted from greater seed dispersion (*e.g.*, seed exchange) and enhanced migration in landrace populations. Because there were reasonable numbers of collection sites in Jordan and Turkey, the extent of local differentiation could be compared between these two countries. Whereas the within- and between-populations components of genetic diversity were nearly equal (each 50%) for wild barley in both countries, cultivated barley populations showed greater differentiation between populations in Turkey (57%) than in Jordan (34%), presumably because of greater intercommunication among agricultural communities mainly localized in a much smaller arable area in northwestern Jordan. It must be emphasized, however, that the evolutionary processes occurring in heterogeneous landrace populations of barley are quite complex, and geographic isolation accompanied by occasional migration might be only partially responsible for the observed level of genetic diversity in landrace populations of cultivated barley.

The development of multilocus structures has been found to be a common feature of closed populations of barley (CLEGG, ALLARD and KAHLER 1972; WEIR, ALLARD and KAHLER 1972, 1974; BROWN, FELDMAN and NEVO 1980; BROWN and FELDMAN 1981; BEKELE 1983c). However, the detection of multilocus associations in experimental barley populations might depend upon the nature of the gene loci employed in the study (MOUNA 1982). Even when multilocus organizations occur, the underlying evolutionary processes might be far from clear (LUCKETT and EDWARDS 1986). We addressed the question of multilocus association in barley landraces and their immediate evolutionary progenitor, wild barley, collected from the

same habitats. Thus the differences in propagation conditions in successive generations of the two species were largely reduced to those associated with the domestication of barley and primitive methods of agriculture in the region. As has been shown in many earlier studies, we found evidence for multilocus association among the four esterase loci (Coded *A, B, C* and *D*). The best-fit log-linear models, [*AB*] [*ACD*] [*BCD*] and [*AD*] [*BD*] [*CD*] [*ABC*], respectively, for wild and cultivated barleys, revealed both two-locus and three-locus associations, but no four-locus association. The association terms in the models are distinct for the wild and cultivated species and wild barley appears to have organized into slightly more complex associations.

The log-linear analysis of the three other isozyme loci, *Acp-3, Pgd-1* and *Pgd-2,* also revealed multilocus associations. Two of these loci, *Acp-3* and *Pgd-1*, are known to be unlinked (KAHLER, HEATH-PAGLIUSO and ALLARD 1981). Like the esterase group, the best-fit model for each species was different, [*P*] [*GH*] for the wild and [*PG*] [*PH*] for the cultivated.

The last group for the log-linear analysis consisted of three isozyme loci, *Pgi-1, Pgd-3* and *Sdh-1,* which showed low or no diversity in either species. One saturated model [*IMS*] was sufficient to describe the associations involving the three loci, represented mainly by the genotype 11 11 11 in both wild and cultivated populations in the region. It is noteworthy that the highest order of multilocus association involving all three loci under consideration was detected only for this last group. Thus, the choice of an appropriate set of loci is crucial to the identification of multilocus associations that are typical representatives of the overall organization of the genome. Whether this has been achieved in our present study is far from clear. We draw the following conclusions from the study: (1) multilocus organizations occurred in both wild and cultivated barleys in the eastern Mediterranean region, and (2) some of the observed associations were specific to the wild and primitive cultivated forms. However, these differential multilocus associations did not lead to a marked increase in genetic distance or wide difference in genetic diversity between the two closely related species.

The research reported in this paper was supported from Natural Sciences and Engineering Research Council of Canada Operating grant A6221. Exploration and collections of materials for the research were supported by a grant from the International Board for Plant Genetic Resources, Rome, Italy.

LITERATURE CITED

ACHARYA, S. N., and S. JANA, 1981 Genetic variability in a heterogeneous population of barley (*Hordeum vulgare*). Can. J. Genet. Cytol. **24:** 257-266.

BEKELE, E., 1983a Some measures of gene diversity analysis on land race populations of Ethiopian barley. Hereditas **98:** 127-143.

BEKELE, E., 1983b Allozyme genotypic composition and genetic distance between the Ethiopian land race populations of barley. Hereditas **98:** 259-267.

BEKELE, E.,1983c The neutralist-selectionist debate and estimates of allozyme multilocus structure in conservation genetics of the primitive land races of Ethiopian barley. Hereditas **99:** 73-88.

BOWMAN, K. O., K. HUTCHESON, E. P. ODUM and L. R. SHENTON, 1971 Comments on the distribution of indices of diversity. Stat. Ecol. **3:** 315-366.

BROWN, A. H. D., 1983 Barley. pp. 57-77. In: *Isozymes in Plant Genetics and Breeding*, Part B, Edited by S. D. TANKSLEY and T. J. ORTON. Elsevier, Amsterdam.

BROWN, A. H. D., and M. W. FELDMAN, 1981 Population structure of multilocus associations. Proc. Natl. Acad. Sci. USA **78:** 5913-5916.

BROWN, A. H. D., and D. R. MARSHALL, 1986 Wild species as genetic resources for plant breeding. pp. 9-15. In: *Proceedings of the Plant Breeding Symposium DSIR 1986*, Edited by T. A. WILLIAMS and G. S. WRATT. Special Publication No. 5, Agronomy Society of New Zealand.

BROWN, A. H. D., and J. MUNDAY, 1982 Population-genetic structure and optimal sampling of land races of barley from Iran. Genetica **58:** 85-96.

BROWN, A. H. D., and J. MUNDAY, 1983 Use of wild barley germplasm in barley breeding. In: *Proceedings of the Australian Plant Breeding Conference*, Adelaide. pp. 151-152.

BROWN, A. H. D., and B. S. WEIR, 1983 Measuring genetic variability in plant populations. pp. 219-239. In: *Isozymes in Plant Genetics and Breeding*, Part A, Edited by S. D. TANKSLEY and T. J. ORTON. Elsevier, Amsterdam.

BROWN, A. H. D., M. W. FELDMAN and E. NEVO, 1980 Multilocus structure of natural populations of *Hordeum spontaneum*. Genetics **96:** 523-536.

BROWN, A. H. D., E. NEVO, D. ZOHARY and O. DAGAN, 1978 Genetic variations in natural populations of wild barley (*Hordeum spontaneum*). Genetica **49:** 97-108.

CLEGG, M. T., R. W. ALLARD and A. L. KAHLER, 1972 Is the gene the unit of selection? Evidence from two experimental plant populations. Proc. Natl. Acad. Sci. USA **69:** 2474-2478.

FELDER, M., 1976 Genetic control of four cathodal peroxidase isozymes in barley. J. Hered. **67:** 39-42.

FIENBERG, S. E., 1980 *The Analysis of Cross-Classified Categorical Data.* MIT Press, Cambridge, Mass.

FREY, K. J., T. S. COX, D. M. RODGERS and P. Bramel-Cox, 1984 Increasing cereal yields with genes from wild and weedy species. Proc. XV Int. Congr. Genet. (New Delhi) **4:** 51-58.

HARLAN, J. R., 1979 On the origin of barley. pp. 10-36. In: *Barley: Origin, Culture, Winter Hardiness, Genetics, Utilization, Pests.* U. S. Department of Agriculture Handbook No. 338. Washington, D.C.

HARLAN, J. R., and D. ZOHARY, 1966 Distribution of wild wheats and barley. Science **153:** 1074-1080.

HUTCHESON, K., 1970 A test for comparing diversities based on the Shannon formula. J. Theor. Biol. **29:** 151-154.

International Union of Biochemistry, Enzyme Nomenclature, 1984 *Recommendations of the Nomenclature Committee.* Academic Press, Orlando, Fla.

KAHLER, A. L., and R. W. ALLARD, 1970 Genetics of isozyme variants in barley. I. Esterases. Crop Sci. **10:** 444-448.

KAHLER, A. L., S. HEATH-PAGLIUSO and R. W. ALLARD, 1981 Genetics of isozyme variants in barley. II. 6-Phosphogluconate dehydrogenase, glutamate oxalate transminase and acid phosphatase. Corp Sci. **21:** 536-540.

LINDE-LAURSEN, I., G. NIELSEN and H. B. JOHANSEN, 1987 Distribution of isoenzyme markers at 37 loci in a pedigree of European spring barley. Hereditas **106:** 241-251.

LUCKETT, D. J., and K. J. R. EDWARDS, 1986 Esterase genes in

parallel composite cross barley populations. Genetics **114:** 289–302.

MARSHALL, D. R., and R. W. ALLARD, 1970 Isozyme polymorphisms in natural populations of *Avena fatua* and *A. Barbata.* Heredity **25:** 373–382.

MOUNA, O. A., 1982 Multilocus study of an experimental barley population. Hereditas **96:** 247–254.

NEI, M., 1972 Genetic distance between populations. Am. Nat. **106:** 283–292.

NEI, M., 1973 Analysis of gene diversity in subdivided populations. Proc. Natl. Acad. Sci. USA **70:** 3321–3323.

NEVO, E., A. BEILES, and D. ZOHARY, 1986 Genetic resources of wild barley in the Near East: Structure, evolution and application in breeding. Biol. J. Linn. Soc. **27:** 255–380.

NEVO, E., A. H. D. BROWN and D. ZOHARY, 1979 Genetic diversity in the wild progenitor of barley in Israel. Experimentia **35:** 1027–1029.

NEVO, E., D. ZOHARY, A. H. D. BROWN and M. HABER, 1979 Genetic diversity and environmental associations of wild barley, *Hordeum spontaneum*, in Israel. Evolution **33:** 815–833.

NEVO, E., D. ZOHARY, A. BEILES, D. KAPLAN and N. STORCH, 1986 Genetic diversity and environmental associations of wild barley, *Hordeum spontaneum*, in Turkey. Genetica **68:** 203–213.

SAGHAI-MAROOF, M. A., K. M. SOLIMAN, R. A. JORGENSEN and R. W. ALLARD, 1984 Ribosomal DNA spacer-length polymorphisms in barley: Mendelian inheritance, chromosomal location and population dynamics. Proc. Natl. Acad. Sci. USA **81:** 8014–8018.

SOKAL, R. R., and F. J. ROHLF, 1984 *Biometry.* W. H. Freeman, San Francisco.

TOLBERT, D. M., C. O. QUALSET, S. K. JAIN and J. C. CRADDOCK, 1979 A diversity analysis of a world collection of barley. Crop Sci. **19:** 789–794.

VON BOTHMER, R., and N. JACOBSEN, 1985 Origin, taxonomy and related species. pp. 19–72. In: *Barley* (Monograph 26), Edited by D. C. RASMUSSON. American Society of Agronomy, Madison, Wisc.

WEIR, B. S., R. W. ALLARD and A. L. KAHLER, 1972 Analysis of complex allozyme polymorphism in a barley population. Genetics **72:** 505–523.

WEIR, B. S., R. W. ALLARD and A. L. KAHLER, 1974 Further analysis of complex allozyme polymorphism in a barley population. Genetics **78:** 911–919.

ZHANG, Q., and R. W. ALLARD, 1986 Sampling variance of the genetic diversity index. J. Hered. **77:** 54–56.

ZOHARY, D., 1969 The progenitors of wheat and barley in relation to domestication and agricultural dispersal in the Old World. pp. 47–66. In: *The Domestication and Exploitation of Plants and Animals*, Edited by P. J. UCO and G. W. DIMBLEBY. Duckworth, London.

Communicating editor: M. T. CLEGG