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Origin, Evolution, Population Genetics and Resources for Breeding of Wild Barley, *Hordeum spontaneum*, in the Fertile Crescent

Eviatar Nevo

Cultivated barley: origins and domestication

Cultivated barley, *Hordeum vulgare* L., is one of the main cereals of the belt of Mediterranean agriculture, a founder crop of Old World Neolithic food production and one of the earliest crops domesticated (Harlan & Zohary, 1966; Harlan, 1968; Zohary & Hopf, 1988). It is an important crop, ranking fifth in world crop production. In order of importance barley is used for: animal feed; brewing malts; and human food. Barley is a short season, early maturing grain with a high yield potential and may be found on the fringes of agriculture, in widely varying environments, including extremes of latitude and altitude where other crops are not adapted (Harlan, 1976a). It extends far into the Arctic, reaching the upper limit of cultivation in high mountains; it grows in desert oases and desert fringes, where it is more salt-and drought-tolerant than other cereals. Barley is a cool season crop; it can tolerate high temperatures if the humidity is low, but is not suited to warm humid climates. It is rarely grown in the tropics except in cool highlands, as in Mexico, the Andes and East Africa. Major production areas are Europe, the Mediterranean fringe of North Africa, Ethiopia, the Near East, Russia, China, India, Canada, the United States and Australia.

Barley was domesticated about 10 000 years ago in the Near East Fertile Crescent from brittle, two-rowed forms, morphologically identical with present-day *Hordeum spontaneum* (Zohary & Hopf, 1988). *Hordeum spontaneum* C. Koch is the wild ancestor of the cultivated barley (Harlan & Zohary, 1966; Zohary, 1969). It is considered systematically the wild race or subspecies of the cultivated crop, and is therefore designated *H. vulgare* L. subsp.

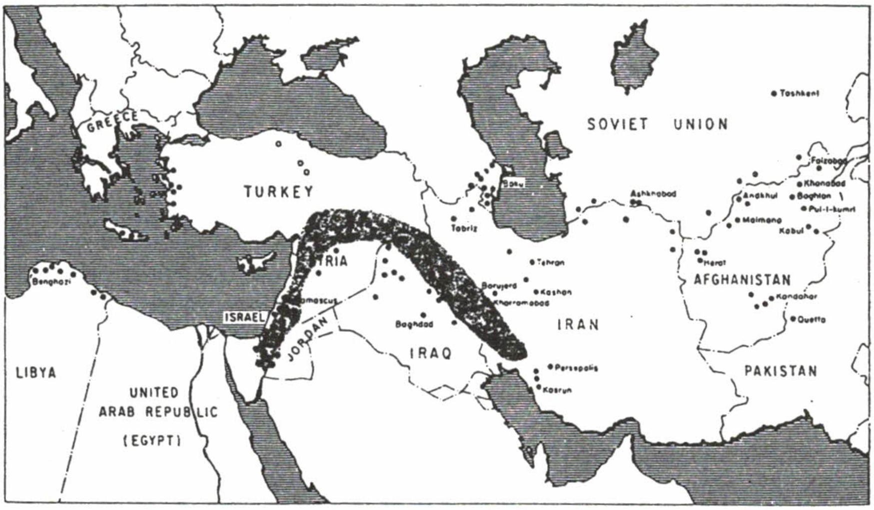

Fig. 2.1. Distribution of wild *Hordeum spontaneum* and of early archaeological sites for cultivated barley, *H. vulgare* (after Harlan & Zohary, 1966).

Population genetics: macrogeographic differentiation

We analysed enzyme polymorphisms encoded by 27 shared loci in 2125 individuals representing 52 populations of wild barley in Israel (Nevo *et al.*, 1979a, b), Iran (Nevo *et al.*, 1986a), Turkey (Nevo, 1986b) and the Near East Fertile Crescent (Nevo *et al.*, 1986c, where all isozyme loci are specified). Our main population genetics results from across the Fertile Crescent are outlined next.

Patterns of genetic variation

H. spontaneum in the Fertile Crescent is very variable genetically (Table 2.1). Overall, 127 alleles at 27 loci were described: 103, 63 and 62 for Israel, Turkey and Iran, respectively. The number of alleles increases with the average range of annual rainfall in the three countries: 100, 19 and 21% of the total range for Israel, Turkey and Iran, respectively; see explanation in Tables 1 and 2 of Nevo *et al.* (1986c) for climatic variation and allele frequencies at 27 loci in the three countries. The mean proportion of polymorphic loci per population (1% criterion of polymorphism) was *P*-1% = 0.312 (range, 0.0–0.41), and gene diversity was *He* = 0.103 (range, 0.0–0.182), displaying high levels and wide ranges of genetic diversity in comparison with mean genetic estimates in nature (Nevo *et al.*, 1984c; Nevo, 1988b).

Genetic differentiation

Wild barley populations in the Near East differ considerably in their allelic content (Nevo *et al.*, 1986c). Out of 127 alleles at 27 shared loci, 65 alleles (51%) were unique, that is they occurred only in one country. Out of these 65 unique alleles, the distribution between Israel, Turkey and Iran was 50, 7 and 8, and their percentage in each of the countries was 48.5, 11.1 and 12.9% respectively. Most of the unique alleles (51 out of 65, or 78.5%) were not widespread but localized or sporadic. Remarkably, 40 out of the 65 unique alleles (61.5%) were common (frequency >10%). Thus, most importantly, a major population genetics pattern of wild barley, like that of wild emmer wheat though somewhat less dramatic, is the 'island' structure. A substantial number of the alleles of *H. spontaneum* are both unique and common locally. This 'island'

Table 2.1. Comparison of overall genetic indices (A, *p*-1%, *p*-5%, *H*, H_e, *F*), mean and ranges, based on 27 shared gene loci in: A, 28 Israeli, 11 Turkish and 13 Iranian populations; and B, three regions (Israel, Turkey and Iran), of wild barley, *H. spontaneum* (from Nevo *et al.*, 1986c).

				Mean proportion of loci					
				Polymorphic per population (*P*)		Heterozygous per individual (*H*)			
	Sample size (*N*)	No. of populations	Mean no. of alleles per locus (*A*)	1%	5%	Mean	S.E.	Wright's fixation index (*F*)	Gene diversity (H_e)
A									
Israel	1179	28	1.509	0.312	0.247	0.003	0.001	0.962	0.103
range			1.000–1.778	0–0.407	0–0.407	0–0.020	0–0.007	0.790–1.000	0–0.182
Turkey	437	11	1.428	0.306	0.253	0	0	0.994	0.099
range			1.111–1.593	0.111–0.370	0.037–0.333	0–0.004	0–0.002	0.954–1.000	0.022–0.156
Iran	509	13	1.507	0.356	0.328	0	0	0.997	0.130
range			1.296–1.778	0.259–0.481	0.185–0.481	0–0.003	0–0.002	0.979–1.000	0.057–0.194
Total	2125	52							
Mean			1.492	0.320	0.271	0	0	0.984	0.108
range			1.000–1.778	0–0.481	0–0.481	0–0.020	0–0.007	0.790–1.000	0–0.194
B									
Israel	1179		3.815	0.667	0.444	0.003	0.001		0.198
Turkey	437		2.333	0.444	0.444	0	0		0.180
Iran	509		2.296	0.519	0.481	0	0		0.184
Mean	2125		2.815	0.543	0.457	0.002	0.001		0.187

population genetics structure has theoretical and practical implications.

The average relative genetic differentiation (*Gst*) (Nei, 1973) was 54% within populations, 39% among populations within countries, and 8% between the three countries. This pattern is also substantiated by the average genetic distances, *D* (Nei, 1972), between and within countries. Mean *D* decreased within countries in the following order: Israel ($D = 0.119$), Turkey ($D = 0.110$), and Iran ($D = 0.065$). The genetic distances also indicate sharp genetic differentiation over short geographic distances. The genetic distance is larger between Israel and either Turkey or Iran ($D = 0.134$ and $D = 0.129$, respectively) than between Turkey and Iran ($D = 0.111$). Discriminant analysis by allele frequencies successfully clustered wild barley of the three countries (96% correct classification) (Fig. 2.2).

Environmental correlates of allozyme diversity

A substantial portion of allozyme diversity in the wild gene pool is significantly correlated with the environment and is predictable ecologically, chiefly by a combination of climatic factors of rainfall, humidity and temperature variables. For example, about a third of the variance of *P*-1% is significantly explained by a three-variable combination of mean annual rainfall, humidity, and August temperature ($R^2 = 0.31$, $P < 0.001$), (Nevo *et al.*, 1986c, p. 370). It appears that rainfall is the best predictor of the genetic indices. Out of 29 alleles representing 11 polymorphic loci, the geographic variation in the frequency of 20 (69%) alleles was explained by a combination of climatic and geographical variables ($R^2 = 17\text{–}46\%$), primarily with factors of water availability and temperature (Table 8 in Nevo *et al.*, 1986c). This is essentially the pattern found earlier, both qualitatively and quantitatively, for each country (Israel, Turkey, Iran). Notably, geographic variation in *H. spontaneum* from Israel was also described for cytoplasmic male sterility genes and in nuclear genes for restoration (Ahokas, 1980).

Multilocus structure of natural populations

The association of alleles among different loci (linkage or gametic phase disequilibrium) has been primarily studied between two-locus associations (e.g. Clegg *et al.*,

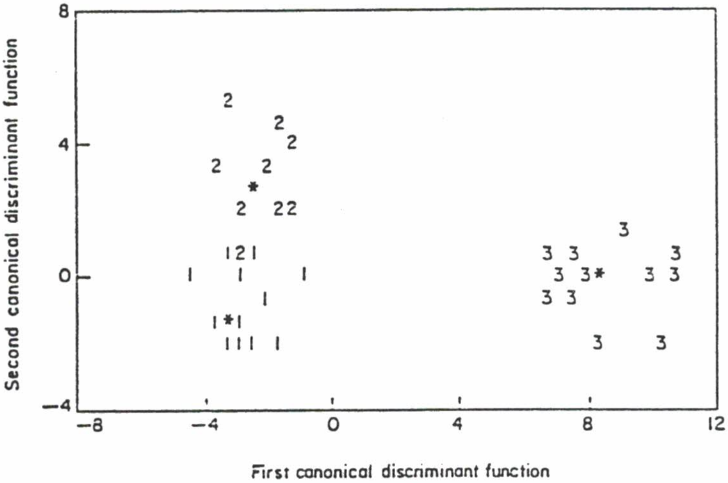

Fig. 2.2. Discriminant analysis of populations of wild barley, *H. spontaneum* from Israel (1), Turkey (2), and Iran (3). *Centroid (from Nevo *et al.*, 1986c).

1972; Karlin, 1975; Hedrick *et al.*, 1978; Weir, 1979; Brown, 1984). We have reported the widespread occurrence of co-adapted combinations of alleles at the four esterase loci in 11 populations of wild barley from Israel (Brown *et al.*, 1977). However, multilocus organization can effectively be summarized over *many* loci rather than by two-locus disequilibria (Brown *et al.*, 1980). The variance of the number of heterozygous loci in two randomly chosen gametes affords a useful measure of such association. Generally, linkage disequilibrium tends to increase the variance above the value expected under complete independence. When data on several loci per individual are available, the observed variance may be tested for agreement with that expected under the hypothesis of complete interlocus independence, using the sampling theory of this model, and generating an index of multilocus organization.

Multilocus organization, based on allozyme data from 26 polymorphic populations of wild barley, was shown to be geographically widespread (Brown *et al.*, 1980). On average, the variance was 80% higher than expected under random association. Most generations of barley composite crosses showed less multilocus structure of four esterase loci than the wild populations. Additional multilocus allozyme analysis indicated a repetitive pattern of the multilocus associations in the composite crosses in contrast to the regionally localized and geographically variable pattern in wild *H. spontaneum* (Brown & Feldman, 1981). While multilocus associations could also be generated by historic and non-selective factors, we interpreted these associations in wild barley and in wild emmer (Nevo & Beiles, 1989) as the result of natural selection.

Population genetics: microgeographic differentiation

Microsite allozyme polymorphisms

Microgeographic allozymic differentiation can take place over remarkably short distances, despite considerable gene flow, and is therefore adaptive at the morphological, physiological (Bradshaw, 1972) and allozymic levels (Nevo *et al.*, 1977, 1981, 1983, 1986d, 1988a, b, in press). Microgeographic allozyme differentiation is partially related to environmental factors (Brown, 1979). We have conducted two microsite allozyme studies in *H. spontaneum* (Nevo *et al.*, 1981, 1986d) and one on the storage protein, hordein (Nevo *et al.*, 1983). Our microsite allozyme studies involved first two soil types, basalt and terra-rossa, along 100 m transects at Tabigha (Nevo *et al.*, 1981); and secondly, six climatic microniches, mosaically distributed, in an open oak forest in the Lower Galilee mountains (Nevo *et al.*, 1986d) involving the following microniches: (i) sun–soil; (ii) sun–rock; (iii) shade–soil; (iv) shade–rock, and the contact zones; (v) soil periphery of the sun–rock microniche; and (vi) soil periphery of the shade–rock microniche. In both microsite allozyme studies, involving 22 and 25 enzyme loci, respectively, we obtained similar results. Allozyme polymorphisms in wild barley are patterned and not random even in a microsite. They are at least partly adaptive and differentiate predominantly by microniche ecological selection, rather than by stochastic processes and/or neutrality of allozyme variants.

Similar results of microsite genetic differentiation were obtained in wild emmer wheat, *T. dicoccoides* by: (i) climatic selection (Nevo *et al.*, 1988a); (ii) edaphic, topographical and temporal selections (Nevo *et al.*, 1988b); and (iii) topographical selection (Nevo *et al.*, in press). The underlying major evolutionary force causing genetic differentiation in overall genic diversity, allele frequencies, gametic phase disequilibria, and multilocus organization of wild barley, as well as wild emmer wheat, appears to be the aridity stress.

Microsite hordein polymorphisms

The hordein storage protein consists of two major groups of polypeptides governed by co-dominant alleles at two loci, *Hor1* and *Hor2*, which are highly polymorphic in cultivated barley, but particularly in *H. spontaneum* (Doll & Brown, 1979). Recently, a third locus, *Hor3*, was described, located with *Hor1* and *Hor2* on chromosome 5 (Blake *et al.*, 1982; Shewry *et al.*, 1983).

Microgeographic edaphic differentiation was also demonstrated in hordein polymorphisms of wild barley (Nevo *et al.*, 1983) along the same 100 m soil transect which displayed allozymic differentiation in an earlier study (Nevo *et al.*, 1981). Genetic diversity in *Hor1* and *Hor2* was analysed electrophoretically in seeds from 123 plants of wild barley, *H. spontaneum*. The test was conducted in two topographically different 100 m transects in Israel, each equally divided into basalt and terra-rossa soil types. Altogether 15 *Hor1* and 16 *Hor2* phenotypes were detected; 7 phenotypes of *Hor1* and 5 of *Hor2* were common. Significant differentiation of both *Hor1* and *Hor2* phenotypes and their associations was found to be correlated with soil type and topography. Likewise, significant correlations were found between hordein phenotypes and allozyme types detected in a previous study (Nevo *et al.*, 1981). Our results suggest that at least part of the hordein polymorphisms in wild barley are adaptive and selected by soil and topographic differences over very short distances. Many different allozymic and hordein homozygous genotypes ('clones') occur differentially on the basalt and terra-rossa soil types, suggesting adaptive 'clonal' microsite distribution (Beiles & Nevo, in preparation).

Genetic diversity in wild and in cultivated barley

We compared total allozymic diversity of 19 shared loci of wild barley in Iran, Turkey and Israel with that of barley landraces from Iran and a collection of European landraces, also including two accessions from Egypt and one from India, and two composite crosses (Tables 2.2 and 2.3). Allozymic diversity was lowest in the composite crosses, intermediate in the landraces, and highest in the wild germplasm in the following order: Iran < Turkey < Israel. These results appear to hold even if the world collection of cultivated barley, which presumably represents the allelic diversity maintained in the domestic gene pool, is compared. When this comparison is made for four esterase loci, the differences between the wild and cultivated gene pools in number of alleles are: *Est1* (8,7); *Est2* (17,12); *Est4* (10,6); *Est5* (6,6) (Nevo *et al.*, 1986c; for cultivars see Kahler & Allard, 1981). These results emphatically demonstrate the potential role of the wild progenitor as well as that of the landraces (Brown & Munday, 1982) as valuable genetic resources for plant breeding. Higher diversity was also obtained for α-amylases than in cultivated barley (Brown & Jacobsen, 1982).

Table 2.2. Comparison of genetic indices among *Hordeum spontaneum*, and landraces and composite crosses of *H. vulgare*, based on 19 shared loci (from Nevo *et al.*, 1986c).

	N	*A*	*P*	H_e
H. vulgare				
Composite cross XXI (F_{17})	50	1.58	0.42	0.099
Composite cross XXXIV (F_4)	50	1.68	0.37	0.139
Landraces				
'European'*	178	2.26	0.47	0.146
Iranian	290	2.21	0.74	0.164
H. spontaneum				
Iran	509	2.58	0.68	0.218
Turkey	437	2.63	0.74	0.226
Israel	1179	4.11	1.00	0.228

* Twenty-nine accessions from the collection of Landbrugets Plantekulturs Sortssamling, Denmark, which include European landraces, plus one Indian and two from Egypt.

Chloroplast DNA (cpDNA) diversity in 11 lines of *H. spontaneum* was significantly higher than in 9 lines of *H. vulgare*, suggesting that the level of cytoplasmic diversity was markedly restricted during barley domestication (Clegg *et al.*, 1984). cpDNA diversity was found within and among

Table 2.3. Comparison of numbers of alleles and total diversity (H_t) among *Hordeum spontaneum* and *H. vulgare* (from Nevo *et al.*, 1986c).

	H. vulgare				*H. spontaneum*							
	European*		Iranian		Near East		Iran		Turkey		Israel	
Locus	Allele	H_t	Allele	H_t	Allele	H_t	Allele	H_t	Allele	H_t	Allele	H_t
Est-2	6	0.28	3	0.38	17	0.83	7	0.61	6	0.72	15	0.86
Acph-3	4	0.47	4	0.57	8	0.73	4	0.48	5	0.63	4	0.66
Est-4	4	0.58	3	0.45	10	0.70	4	0.62	4	0.63	7	0.70
Est-5	4	0.40	2	0.01	6	0.59	4	0.57	5	0.64	6	0.53
Nadh-1	2	0.01	3	0.50	4	0.47	3	0.29	2	0.48	4	0.54
Adh-1	1	0	2	0.04	3	0.29	2	0.17	3	0.52	3	0.24
Est-1	3	0.48	3	0.44	8	0.25	4	0.44	3	0.18	6	0.13
Aat-1	1	0	1	0	3	0.17	2	0.30	2	0.28	2	0.03
Pgi	1	0	3	0.19	5	0.16	4	0.22	4	0.17	3	0.13
Pgm	1	0	2	0.01	3	0.10	2	0.004	2	0.02	3	0.18
Adh-2	1	0	1	0	5	0.10	3	0.11	2	0.04	3	0.11
Cat	1	0	2	0.15	3	0.09	2	0.34	2	0.01	2	0.01
Mdh-2	1	0	1	0	7	0.05	2	0.004	3	0.02	4	0.08
Gdh	1	0	2	0.05	3	0.04	1	0	1	0	3	0.07
Aat-2	2	0.04	2	0.02	4	0.02	1	0	1	0	4	0.03
6Pgd-2	4	0.46	3	0.21	3	0.02	1	0	1	0	3	0.02
Acph-1	1	0	1	0	2	0.01	1	0	1	0	2	0.01
6Pgd-1	6	0.07	1	0	3	0	1	0	1	0	3	0.01
Mdh-1	1	0	2	0.11	2	0	1	0	2	0.002	2	0.01

*Twenty-nine accessions from the collection of Landbrugets Plantekulturs Sortssamling, Denmark which include European landraces, plus one Indian and two from Egypt.

populations of *H. spontaneum* from Israel and Iran, displaying ecogeographic correlates, and diversity was higher in *H. spontaneum* than in *H. vulgare* (Neale *et al.*, 1988). By contrast, however, landraces of *H. vulgare* proved more polymorphic in cpDNA and in mitochondrial DNA (mtDNA) diversity than *H. spontaneum* (Holwerda *et al.*, 1986). More genotypes and populations need to be studied to make a meaningful comparison.

Outcrossing in natural populations of *H. spontaneum*

The mating system is crucial to understanding the evolution of plant populations. We used our allozyme data to estimate outcrossing rates across the range of wild barley in Israel (Brown *et al.*, 1978a). The extent of cross-pollination was estimated quantitatively in 26 populations of wild barley (*H. spontaneum*) in Israel, using allozyme variation at 22 polymorphic loci. Individual population estimates varied from 0 to 9.6% outcrossing. The overall average was a very low rate, 1.6%, with a 95% confidence range of 0.8–2.7%. Outcrossing varied with ecology and was significantly higher in populations from mesic (2.1%), than from xeric regions (0.4%). The 0.037 multilocus heterozygosity encountered at 22 loci displayed a very high degree of multiple disequilibrium. In general, these results indicate that extensive genetic polymorphisms in the progenitor probably predate the domestication of the crop, and are maintained independently of introgression, presumably by natural selection in accordance with environmental heterogeneity.

Phenotypic and genotypic quantitative morphological and physiological variation within and between populations of *H. spontaneum*

Cultivated barley, even some composite crosses, harbour substantially less genetic diversity as compared with the wild gene pool (Nevo *et al.*, 1979a, b), or some tested landraces (Brown & Munday, 1982). Opposite results have been reported on landraces from the eastern Mediterranean countries Jordan, Syria, Turkey and Greece by Jana & Pietrzak (1988). This discrepancy may be derived from a lower number and a somewhat different set of tested loci. The reduction in genetic diversity of purebred lines makes cultivated barley increasingly vulnerable to new pathogens, pests and adverse climates, primarily hot ones. We therefore tested variation in quantitative traits of agronomic importance of *H. spontaneum* as potential genetic resources for breeding.

Variations in morphological and phenological characteristics

Populations of wild barley, *H. spontaneum*, in Israel, originating from diverse habitats, and tested earlier for allozymes (Nevo *et al.*, 1979a, b) and disease resistance polymorphisms (Moseman *et al.*, 1983; Nevo *et al.*, 1984b), were compared and contrasted for performance in agronomically important quantitative phenotypic traits (Nevo *et al.*, 1984a). The traits compared involved ten variables of germination, earliness, biomass and yield. The field experiments were conducted in 1980–2 in two relatively standardized and contrasting environments: mesic (Mount Carmel, Haifa) and xeric (Avedat farm and Sede Boqer, both in the northern Negev desert). The experimental design involved 26 population quadrangles at Avedat farm (1980), and rows of randomized plants of 11 populations in both Haifa and Sede Boqer (1981 and 1982).

The results indicated that the characters studied are partly genetically determined (Fig. 2.3). Striking genetic variation was found between and within populations in each site, whereas remarkable environmental variation, including genetic × environmental interaction, was found between the mesic and the xeric sites, as well as between populations and years. We concluded that wild barley in Israel varies not only in

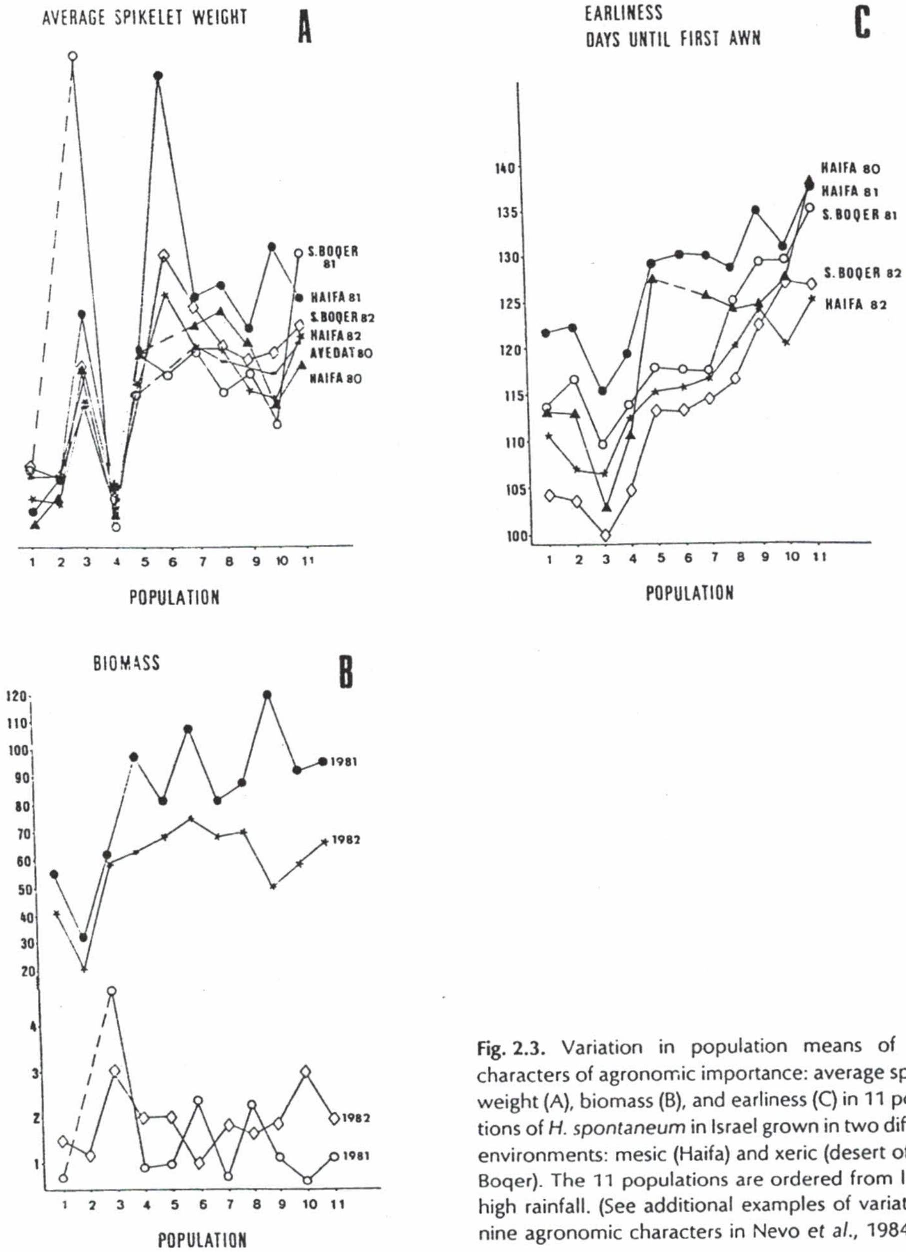

Fig. 2.3. Variation in population means of three characters of agronomic importance: average spikelet weight (A), biomass (B), and earliness (C) in 11 populations of *H. spontaneum* in Israel grown in two different environments: mesic (Haifa) and xeric (desert of Sede Boqer). The 11 populations are ordered from low to high rainfall. (See additional examples of variation in nine agronomic characters in Nevo *et al.*, 1984a.)

allozyme polymorphisms and disease resistances, but also in quantitative traits of agronomic importance. Similar results were obtained by others (Vega & Frey, 1981; Snow & Brody, 1984; Giles & Lefkovitch, 1985; Jaradat, 1989a). These traits are economically significant and should be conserved and utilized in barley improvement.

These agronomically important traits, which differ remarkably both within and between populations, are also geographically structured, and originated by natural selection as adaptations to macro- and micro-geographic environments. The variance in earliness, for example, is highly and significantly explained ($R^2 = 0.70$, $P < 0.001$) by a three-variable combination involving evaporation, humidity and the number of rainfall days (see other examples in Table 5 in Nevo *et al.*, 1984a). Outstanding earliness was found, as expected, in populations from steppe (Beth Shean, Mehola) and desert (Wadi Qilt), warm and dry habitats. Likewise, the yield in both the mesic and xeric test sites was higher in populations derived from optimal rather than marginal habitats for wild barley.

Advanced cultivars have been purebred throughout the last hundred years for high performance under intensive high-input cultivation, which tends to even out environmental, as well as genetic differences of site and season. Modern varieties, in contrast to either their progenitors or to landraces, are purebred cultivars. They are deliberately selected for performance over a range of environments, thus reducing the need for specific local adaptation. Hence, they are selected for a high degree of genetic homogeneity. Consequently, the genetic bases of cultivated crops have been narrowed and placed under serious risks and their future evolution placed in jeopardy (Frankel & Soule, 1981; Plucknett *et al.*, 1987). Our results substantiated earlier claims that wild barley in Israel displays remarkable morphological and physiological variation both within and between populations in each of the agronomic characters studied (Table 2, Fig. 2 in Nevo *et al.*, 1984a). Geographic variation in the Near East was also described in another study of reproductive structures of *H. spontaneum*, but its biological correlates require further investigation (Giles & Bengston, 1988).

The interest in the progenitors of crop species should not reside only in their wealth of resistance genes to pathogens acquired over long periods of host–pathogen co-evolution. *H. spontaneum* harbours a wealth of additional genetic traits of economic significance, such as earliness, high yield and high biomass. Apart from the direct importance of these traits in breeding, they can also improve breeding indirectly. When parental genotypes of the progenitor are used as donors of alien genes for disease resistance to a cultivar, it is desirable that they also combine the genetic capacity for high yield and biomass to avoid yield depression in the resulting crosses.

Variation in physiological performances: drought and salt tolerance

Natural populations of *H. spontaneum* involve abundant genetic variation in resistance to physiological stresses, such as drought and salinity. This is highlighted by the tremendous variation both between and within populations observed in our extreme desert station at Sede Boqer (Table 2 and Fig. 2 in Nevo *et al.*, 1984a). Recently, we tested populations and genotypes of wild barley *H. spontaneum* and wild emmer wheat, *T. dicoccoides*, for salt tolerance under controlled conditions, using 150, 250 and 350 mM NaCl (equivalent to 25, 40 and 60% sea water) with non-saline controls (Nevo, Krugman & Beiles, unpublished). We found high tolerances for salt within and between populations of *H. spontaneum* and *T. dicoccoides*, and identified genotypes of wild barley from coastal Mediterranean populations (e.g. Caesarea), the Jordan Valley (Mehola) and the northern Negev desert (Makhtesh Gadol) that spiked in 350 mM NaCl. Natural populations of wild barley extend southwards to the nothern Negev, yet they only grow there in dry water courses thereby effectively utilizing the extra run-off water. However, in our Sede Boqer experiments, under a water regime of 130 mm and, under highly saline soil conditions, some populations and superior genotypes have proved relatively outstanding in both growth and yield, despite these extremely harsh ecological conditions. Thus, the genetic resources of the progenitor display striking morphological and physiological performances, which are of potential economic importance for barley improvement.

Variation in vegetative parameters related to the nitrogen economy

The nitrogen contents and dry weights of leaf and 'stem' (stem plus sheath) at anthesis, and the final grain size and grain protein content were measured in 33 *H. spontaneum* and two *H. vulgare* genotypes (Corke *et al.*, 1988). *H. spontaneum* was generally higher in nitrogen content of leaves and stems, but lower in dry weight at anthesis. Consistent with previous reports, the *H. spontaneum* genotypes were considerably higher in grain protein (see next section) than the cultivars. There was wide variation between and within populations of *H. spontaneum*, suggesting that lines combining high vegetative nitrogen content, dry weight and grain protein content can be selected for breeding.

Variation in protein resources

The initial protein studies of *H. spontaneum* were conducted by Ladizinsky (1975) and Ahokas (1977, 1982). These studies indicated many significant differences in protein content between wild barley populations from different biogeographical regions. We have recently determined the protein content of *H. spontaneum* in Israel, and tested for associations with ecological and allozyme markers in an attempt to derive predictive guidelines for conservation and utilization in breeding programmes (Nevo *et al.*, 1985). The study involved 195 genotypes of wild barley from 25 populations, 15 central and 10 marginal, tested earlier for allozymic variation (Nevo *et al.*, 1979a, b). The results indicated that protein content varies within but particularly between populations. Notably, the ten marginal populations exhibited high protein contents (15.06%, S.E. ± 0.281), but low kernel weights (21.4 mg, S.E. ± 5.8), as compared with the 15 central populations which displayed lower protein contents (13.92%, S.E. ± 0.138), but high kernel weights (36.0 mg, S.E. ± 0.914). Thus, we demonstrated negative correlation between mean population protein percentage and mean kernel weight ($r_s = -0.56$; $P = 0.004$, for $n = 25$ populations). Notably 96% of our populations were correctly classified in a discriminant analysis to either marginal or central populations. Three-variable combinations of climatic factors explain 40% of the variability in protein content among populations. Likewise, three-variable combinations of allozyme allele frequencies explain a significant degree of spatial variance in protein content ($R^2 = 0.63$). The genetic determination estimate *within* populations was 57% and the overall genetic determination was 80%. Thus, protein content is amenable to cultivar improvement. Later, 21.5% grain protein content was described in *H. spontaneum* versus 13% in a standard Israeli barley cultivar (Friedman & Atsmon, 1988). We concluded that natural populations of wild barley in Israel contain large amounts of yet untapped genes for protein content. These could be effectively screened and utilized for producing high-protein cultivars of barley by following ecological and allozymic markers as predictive guidelines in screening natural populations of wild barley.

Disease resistance polymorphisms in *Hordeum spontaneum*

Host–pathogen co-evolution in the centre of diversity

Crop diseases prevent a rapid increase in food production. Crop improvement should, therefore, aim to minimize the risks of both epidemic and endemic diseases in an attempt to increase production efficiency, without affecting the agronomic properties of existing varieties (Horsfall & Cowling, 1977). In general, natural plant ecosystems are not devastated, but develop efficient defence against diseases, due to the long-lasting host–pathogen co-evolution. In a centre of diversity, this evolutionary interaction results in a balanced genetic polymorphism with the highest genetic diversity for virulence in the pathogen, and for resistance in the host (Dinnor, 1974; Anikster & Wahl, 1979).

Israel is one of the epicentres where active co-evolution of several crop ancestors and their pathogens occurs, including wild barley, wild wheat and their rust and powdery mildew pathogens. Following the theory and genetics of host–parasite co-evolution, the highest and broadest genetic immunity against devastation in the progenitors of some crops would be expected in the Fertile Crescent in general, and in Israel in particular. Israel is ideal for the exploitation of resistance genes which could provide useful material for crop improvement, for both the short-term, and more importantly, the long-term solution to disease problems in agriculture (Segal *et al.*, 1980, 1982). This includes the clarification of the controversy related to specific and general resistance (Anikster & Wahl, 1979).

Resistance to powdery mildew (*Erysiphe graminis hordei*)

The world-wide importance of yield losses in barley caused by the powdery mildew disease of barley (*Erysiphe graminis hordei*) is well known (e.g. Brooks, 1970), and was discussed as an objective in breeding cereal varieties (Slootmaker, 1974). Many sources of barley resistant to *E. graminis hordei* have been identified (Moseman *et al.*, 1983), and used extensively in developing resistant cultivars in many countries. Plant diseases in natural populations of wild barley were recently reviewed by Dinoor & Eshed (1990a, b). Many *H. spontaneum* accessions obtained from plants growing in Israel have been found to be highly resistant to *E. graminis hordei* (Moseman *et al.*, 1980). Moseman & Craddock (1976) reported that 75% of 277 accessions of *H. spontaneum* collected in Israel were resistant to two cultures of *E. graminis hordei*. Fischbeck *et al.* (1976a) reported that about 50% of 2700 unselected accessions of *H. spontaneum* were attacked only slightly or not at all by European field isolates of the pathogen. They found accessions resistant to the pathogen in all 69 collection sites in Israel with natural stands (see also Segal *et al.*, 1980, 1982). Baenziger *et al.* (1981) have developed a composite cross population with recessive male-sterile genes consisting of 19 *H. spontaneum* accessions which are resistant to many cultures of *E. graminis hordei*.

The percentage of *H. spontaneum* accessions resistant to *E. graminis* depends on where the plants are collected in Israel. Wahl *et al.* (1978) found that *H. spontaneum* plants with resistant types were prevalent in the Golan Heights, the Galilee and in the Samarian and Judean highlands. Fischbeck *et al.* (1976b) showed that there are few plants resistant to *E. graminis hordei* in regions of Israel with low rainfall. The number and relationships of resistance genes in cultivated barley and in *H. spontaneum* have been determined by using cultures of *E. graminis hordei* collected in Israel and other cultures with specific virulences. Moseman *et al.* (1981) showed that the number of identifiable genes conditioning the resistance of *H. spontaneum* accessions was determined by the virulence of cultures of *E. graminis hordei*. They used culture CR3 and culture 64–54 isolated from a plant in Israel. Moseman & Jørgensen (1973) used culture 64–54 and other cultures with specific virulences to identify and differentiate between resistance genes within the complex *Ml-a* locus on chromosome 5 of barley. A total of 56 mildew resistance genes participate in the inheritance of mildew resistance of *H. spontaneum* derived lines (Jahoor & Fischbeck 1987a). Thus, *H. spontaneum* in Israel forms a large gene pool for mildew resistance which is not yet widely used in barley breeding (Jahoor & Fischbeck, 1987b).

In the work conducted at the Institute of Evolution we found geographic variation in resistance of *H. spontaneum* against powdery mildew (Moseman *et al.*, 1983). Eighty-one resistant accessions and 180 moderately resistant accessions were identified against cultures of powdery mildew. Resistance was prevalent in northern and central Israel whereas sensitivity was distinct in the Negev and on Mt Hermon, where the pathogen is seldom observed. The resistance against powdery mildew is predictable ecologically and allozymically (Nevo *et al.*, 1984b).

Resistance to leaf rust (*Puccinia hordei*)

The reactions to infection with two cultures of *Puccinia hordei* were determined for 292 *H. spontaneum* accessions, collected at 16 sites which encompassed the entire ecological range of *H. spontaneum* in Israel (Moseman *et al.*, 1990). Culture Tel-Aviv was from Israel and culture 57.19 was from the United States. Of the accessions tested, 52% were resistant to culture Tel-Aviv, 67% were resistant to culture 57.19, and 43% were resistant to both cultures. The average infection type (IT) of accessions within sites ranged from 2.7 to 7.5 on a 0–9 rating scale. The results showed that the presence of *Ornithogalum* species, the alternate host of *P. hordei*, may increase the percentage of *H. spontaneum* accessions resistant to *P. hordei*. More accessions were resistant at sites where average annual humidity at 14:00 hours was higher, the annual evaporation was lower, and where the glumes were shorter. Kernel weight and annual rainfall were not correlated with resistance. A lower percentage of *H. spontaneum* accessions was resistant to *P. hordei* culture Tel-Aviv from Israel, than to culture 57.19 from the United States. Earlier, a lower percentage of *H. spontaneum* accessions was also found to be resistant to a culture of *Erysiphe graminis hordei* from Israel than to cultures from other countries. Previous studies have also shown that cultures of *P. hordei* and *E. graminis hordei* from Israel have many genes for virulence on barley, and that *H. spontaneum* accessions from Israel have many genes for resistance to these two pathogens. Previous results (e.g. Manisterski *et al.*, 1986; Treeful & Wilcoxson, 1986) and the results discussed here confirm that resistance to leaf rust is common in wild barley. The evidence supports the hypothesis of co-evolution of resistant host genes and virulent pathogen genes where hosts and pathogens have co-existed for a long evolutionary period.

We compared and contrasted disease resistance polymorphisms to infection with *Erysiphe graminis hordei* and *Puccinia hordei* in the Fertile Crescent (Jana & Nevo, in press). Random samples of 330 genotypes of wild barley plants collected from 14 sites in Iran, Turkey and Syria were compared and contrasted with 258 genotypes from 15 sites in Israel, studied earlier for allozyme diversity by Nevo *et al.* (1979a, b), and later for disease resistance for their reactions to infection with three cultures of *Erysiphe graminis hordei* (Moseman *et al.*, 1983) and two cultures of *Puccinia hordei* (Moseman *et al.*, 1990). One culture of each of the two pathogens was isolated in Israel, and the other cultures were isolated either in Japan or the United States. Of a total of 330 wild barley plants collected from 14 sites in Iran, Turkey and Syria, only 18.8% were resistant to the Israeli culture, and 14.8% were resistant to a composite of the Japanese and American cultures of *E. graminis hordei*. Of 105 plants collected from six sites in Iran and Turkey, none was found to be resistant to the Israeli culture and only 34.3% were resistant to the American culture of *P. hordei*. These frequencies were significantly lower than the corresponding frequencies of resistant wild barley plants from Israel. Phenotypic diversity for reactions to different cultures of the two pathogens was also higher in Israel. Considerable variations were observed both within and among sites for reactions to infection with different cultures of each of the two pathogens. These results illustrate the relative importance of wild barley accessions from Israel as a source of new genes for resistance to *E. graminis hordei* and *P. hordei*. Israel also appears to be one of the most desirable locations in west Asia for the *in situ* conservation of genetic diversity in wild barley in a dynamically evolving state (Dinoor & Eshed, 1990b; Ministry of Science and Technology, Israel, 1990).

Chromosomal localization and isolation of resistance genes

The utilization of major genes to detect and map genes controlling quantitative traits was described by Thoday (1961), and elaborated by Thompson & Thoday (1979). It was pioneered by Tanksley *et al.* (1982), using isozyme markers as major genes in analysing quantitative traits in tomato. The chromosomal localization of genes for isozymes has been summarized by Brown (1983).

As described earlier, we have used isozyme marker genes to identify élite genotypes of wild cereals (Nevo, 1987). However, the weakness of this predictive technique is in establishing correlations between the isozyme markers and the traits in question, while indisputable confirmation calls for tests by crossings. The segregation analysis of several generations can unequivocally determine the association or linkage relationships between isozyme loci and genes controlling the quantitative trait under study. We are currently analysing time of flowering (earliness) through breeding programmes in *H. spontaneum*. This trait displays wide geographic variation and has agronomic importance in enhancing cultivated germplasm.

Aside from its theoretical aspects, chromosomal localization and linkage analysis of isozyme loci (McIntosh, 1983; Brown 1983; Brown & Clegg, 1983; Brown *et al.*, 1989c; Tanksley & Orton, 1983; Hart & Gale, 1990) may permit direct genetic analysis of quantitative traits, and substantiate correlative results. It may also facilitate identification of these traits in segregants in breeding programmes, and of traits determined mainly by major genes, such as those for herbicide resistance in wild emmer wheat (Snape *et al.*, 1991a, b). Chromosomal localization of genes can be determined by analysis of addition lines (Islam *et al.*, 1981). As more enzymes and other DNA markers (Beckman & Soller, 1986) are located on the chromosomes, it will become easier and faster to analyse quantitative and single major gene traits of agronomic importance. A detailed review of isozymes in plant genetics and breeding appears in Tanksley & Orton (1983); of DNA markers in Beckman & Soller (1986); and of genetic engineering in Gasser & Fraley (1989). Chromosomal localization of the complex powdery resistant locus *Ml-a* (Moseman & Jorgensen, 1973), as well as the location of *Hor1, 2, 3* (Blake *et al.*, 1982; Shewry *et al.*, 1983), on chromosome 5 of barley, was described earlier. Chromosomal localization of salt-tolerant genes in wheat and barley was described recently by Forster *et al.* (1990). Genes with positive salt tolerance effects were located to chromosomes 4 (4H) and 5 (1H) of *H. vulgare*. The transfer of these genes from *H. spontaneum* to *H. vulgare* should be straightforward.

Genetically engineered plants for crop improvement

Through recombinant DNA technology, molecular biology can now probe much deeper into the genome, giving detailed information on the structure and function of genes. It also provides plant breeders with numerous potential genetic markers (reviewed in Beckman & Soller, 1986) for isolating genes of interest from genomic libraries. Dramatic progress has been made in the development of gene transfer systems for higher plants (Schell, 1987; Gasser & Fraley, 1989). The ability to introduce foreign genes into plant cells and tissues and to regenerate viable, fertile plants, has facilitated an explosive expansion of our understanding of plant biology and provided an unparalleled opportunity to modify and improve crop plants. Genetic engineering of plants offers significant potential for crop improvement. Transgenic plants have already been produced in many species, including herbaceous dicots (e.g. tomato, potato, tobacco), monocots (e.g. asparagus, rice, corn, orchard grass, rye), and woody dicots (e.g. poplar, walnut, apple). In particular, virus-, herbicide- and insect-resistant plants have been produced, and other genes conferring traits of agronomic importance will be transferred in the future.

The wild gene pool of barley and future barley breeding

The wild gene pool of *H. spontaneum* in the entire Near East Fertile Crescent is very rich in genetic variation, notably in important agronomic characters, such as earliness, biomass and yield (Nevo *et al.*, 1984a; Ceccarelli & Grando, 1987; Giles & Lefkovitch, 1985), proportions of lysine and other amino acids (Ahokas, 1977, 1982; Corke & Atsmon, 1988), nitrogen content (Corke *et al.*, 1988), protein content (Nevo *et al.*, 1985; Friedman & Atsmon, 1988), carbohydrate composition (Henry & Brown, 1987; Ahokas & Nashali, 1990), hordein patterns (Doll & Brown, 1979; Nevo *et al.*, 1983) and disease resistances (Moseman *et al.*, 1980; Lehmann & Bothmer (in Jorna & Slootmaker, 1988); Dinoor & Eshed 1990a, b), including a high proportion of resistant genotypes against powdery mildew (Fischbeck *et al.*, 1976a, b; Moseman *et al.*, 1983; Jahoor & Fischbeck 1987a, b; Jana & Nevo, in press) or leaf rust (Moseman *et al.*, 1990; Jana & Nevo, in press); and grain milling energy variation (Ellis, R.P., Forster, B.P. & Nevo, E., in preparation). Furthermore, we now have preliminary evidence that this vast biochemical, morphological and physiological diversity is distributed non-randomly in nature. This information is of paramount importance for optimizing sampling strategies, and for outlining guidelines for *in situ* conservation sites in nature.

The association of ecological (primarily climatic and edaphic factors) and allozyme markers as a predictive method to screen for genotypes resistant against powdery mildew was explored by Nevo *et al.* (1984b). *H. spontaneum* populations in Israel, which grow in the species centre of diversity, contain large amounts of unexploited disease-resistant polymorphisms significantly exceeding in resistance genotypes from other regions of the Fertile Crescent (Iran, Turkey, Syria) (Jana & Nevo, in press). This may also be true for other important agronomic characters discussed above. These traits could be effectively screened and utilized for producing resistant barley varieties by using ecological factors and allozymic markers as guidelines. Transfer of alien genes could proceed by classical plant breeding and/or by modern biotechnology. The use of isozyme-marked segments from *H. spontaneum* in barley breeding was described by Brown *et al.* (1988). Chromosomal localization of major genes and their transgenic utilization in barley and improvement of other crops, may become of paramount importance in the future.

The studies of population genetics structure reported here, as well as the availability of predictive screening methods based on ecology and allozymes, support a basic change in sampling strategies for *in situ* conservation in nature and in gene banks, respectively, and utilization in breeding. The number of sample sites based on the largest ecological spectrum available, should increase. This will increase the probability of collecting and/or preserving *in situ* the locally common alleles rather than concentrating on capturing the rare conspicuous morphological variant by intensive or biased sampling (see critical discussions in Marshall & Brown, 1975; Brown & Munday, 1982; Brown, 1983). Furthermore, if allozymes and restriction fragment length polymorphisms (RFLPs) are indeed good markers for screening disease-resistant genotypes, or genotypes with important agronomic traits such as high yield or earliness, then they could be used on an extensive scale because electrophoresis and RFLP analysis can be conducted quickly and relatively cheaply on a massive scale. By using allozyme markers (Tanksley & Orton, 1983) and RFLPs (Beckman & Soller, 1986) genes of agronomic interest could be chromosomally located, isolated from genomic libraries, and used to engineer improved cultivated barley (Gasser & Fraley, 1989).

The utilization of wild relatives in barley breeding was reviewed by Moseman *et al.* (1980), Grando *et al.* (1985), Brown &

Marshall (1986), and by several papers in Jorna & Slootmaker (1988). The potential of *H. spontaneum* for malting barley was described by Ahokas & Nashali (1990). High-yielding genotypes can be bred from *H. spontaneum* × *H. vulgare* crosses (Vega & Frey, 1981; Brown *et al.*, 1988). The wild germplasm of barley across the Fertile Crescent exhibits vast intra- and inter-population variation in a range of agronomic and quality traits (see earlier), as well as ecological tolerances to extremes of drought, salt and temperature. This vast potential store of genetic resources is as yet largely unexploited. Exploration, sampling, evaluation, documentation *in situ* and *ex situ* conservation, and utilization of these wild resources are of a supreme importance for future breeding. They should be actively and wisely explored and exploited to improve the genetically impoverished cultivated germplasm of barley.

Conclusions and prospects

The demands of an increasing and stabilized food production are extremely urgent in view of the population explosion (11–14 milliard people expected at the end of the twenty-first century). This dictates a concerted effort to advance crop improvement, not only agrotechnically, but, most importantly, genetically. Yet a major problem preventing effective crop improvement, and causing growing concern, lies in the drastic erosion of the genetic resources of the world's crops as compared with those of their ancestors. This process has been accelerated during domestication, particularly over the last century, due to modern pureline breeding practices which have increased genetic homogeneity in the cultivars. Thus, many important food crops have become increasingly susceptible to diseases, pests and environmental stresses.

The present interdisciplinary review of wild barley, *H. spontaneum*, the progenitor of cultivated barley, supports the idea that the greatest hope for future crop improvement lies in rationally and effectively exploring and exploiting the rich gene pool of the plant's wild relative. The centre of origin and diversity of wild barley is the Near East Fertile Crescent. Particularly in Israel, with its extraordinary biotic and genetic diversity, wild barley developed over a long evolutionary history, both within and between populations, a wide range of adaptive diversity to multiple diseases, pests and ecological stress. Most importantly, this variation is neither random nor neutral. By contrast, it displays at all levels adaptive genetic diversity for biochemical, morphological, physiological, and immunological characteristics which contribute to its ability to adapt to diverse climatic and edaphic conditions. The long-lasting co-evolution with parasites and with the ecologically heterogeneous nature of the Fertile Crescent, particularly in Israel, caused the development of numerous adaptive traits. These involve single variable genes, as well as multilocus co-adapted structures, locally and regionally, for both short- and long-term survival. Genetic resources of *H. spontaneum* harbour disease resistances, physiological adaptations for environmental stresses, high protein and nitrogen contents, nutritional quality, and diverse agronomic traits of economic importance. The last group includes growth rates, ripening and yield, in accordance with specific habitats, as well as grain size, grain milling energy variation and malting quality. A sound prediction would be that wild barley will display parallel patterns in other characters already found in wild emmer wheat, such as herbicide resistance (Snape *et al.*, 1991a, b) and photosynthetic yield (Carver & Nevo, 1990; Nevo *et al.*, 1991).

The genetic resources of wild barley, wheat and oats, and most probably of other progenitors of many crops found in Israel and elsewhere across their entire ranges, exhibit non-random, geographic distribution. This distribution is correlated with, and predicted by, climatic and soil factors as well as by allozyme and RFLP markers. We have suggested a predictive methodology, based on ecology and genetic markers to optimize sampling strategies, and maximize the screening and evaluation of élite populations and genotypes appropriate for breeding.

Chromosomal localization, crossing and recombinant DNA techniques are available, and pioneering success has been achieved in transferring alien genes from wild emmer and wild barley to their respective cultivars. The diverse genetic resources of these wild cereals are far from being fully exploited. Our predictive method of screening for optimal genotypes may also be extended to other progenitors, to help in maximizing the conservation and utilization of the genetic resources of wild germplasm. Thus, the genetic resources from the wild gene pool could substantially contribute to crop improvement by means of traditional plant breeding, complemented by the new biotechnology of gene transfer to overcome barriers to crossing due to incompatibility.

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