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Genetic Diversity and Environmental Associations of Wild Wheat, *Triticum dicoccoides*, in Israel

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Summary. Allozyme variation in the tetraploid wild progenitor of wheat, *Triticum dicoccoides*, was studied for the proteins encoded by about 50 gene loci in 457 individuals representing 12 populations from Israel. Six spikelet morphological traits were measured in the same populations. The results indicate that: (a) 16 loci (=32%) were monomorphic in all 12 populations, 15 loci (=30%) were locally polymorphic, and 19 loci (=38%) were regionally polymorphic. All polymorphic loci (but one) displayed high levels of polymorphism (≧ 10%). In Israel, the proportion of polymorphic loci per population, P, in wild wheat averaged 0.25 (range, 0.16 – 0.38), and the genetic diversity index, H_e averaged 0.07, (range, 0.03 – 0.12). (b) Altogether there were 110 alleles at the 50 putative loci tested (c) Genetic differentiation of populations included regional and local patterns: (i) The coefficients of genetic distance between populations were high (mean D=0.10 range, 0.02 – 0.25), and indicated sharp genetic differentiation over short distances. (ii) Common (≧ 10%) but sporadic and localized alleles were frequent (76%), and (iii) Rare alleles were few (only 5 alleles). (d) The patterns of allozyme and spikelet variation in the wild gene pool were significantly correlated with, and partly predictable by, water factors, including those of precipitation, evaporation, and relative humidity as well as of soil type. (e) All six spikelet characters showed statistically significant variation among localities and (f) Allozymic variation was correlated with spikelet variation.

These results suggest in *T. dicoccoides:* (i) the operation of natural selection in population genetic structure, (ii) local adaptive genetic differentiation caused by diversifying selection through climate and soil, and (iii) the guidelines for sampling these resources for use in wheat breeding programs.

Key words: *Triticum dicoccoides* – Allozyme polymorphisms – Genetic and ecological diversity – Sampling and conservation strategies

Introduction

Genetic diversity is the raw material essential to meet the diverse goals of modern plant breeding, namely producing cultivars with increased yield, wider adaptation, desirable quality, and pest and disease resistance. The naturally occurring wild progenitors of crop plants are one potential source of such diversity now receiving increasing attention (Harlan 1976). Plant breeders have used them primarily as a source of specific characters, notably disease resistance (Harlan 1976). This pragmatic approach has proceeded despite the limited basic knowledge of the levels and patterns of genetic variation in the wild species, and the evolutionary forces responsible for them. However, the efficient collection, study and use of such wild genetic resources would be greatly enhanced by answers to such questions as: (1) How genetically variable are the natural populations of the wild relatives? (2) How is this variation apportioned among populations? and (3) Do variability patterns reflect the varying ecological demands for survival or are they random? Electrophoretic surveys of genetic variation, perhaps the most convenient mode for assessing variation for this purpose (Brown 1978), have recently been made in *Lycopersicon pimpinellifolium* (Rick et al. 1977), and *Hordeum spontaneum* (Brown et al. 1978 a, b; Nevo et al. 1979). In this paper, we report the results of an electrophoretic survey of wild emmer wheat *Triticum dicoccoides*, the tetraploid wild source from which modern cultivated wheats were derived.

There are several reasons for choosing to address the above questions in samples of wild emmer. First, the wild relatives of wheat have been studied biogeographically, ecologically, physiologically, cytologically, and morphologically. Second, the different levels of ploidy in the wheat group allow a comparison of their genetic and ecological strategies. Third, cytogenetic, morphological and archaeological evidence indicate that wild emmer is the evolutionary progenitor of

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tetraploid cultivated emmer (*T. dicoccum*) and durum (*T. durum*) wheats (Zohary 1970). All three are tetraploids (2n=28), and hybrids between them are interfertile. Therefore, genes from *T. dicoccoides* can be easily transfered to cultivated tetraploids. In addition, the A and B genomes of tetraploid *T. dicoccoides* are present also in the hexaploid bread wheats. Here also, wild to cultivated gene transfer is possible through a partially fertile pentaploid bridge (Grama and Gerechter-Amitai 1974). Fourth, Israel is located in the primary distribution of the species, displays a large ecological amplitude for this species, and shows wide morphological diversity (Zohary 1970). Fifth, the discoveries of yellow-rust resistance (Gerechter-Amitai and Stubbs 1970), large grain size with high quality and quantity of grain protein (Avivi 1979a) justify the further study of this species as a genetic resource of wheat breeding (Avivi 1979b; Feldman, 1977, 1979; Feldman and Sears 1981). Sixth, the genetics of isozyme variation has been extensively studied in the wheat group (see review by Hart 1979), especially by aneuploidy. In general, these studies have shown the additivity of isozymes with homoeologous chromosomes in euploid and aneuploid stocks. In hexaploid wheat, most sets (16 out of 18) of triplicate structural genes for enzymes remain discernible.

The present analysis deals mainly with the central populations of *T. dicoccoides* in Israel. Our results show that allozymic variation in these populations is geographically structured and is associated with, and predictable by, environmental factors, primarily those of water availability, temperature and soil types. These results are in line with those found in our wild barley (Nevo et al. 1979) and wild oat (Kahler et al. 1980) studies, and they can provide a better basis for sampling and use of the wild germplasm.

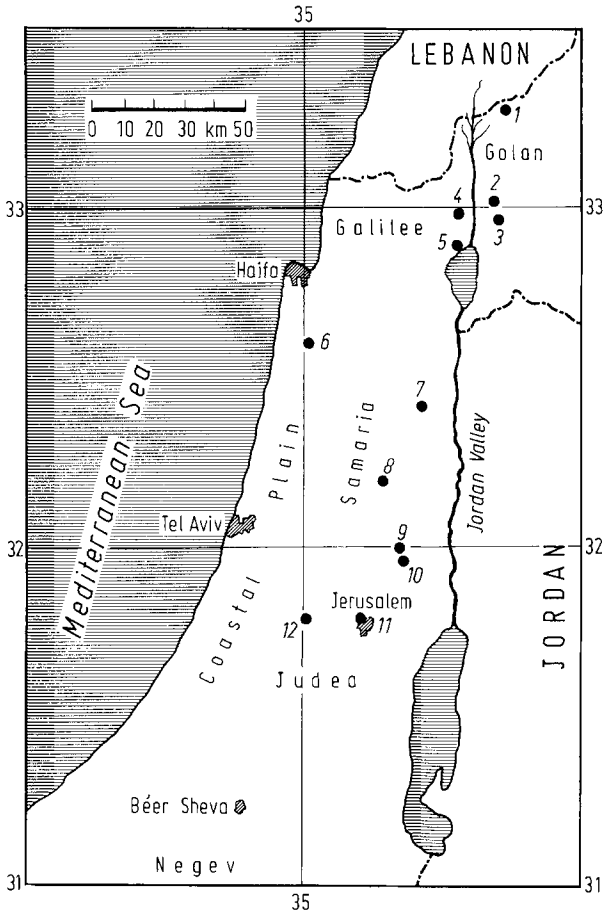

Fig. 1. Geographic distribution of sampling localities of *T. dicoccoides*

Materials and Methods

Ecological Background

Wild emmer (*T. dicoccoides*, genomic constitution AB) is distributed over the Near East Fertile Crescent including Israel, South Syria, Jordan (Harlan and Zohary 1976), South Turkey, North Iraq and West Iran (Rao and Smith 1968; Zohary 1969, 1970). The center of distribution of *T. dicoccoides* is found in the catchment area of the Upper Jordan Valley (East Galilee, Golan, Gilead, Hauran, Mt. Hermon). In this area, *T. dicoccoides* grows as an annual component in several steppe-like herbaceous formations and in the *Quercus ithaburensis* or in the *Q. brantii* park-forest belts. It grows chiefly on basaltic, hard limestone and dolomitic bedrocks. *T. dicoccoides* is restricted mainly to primary habitats growing together with wild barley, *H. spontaneum* and wild oats, *Avena barbata* and *A. sterilis*. It seldom occurs as a weed. Natural populations are often polymorphic for the color and hairiness of the spike. Wild emmer ranges over a wide altitudinal amplitude. Robust, early maturing types grow in the winter warm slopes facing the sea of Galilee (as low as 100 m below sea level). More slender and late flowering types occur in higher elevations reaching 1400 m on Mt. Hermon (Zohary 1970).

Sampling

Individual plants of *T. dicoccoides* were collected at random from 12 populations in April-June, 1975 – 1978 across the major ecogeographical range in Israel. The localities and their major ecogeographical parameters are given in Table 1, and the distribution of sites is mapped in Fig. 1. The localities occur in seven ecological regions: (1) Mt. Hermon (pop. 1); (2) Golan (pop. 2, 3); (3) Upper Jordan Valley (pop. 4, 5); (4) Ramot Menashe (pop. 6); (5) Samaria (pop. 7, 8); (6) Judean Desert (pop. 9, 10); and (7) Judean Mountains (pop. 11, 12). These regions encompass a wide range of climates and vegetation types and two main soil types, terra rossa (T) and basalt (B). The two geographically most distant sites (Mt. Hermon and Bet-Meir) are only about 180 km apart. The populations sampled essentially follow north-south and high-low altitudinal transects of increasing aridity (precipitation 1424 to 400 mm with some exceptions such as the western Bat Shelomo and Judean Mountains populations of Sanhedriyya and Bet-Meir). The Bat Shelomo population differs from all other 11

Table 1. Geographical and climatological data for 12 populations of *Triticum dicoccoides* in Israel

Population No.	Locality	Sample size (N)	Latitude (dec)	Longitude (dec)	Altitude (m)	Temperature (°C) annual Mean	annual s. d.	Jan. Mean	Aug. Mean	Rainfall annual (mm)	Humidity at 14:00 Annual mean (%)	Humidity at 14:00 s. d.	Evaporation annual (cm)	Soil type[a]	Plant community[b]
1	Mt. Hermon (Mt. Dov)	40	33.30	35.73	1300	11.1	7.3	3.2	21.0	1424	48.2	11.0	225[c]	T	2
2	Qazrin	40	33.02	35.67	350	18.0	–	10.0	26.0	616	43.0[c]	–	220[c]	B	5
3	Yehudiyya	39	32.93	35.70	200	19.0	–	10.5	27.0	678	42.0[c]	–	225[c]	B	7
4	Rosh Pinna	40	32.97	35.55	500	19.0	–	8.0	24.0	697	43.6	10.5	220	T	4
5	Tabigha	40	32.88	35.55	0	24.1	6.3	15.0	32.0	436	42.2	9.1	225	B	3
6	Bat Shelomo	40	32.60	35.02	75	19.9	4.9	13.1	26.0	596	55.2	3.4	185	R	6
7	Mt. Gilboa	32	32.48	35.42	350	21.9	6.2	13.4	29.6	405	43.8	8.2	200	T	8
8	Mt. Gerizim	25	32.20	35.28	800	21.3	6.5	13.0	29.0	618	46.9	8.1	210	T	8
9	Kokhav Hashahar	40	31.95	35.34	600	20.0	–	10.0	26.0	400	42.5	–	240	T	8
10	Taiyiba	41	31.92	35.35	450	20.0	–	10.0	26.0	400	42.5	–	240	T	1
11	Sanhedriyya	40	31.80	35.22	800	17.1	5.8	8.8	23.8	548	51.4	8.9	220	T	8
12	Bet Meir	40	31.80	35.03	500	18.0	–	9.0	26.0	582	47.1	10.8	210	T	9

[a] Soil type – T = terra rossa; B = basalt; R = rendzina

[b] Plant community: 1 = Marginal Mediterranean desert batha; 2 = Tragacantic batha (phyrgana); 3 = Marginal Mediterranean batha with *Zizyphus loti*; 4 = Marginal Mediterranean batha with perennial weeds; 5 = Primary climax of *Quercus ithaburensis* (sagital); 6 = Primary climax of *Q. ithaburensis* (batha); 7 = *Quercus ithaburensis* park forest; 8 = Batha of *Sarcopterium spinosum* (primary evergreen climax); 9 = Batha of *S. spinosum* with macquies of *Q. caliprinos – Pistacia palestina*

[c] Extrapolated

largely central populations. Bat Shelomo is isolated and occurs near the Coastal Plain (hence it has the lowest evaporation and highest humidity levels). It is also the only site with dark rendzina soil. Having no replicates from rendzina soil, we omitted the Bat Shelomo population from the soil correlations and from the multiple regression analysis (Table 6). In each site, spikes were collected from about 50 plants, at least 1 meter apart, along a transect of over one hundred meters. Seedling progeny from a total of 457 spikes were assayed electrophoretically.

Electrophoresis

Tissue preparative procedures, electrophoretic techniques, locus and allele designations were similar to those used for wild barley (Brown et al. 1978a). The 50 loci coding for the soluble proteins and their abbreviations are given below. The electrophoretic variants referred to in this paper as alleles, were labeled alphabetically in order of decreasing mobilities of their allozymes. We designated the first locus as A and the second one as B.

Our A and B designations represent the two contributing diploid genomes, although they are not necessarily the same A and B genomes commonly designated so on cytogenetical grounds.

When only one genomic contribution was found, either letter was omitted. The loci code for acid phosphatases (E.C.3.1.3.2) five loci (*Acph-1* A, B; *Acph-2*; *Acph-3*; *Acph-x*); alcohol dehydrogenases (E.C.1.1.1.1) four loci (*Adh-1* A, B; *Adh-2* A, B); catalases (E.C.1.11.1.6) two loci (*Cat* A, B); esterases (E.C.3.1.1.2) eight loci (*Est-1* A, B; *Est-2* A, B,; *Est-4* A, B; *Est-5* A, B); glutamate dehydrogenases (E.C.1.2.1.2) two loci (*Gdh* A, B); glucosidase (E.C.3.2.1.21) (*Gluc*); aspartate aminotransferase (E.C.2.6.1.1) five loci (*Aat-1* A, B; *Aat-2*; *Aat-3* A, B; previously *Got*); glucose-6-phosphate dehydrogenase (E.C.1.1.1.49) (*G-6pd*); hexokinase (E.C.2.7.1.1) (*Hk*); indophenol oxidases (E.C.1.10.3.1) three loci (*Ipol*; *Ipor* A, B) leucine aminopeptidase (E.C.3.4.1.1) (*Lap*); malate dehydrogenases (E.C.1.1.1.37) three loci (*Mdh-1* A, B; *Mdh-2*); lipoamide diaphorases (E.C.1.6.4.3) three loci (*Nadhd-1* A, B; *Nadhd-2*); phosphoenol pyruvate carboxylases (E.C.4.1.1.31) (*Pepc*); peptidases (E.C.3.4.13.11) three loci (*Pept-1* A, B; *Pept-2*); glucosephosphate isomerases (E.C.5.3.1.9) two loci (*Pgi* A, B); phosphoglucomutases (E.C.2.7.5.1) two loci (*Pgm* A, B) and phosphogluconate dehydrogenases (E.C.1.1.1.44) three loci (*6Pgd-1* A, B; and *6Pgd-2*).

Spikelet Morphology measurements

As varieties of wild emmer have previously been described from spike morphology, six spikelet characters were measured in the 12 populations on 10 random spikes in each. These were (a) the total length of the spikelet, including the first awn; (b) the total length of the spikelet including the second awn; (c) the length of the longest glume; (d) the length of the larger grain; (e) the weight of the larger grain, and (f) mature spikelet color on a graded scale of 15 categories from pure yellow through degrees of yellow mixed with a darker color: green, brown, to black.

Statistical Analysis

Stepwise multiple regression (Draper and Smith 1966) was employed to determine whether environmental factors were associated with gene frequencies of allozymes and phenotypic variation in spikelet morphology. In addition, Pearsonian correlations were computed between all variables.

Results

Pattern of Variation

Allele Frequencies

The frequencies of the individual alleles at each of the 50 putative loci are presented in Table 2. Eighteen systems exhibited both contributions from genomes A and B (36 loci = 72%), whereas 14 systems (*Acph-2, Acph-3, Acph-x, Gluc, Aat-2, G6pd, Hk, Ipol, Lap, Mdh-2, Nadhd-2, Pepc, Pept-2, 6Pgd*) displayed one genome only. Activity for the homoeologous loci was not distinguishable in these cases. In three systems (*Cat* A, B; *Aat-1* A, B; *Aat-3* A, B) we assumed contributions from both the A, B genomes owing to the distinct width of the zone in the tetraploid which corresponded to the combined width of the band in the diploids (*T. boeticum* and *Aegilops speltoides*, which were run simultaneously with the tetraploid). This interpretation of *Aat* zymograms is supported by the evidence of Hart (1975) and Jaaska (1976). Our computed genetic values are therefore based on the assumption of 32 systems presumably encoded by 50 gene loci. Although the variation we scored is real, its interpretation should be considered tentative until resolved by genetic crosses. This is particularly true for the *Acph* loci.

Out of the 50 loci, 16 loci (=32%) were monomorphic in all 12 populations, 15 loci (=30%) were locally polymorphic (polymorphism in 1 – 3 populations out of the 12), and 19 loci (=38%) were regionally polymorphic (polymorphism in 4 – 12 populations). The variation can be classified on the basis of genomes represented and degree of polymorphism as follows:

(A) Only one genome is represented

Three groups progressively more polymorphic were recognized:

(i) Monomorphic, 4 loci or 8% (*G-6pd, Hk, Mdh-2, Pepc*). Of these, the *Hk* locus was monomorphic within, but polymorphic between, sites, i.e. it was alternatively fixed.

(ii) Locally polymorphic, 5 loci or 10% (*Acph-2, Ipol, Lap, Nadhd-2, 6Pgd-2*).

(iii) Regionally polymorphic, 5 loci or 10% (*Acph-3, Acph-x, Gluc, Aat-2, Pept-2*).

(B) Both genomes are represented

Six groups progressivly more polymorphic were recognized:

(i) Monomorphic in both genomes, 6 loci or 12% (*Cat* A,B; *Aat-1* A, B; *Aat-3* A, B)

(ii) Monomorphic in one genome and locally polymorphic in the second genome, 4 loci or 8% (*Pgm* A, B; *6Pgd-1* A, B).

Table 2. Allele frequencies at 35 polymorphic loci of 12 populations of *Triticum dicoccoides* in Israel[a]

Population and code number		Mt. Hermon 1	Qazrin 2	Yehudiyya 3	Rosh Pinna 4	Tabigha 5	Bat Shelomo 6	Mt. Gilboa 7	Mt. Gerizim 8	Kokhav Hashahar 9	Taiyiba 10	Sanhedriyya 11	Bet Meir 12	Mean (P)
Locus	Allele	N = 40	40	39	40	40	40	32	25	40	41	40	40	457
Acph-1	A a	1.00	1.00	0.95	1.00	0.48	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95
	b			0.05		0.52								0.05
	B a							0.13		0.10				0.02
	b	1.00	1.00	1.00	1.00	1.00	1.00	0.87	1.00	0.90	1.00	1.00	1.00	0.98
Acph-2	a	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00	0.97	0.99
	Null						0.10						0.03	0.01
Acph-3	a		0.03	0.59		0.97								0.14
	b	1.00	0.95	0.41	0.82	0.03	0.72	1.00	1.00	1.00	1.00	1.00	1.00	0.82
	c		0.03		0.18		0.28							0.04
Acph-x	a				0.03		0.40	0.21	0.22			0.23		0.08
	b	1.00	1.00	1.00	0.97	1.00	0.60	0.79	0.78	1.00	1.00	0.77	1.00	0.92
Adh-1	A a	0.16	1.00	0.79	1.00	0.87	0.97	1.00	1.00	1.00	0.97	1.00	0.97	0.89
	b	0.84		0.21		0.13	0.03				0.03		0.03	0.12
	B a						0.03			0.89	0.09			0.09
	b	1.00	1.00	1.00	1.00	1.00	0.97	1.00	1.00	0.11	0.91	1.00	1.00	0.91
Adh-2	A a	1.00	1.00	0.74	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98
	b			0.26										0.02
	B a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.30	0.94
	b												0.70	0.06
Est-1	A a	0.02				0.05	0.26	0.90		0.03		0.10	0.24	0.12
	b	0.14		0.03		0.04	0.13							0.03
	c	0.84	1.00	0.97	1.00	0.89	0.60	0.10	0.83	0.97	1.00	0.75	0.75	0.82
	Null					0.02	0.01		0.17			0.15	0.01	0.03
	B a	0.04						0.09					0.25	0.03
	b	0.05	0.03	0.84	0.10	0.72	0.24		0.09	0.03	0.05	0.13		0.19
	c	0.33	0.05	0.05	0.72	0.20	0.67	0.91	0.91	0.45	0.45	0.17	0.05	0.39
	Null	0.59	0.92	0.11	0.18	0.08	0.09			0.52	0.50	0.70	0.70	0.39
Est-2	A a	0.01			0.16	0.03				0.15				0.03
	b			0.14	0.05						0.23		0.20	0.06
	c	0.75	1.00	0.39	0.61	0.44	0.83	0.54	1.00	0.35	0.62	0.87	0.80	0.68
	d	0.14				0.41				0.47	0.12			0.11
	e			0.08				0.38						0.03
	Null	0.10		0.39	0.18	0.12	0.17	0.08		0.03	0.03	0.13		0.10
	B a	1.00	1.00	1.00	1.00	1.00	0.59	1.00	1.00	0.92	0.90	1.00	1.00	0.95
	b						0.41			0.03				0.04
	c									0.05	0.02			0.01
	Null										0.07			0.01
Est-4	A a	0.95	1.00	0.90	0.85	1.00	1.00	1.00	0.80	1.00	1.00	1.00	1.00	0.96
	b	0.05		0.10	0.15				0.20					0.04
	B a	0.43	0.90	0.03	0.47	0.36	0.89	0.25	0.20	0.47	0.84	1.00	1.00	0.58
	b				0.12									0.01
	c	0.57	0.10	0.97	0.41	0.64	0.11	0.75	0.08	0.38	0.16			0.35
	d								0.72	0.15				0.06
Est-5	A a	1.00	0.09	1.00	0.92	1.00	0.72	1.00	1.00	0.94	1.00	1.00	1.00	0.88
	b		0.91		0.08		0.28			0.06				0.12
	B a	0.92	0.04	1.00	0.92	0.97	0.56	1.00	1.00	0.85	1.00	0.10	0.33	0.70
	b						0.15			0.07		0.71		0.09
	c		0.94				0.29							0.11
	d				0.08									0.01
	e	0.03	0.02			0.03				0.07		0.18	0.67	0.09
	f	0.05												0.00

[a] The following loci were monomorphic in all 12 populations: *Cat* A, B; *Gdh* A; *Aat-1* A, B; *Aat-3* A, B; *G6pd*; *Mdh-1* B; *Mdh-2*, *Pepc*, *Pept-1A* *Pgi* B; *Pgm* B; *6Pgd-1A*

Table 2. (continued)

Population and code number		Mt. Hermon 1	Qazrin 2	Yehudiyya 3	Rosh Pinna 4	Tabigha 5	Bat Shelomo 6	Mt. Gilboa 7	Mt. Gerizim 8	Kokhav Hashahar 9	Taiyiba 10	Sanhedriyya 11	Bet Meir 12	Mean (P)
Locus	Allele	N = 40	40	39	40	40	40	32	25	40	41	40	40	457
Gdh	B a	0.95	0.95	1.00	1.00	0.97	0.97	1.00	0.88	0.92	1.00	1.00	1.00	0.97
	b	0.05	0.05			0.03	0.03		0.12	0.08				0.03
Gluc	a	0.09			0.02				0.04	0.18				0.03
	b	0.91	0.96		0.95		0.58	1.00	0.96	0.82	1.00	1.00	1.00	0.75
	Null		0.04	1.00	0.03	1.00	0.42							0.22
Aat-2	a		0.03	0.38	0.18	0.05								0.05
	b	1.00	0.97	0.62	0.82	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95
Hk	a	1.00	1.00		1.00		1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.82
	b			1.00		1.00								0.18
Ipol	a										0.15			0.01
	b	1.00		1.00	1.00	1.00	0.75	1.00	0.64	1.00	0.83	1.00	1.00	0.87
	c		1.00						0.36					0.09
	Null						0.25				0.02			0.03
Ipor	A a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.85	1.00	1.00	0.99
	Null										0.15			0.01
	B a	1.00	1.00	1.00	1.00	1.00	0.86	0.81	1.00	1.00	0.63	0.36	1.00	0.89
	b						0.14	0.19			0.37	0.64		0.11
Lap	a	0.17	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.78	1.00	1.00	0.91
	b	0.14												0.01
	Null	0.69									0.22			0.08
Mdh-1	A a	0.06	0.01	1.00		0.95						0.06		0.19
	b	0.94	0.99		1.00	0.05	1.00	1.00	1.00	1.00	1.00	0.94	1.00	0.81
Nadhd-1	A a				0.35									0.03
	b	0.62	0.22	1.00	0.65	1.00	1.00	0.91	1.00	1.00	0.90	0.31	1.00	0.79
	c	0.38	0.78					0.09			0.10	0.69		0.18
	B a	1.00	1.00	1.00	0.44	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95
	b				0.56									0.05
Nadhd-2	a	1.00	0.95	1.00	0.82	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	0.98
	b		0.05		0.18								0.03	0.02
Pept-1	B a			1.00		0.68	0.38	0.03	0.10					0.19
	b	1.00	1.00		1.00	0.32	0.62	0.97	0.90	1.00	1.00	1.00	1.00	0.81
Pept-2	a	0.69												0.06
	b	0.31	1.00	1.00	1.00	0.97	0.90	0.47	1.00	0.23	1.00	1.00	1.00	0.82
	c					0.03	0.10	0.53		0.77				0.12
Pgi	A a		0.03	0.03	0.67	0.19	0.03		0.62					0.12
	b	1.00	0.97	0.97	0.33	0.81	0.97	1.00	0.38	0.41	0.76	1.00	1.00	0.81
	c									0.59	0.24			0.07
Pgm	A a		0.06											0.01
	b	1.00	0.94	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
6Pgd-1	B a	0.86	1.00	1.00	1.00	1.00	1.00	0.94	1.00	1.00	1.00	1.00	1.00	0.98
	b	0.14						0.06						0.02
6Pgd-2	a	1.00	1.00		0.63	0.33	1.00	1.00	1.00	1.00	0.94	1.00	1.00	0.81
	b				0.31						0.06			0.03
	c			1.00	0.06	0.67								0.16

(iii) Monomorphic in one genome and regionally polymorphic in the second genome, 8 loci or 16% (*Gdh* A, B; *Mdh-1* A, B; *Pept-1* A, B; *Pgi* A, B)

(iv) Locally polymorphic in both genomes, 4 loci or 8% (*Acph-1* A, B; *Adh-2* A, B)

(v) Locally polymorphic in one genome and regionally polymorphic in the second genome, 8 loci or 16% (*Adh-1* A, B; *Est-2* A, B; *Ipor* A, B; *Nadhd-1* A, B)

(vi) Regionally polymorphic in both genomes, 6 loci or 12% (*Est-1* A, B; *Est-4* A, B; *Est-5* A, B)

In the monomorphic and locally polymorphic groups (A i, ii; B i, ii, iv) the same allele was either fixed or predominant in most populations. In contrast, the pattern of the regionally polymorphic groups (A iii; B iii, v, vi) displayed chiefly either sharp geographic differentiation over short distances, or shifts in the predominant allele between populations. In 37 out of the 50 loci (=74%) the same allele was common, throughout the range in at least 11 out of the 12 tested populations. In contrast, sharp geographic differentiation in 13 loci (=26%) characterized the northern populations in the Golan, Jordan valley and Bat Shelomo.

In the northern region, but chiefly in Mt. Hermon and the Golan, near or total alternative fixation occured in the following 8 loci (population numbers appear in parentheses); (i) *Acph-3*$^{a-b}$ (4–5); (ii) *Est-5* A^{a-b} (1–2); (iii) *Gluc*$^{b-null}$ (2–3, 4–5); (iv) *Hk*$^{a-b}$ (2–3, 4–5); (v) *Ipol*$^{b-c}$ (1–2); (vi) *Mdh-1* A^{a-b} (2–3, 4–5) (vii) *Pept-1* B^{a-b} (2–3); (viii) *6Pgd-2*$^{a-c}$ (2–3). The Qazrin-Yehudiyya populations (2–3), 10 km apart, were markedly differentiated at 6 loci; the Rosh Pinna-Tabigha populations (4–5), 10 km apart, at 5 loci, and the Hermon-Qazrin populations (1–2), 15 km apart, at 2 loci.

A summary of the genetic data on the 12 populations of *T. dicoccoides* in Israel is given in Table 3. The major features were: (a) lower mean values of genetic variation compared with diploid wild barley (Nevo et al. 1979), but similar to those of tetraploid wild oats (Kahler et al. 1980); and (b) distinct local differences over short geographic distances. The estimates based on 50 loci involve the average number of alleles per locus, A, (mean 1.33, range 1.20–1.46); the proportion of polymorphic loci per population, P (mean 0.25, range 0.16–0.38); and the proportion of heterozygosity per locus per individual, H (mean 0.002, range 0.000–0.006). The index of genic diversity, H_e, which is the average per locus probability that two random gametes from the population carry different alleles at a locus (Nei 1975), was appreciable (mean 0.070) and varied geographically (range 0.031–0.118). The mean of Wright's fixation index (Wright 1965) was high, but also varied geographically (F=0.96, range 0.82–1.00). Such values imply that *T. dicoccoides* in predominantly self-pollinated, with outcrossing of the order of 3%. Northern populations (1–6) were genetically more variable than southern populations (7–12). The three genetic indices A, P, H_e, were 1.38, 0.29, 0.079 for the former, and 1.27, 0.21, 0.062 for the latter (Table 3; The differences in A and P are significant, t-test, $P<0.05$). This significant difference persists also after the exclusion of the exceptional highly polymorphic Bat

Table 3. Genetic variation based on 50 loci in 12 populations of *Triticum dicoccoides* in Israel

No.	Locality	Sample size (N)	Alleles per locus (A)	Mean proportion of loci		Diversity index (H_e)	Mean distance to other populations	
				Polymorphic per population (P)	Heterozygous per individual (H)		Geographic (km)	Genetic (D)
1	Mt. Hermon (Mt. Dov)	40	1.42	0.28	0.002	0.084	103	0.093
2	Qazrin	40	1.32	0.26	0.004	0.031	77	0.123
3	Yehudiyya	39	1.28	0.22	0.001	0.061	74	0.170
4	Rosh-Pinna	40	1.42	0.30	0.001	0.101	72	0.016
5	Tabigha	40	1.40	0.29	0.005	0.080	68	0.148
6	Bat Shelomo	40	1.46	0.38	0.005	0.118	73	0.070
7	Mt. Gilboa	32	1.24	0.22	0.000	0.060	61	0.084
8	Mt. Gerizim	25	1.22	0.20	0.006	0.059	66	0.078
9	Kokhav Hashahar	40	1.38	0.26	0.003	0.079	75	0.092
10	Taiyiba	41	1.36	0.26	0.001	0.075	76	0.062
11	Sanhedriyya	40	1.22	0.16	0.000	0.057	90	0.086
12	Bet Meir	40	1.20	0.16	0.002	0.043	96	0.081
Total		457						
Mean			1.33	0.25	0.002	0.070	77.7	0.097
Range			1.20–1.46	0.16–0.38	0.000–0.006	0.031–0.118	61–102	0.062–0.170

Shelomo population, No. 6. The overall number of alleles detected in the 50 loci in the 12 populations of *T. dicoccoides* in Israel amounts to 110 (mean per locus 2.20, range 1 – 6).

Geographic Patterns of Allele Distribution

The values of A, P and H_e decreased southwestwards from Mt. Hermon to Southern Golan and from Rosh Pinna to Bet Meir, with some exceptions (population 6, 9 and 10). Simple clinal patterns in allele frequencies were rare or nonexistant. When they occurred, they were regional and short such as in: *Est-1* A^c (7 – 10), *Est-1* B^c (7 – 12); *Est-4* B^a (7 – 12). The major pattern of allelic distribution was regional and local.

Regional distribution of alleles (appearance in 2 or more regions) included *Est-1* A^a, *Est-5* B^e, *Gluc*^{null}, *Ipor* B^b, *Lap*^{null}, *Pept-1* B^a, *Pept-2*^{c}, *Pgi* A^a, and *6Pgd-1* B^b. Local distribution (appearance in only one region) included: *Adh-2* A^b, *Adh-2* B^b, *Est-2* B^{null}, *Est-4* B^b, *Est-5* B^d, *Ipol*^{a}, *Ipor* A^{null}, *Lap*^{b}, *Nadhd-1* A^a, *Pgi* A^c.

To assess the various kinds of allele distributions we followed the classification proposed by Marshall and Brown (1975) and Brown (1978). Each of the 110 alleles found in the 12 populations of *T. dicoccoides* in Israel was classified into one of the following five classes: (i) Common (=at least one sample with frequency ≧ 10%): (a) widespread, common occurrence in more than two regions (64 alleles, or 23% of the variants); (b) sporadic, common occurrence in two regions (19 alleles, or 31%); (c) localized, common occurrence in only one region (22 alleles, or 37%); (ii) Rare (=never occurs with frequency ≧ 10%): (d) widespread, in more than one region (0 alleles), and (e) localized, in only one region (5 alleles, or 8%). The percentage of the variants was computed by subtracting the number of loci studied from the number of alleles in class (i) (a). This adjustment standardized any differences in the number of invariant loci recorded. Note that 76% of the variant alleles were not widespread. These figures suggest that natural populations of wild wheat in Israel differ considerably in their allelic content.

Genetic Distance

Coefficients of genetic similarity (I) and distance (D) were calculated for paired comparisons of all 12 populations, based on the normalized identity of all loci be-

Table 4. Coefficients of genetic similarity (I, upper figure) and genetic distance (D, lower figure) between 12 populations of *Triticum dicoccoides* in Israel

Population												
Locality	No.	1	2	3	4	5	6	7	8	9	10	11	12
Mt. Hermon (Mt. Dov)	1		0.894 0.112	0.832 0.184	0.930 0.073	0.846 0.168	0.926 0.077	0.934 0.068	0.927 0.075	0.926 0.077	0.955 0.046	0.927 0.075	0.931 0.072
Qazrin	2			0.780 0.248	0.900 0.105	0.802 0.221	0.923 0.080	0.878 0.130	0.905 0.100	0.883 0.124	0.924 0.079	0.934 0.068	0.921 0.082
Yehudiyya	3				0.853 0.159	0.977 0.023	0.862 0.148	0.838 0.177	0.839 0.176	0.823 0.194	0.848 0.165	0.815 0.205	0.825 0.192
Rosh-Pinna	4					0.870 0.139	0.949 0.052	0.945 0.056	0.970 0.030	0.939 0.063	0.968 0.033	0.934 0.068	0.941 0.061
Tabigha	5						0.884 0.124	0.854 0.158	0.861 0.150	0.848 0.165	0.870 0.139	0.838 0.177	0.849 0.164
Bat Shelomo	6							0.956 0.045	0.958 0.043	0.932 0.071	0.967 0.034	0.952 0.049	0.953 0.048
Mt. Gilboa	7								0.951 0.050	0.942 0.059	0.956 0.045	0.930 0.073	0.935 0.067
Mt. Gerizim	8									0.938 0.064	0.966 0.034	0.930 0.072	0.939 0.063
Kokhav Hashahar	9										0.959 0.042	0.918 0.086	0.931 0.072
Taiyiba	10											0.967 0.034	0.968 0.033
Sanhedriyya	11												0.959 0.042
Bet Meir	12												

I: Mean 0.909, Range 0.780 – 0.978; D: Mean 0.097, Range 0.023 – 0.248; standard errors of D range 0.002 – 0.005

tween each pair of populations (Nei 1972). The results are given in Table 4. The mean value of D was 0.097, (range 0.023 – 0.25). The standard errors of individual values of D were less than 0.005. The estimates of D indicated sharp genetic differentiation over short geographic distances; i.e., geographically close populations can have distinctly high D's whereas geographically distant populations can have lower D's. An extreme example was that of localities 2 and 3, separated by only 10 km for which D was 0.248, whereas between localities 2 and 12, separated by 160 km, D was 0.082. The average distances (both geographic in kilometers, and genetic in D) from each population to every other sampled population are listed in Table 3. There was no significant relationship between geographic separation and genetic distance, D ($r = -0.15$) or diversity level, H_e and D ($r = -0.26$), again indicating sharp local differentiation rather than gradual change in allele frequencies across the range of *T. dicoccoides* in Israel.

Spikelet Morphology

Table 5 gives the means and analysis of variance of the five spikelet characters which were intercorrelated ($0.49 < r < 0.72$, with the exception of color) for the 12 sampled populations of *T. dicoccoides.* Geographic variation was displayed by all five traits. A statistically significant amount of variation ($p < 0.001$) was present between localities. This spatial variation in spikelet morphology has been previously indicated by Zohary (1970), who emphasized the presence of morphologically ecogeographic races of *T. dicoccoides* in Israel. Spike color varies from yellow to black. The Tabigha population was pure yellow, whereas pure yellow spikes were absent from Rosh Pinna. The entire range of color morphs was present in three populations (Yehudiyya, Mt. Gerizim, and Bet Meir).

Environmental Correlates of Allozyme Polymorphism, and Spikelet Variation

Correlation Among Environmental Variables

In our search for environmental correlates with morphological and allozymic variation, we used several variables: (a) Geographical (Longitude, Ln, Latitude, Lt, and Altitude, Al), (b) Climatic (i) Temperature (mean annual, Tm, mean January, Tj, mean August,

Table 5. Spikelet morphometrics of 12 populations of *Triticum dicoccoides* in Israel

Population		Length (mm)								Weight (mg)	
		1st Awn		2nd Awn		Glume		Grain		Grain	
No.	Locality	Mean	S. D.	Mean	S. D.	Mean	S. D.	Mean	S. D.	Mean	S. D.
1.	Mt. Dov, Hermon	140	22	95	32	18	2.1	20	1.5	511	82
2.	Qazrin Junction	176	23	107	24	20	1.9	23	1.7	571	147
3.	Yehudiyya	202	19	188	21	22	1.7	22	2.5	574	263
4.	Rosh Pinna	200	16	192	16	19	1.1	23	0.9	592	83
5.	Tabigha	199	16	191	16	22	1.5	21	1.3	689	79
6.	Bat-Shelomo	164	15	141	35	20	2.6	22	1.7	456	77
7.	Mt. Gilboa	182	46	98	49	19	2.6	20	2.4	500	255
8.	Mt. Gerizim	146	17	118	21	16	3.5	17	1.0	463	118
9.	Kokhav Hashakhar	172	30	140	30	19	1.3	20	1.2	491	137
10.	Taiyiba	162	21	142	29	18	1.9	22	1.8	474	110
11.	Sanhedriyya	180	16	83	54	19	1.0	20	1.4	303	93
12.	Bet Meir	158	16	113	28	16	1.2	19	1.3	244	78
Mean		173	29	131	48	19	2.6	21	2.3	489	177
Range		140 – 202		83 – 192		16 – 22		17 – 23		244 – 689	

Analysis of variance
(Sum of squares appear as percentage of total)

Variation	Degrees of freedom	1st awn length	2nd awn length	Glume length	Grain length	Grain weight
Within localities	102[a] – 109	55.5	41.2	54.8	44.1	55.6
Between localities[b]	11	44.5	58.8	45.2	55.9	44.4

Sample size for each locality is N = 10 (for Mt. Dov, Hermon, N = 11)
[a] Some measurements are missing, therefore the variation in degrees of freedom
[b] The variation between localities in each of the 5 variables is statistically significant at $P < 0.001$

Table 6. Coefficients of multiple regression (R^2) with dependent variables P, H_e, and representative allele frequencies at 17 loci[a] and 5 spikelet variables of 11 populations[b] of *Triticum dicoccoides*, and as independent variables (A) geographic, climatic and edaphic, and (B) only climatic and edaphic factors[c]

Variable	Allele		Stepwise Model								
			A) Geographic, climatic and edaphic					B) Only climatic and edaphic			
			$X_1X_2X_3X_4$	R^2_1	R^2_{12}	R^2_{123}	R^2_{1234}	$X_1X_2X_3X_4$	R^2_1	R^2_{12}	R^2_{123}	R^2_{1234}
P			LtEvHuSo	0.44*	0.69**	0.76**	0.84**	HuRnEvTa	0.37*	0.60*	0.65	0.66
H_e			EvSoLtTa	0.17	0.28	0.58	0.75*	EvSoHuRn	0.17	0.28	0.35	0.66
Acph-1	A	a	TaSoEvRn	same as in B				TaSoEvRn	0.39*	0.51	0.55	0.64
Acph-3		a	SoTaEvRn	same as in B				SoTaEvRn	0.58**	0.67	0.70	0.77
Acph-x		b	EvLtLnHu	0.36	0.51	0.66*	0.77*	EvHuRnSo	0.36	0.49	0.65*	0.67
Adh-1	A	a	RnEvTaLt	0.82****	0.85****	0.90****	0.91***	RnEvTaSo	0.82****	0.85****	0.90****	0.91***
	B	a	EvLtHuAl	0.32	0.42	0.46	0.59	EvSoRnHu	0.32	0.40	0.48	0.51
Est-1	A	c	EvSoTaLn	0.53**	0.59*	0.64	0.68	EvSoTaHu	0.53**	0.59*	0.64	0.65
	B	c	SoTaLnEv	0.32	0.55*	0.87***	0.88***	SoTaHuRn	0.32	0.55*	0.60	0.69
Est-2	A	c	HuEvSoAl	0.38*	0.43	0.45	0.49	HuEvSoTa	0.38*	0.43	0.45	0.47
		d	EvTaAlLt	0.38*	0.56*	0.64	0.65	EvTaRnSo	0.38*	0.56*	0.60	0.65
	B	a	EvLtHuAl	0.56***	0.75***	0.83***	0.91***	EvSoRnHu	0.56***	0.69***	0.84***	0.88***
Est-4	B	c	LnTaSoAl	0.42*	0.53*	0.58	0.62	HuRnTaEv	0.25	0.40	0.49	0.50
Est-5	B	b	HuRnLnEv	0.47**	0.64**	0.82***	0.94****	HuRnEvSo	0.47**	0.64**	0.74**	0.80*
Gluc		b	SoTaEvRn	same as in B				SoTaEvRn	0.58***	0.61**	0.66*	0.73
Hk		a	SoTaRnEv	same as in B				SoTaRnEv	0.56***	0.57*	0.63	0.67
Ipor	B	a	LtHuLnRn	0.29	0.40	0.61	0.77*	HuRnEvTa	0.23	0.49	0.59	0.62
Lap		a	RnEvSoTa	same as in B				RnEvSoTa	0.72****	0.78***	0.82***	0.86**
Mdh-1	A	a	SoTaRnEv	same as in B				SoTaRnEv	0.59***	0.61**	0.64	0.69
Nadhd-1	A	b	TaSoHuRn	same as in B				TaSoHuRn	0.29	0.41	0.51	0.60
Pept-1	B	a	SoTaRnAl	0.55***	0.58*	0.60	0.63	SoTaRnEv	0.55***	0.58*	0.60	0.63
Pgi	A	c	EvLtHuAl	0.48**	0.63**	0.70*	0.83**	EvSoRnHu	0.48**	0.59*	0.72**	0.75*
6Pgd-2		c	SoAlRnLt	0.56***	0.57*	0.63	0.67	SoTaRnEv	0.56***	0.57*	0.58	0.61
First awn length			AlTaLtHu	0.57***	0.66**	0.69*	0.73	SoRnTaEv	0.29	0.44	0.47	0.49
Second awn length			HuAlRnEv	0.47**	0.50	0.56	0.63	HuEvSoTa	0.47**	0.49	0.51	0.51
Grain length			HuTaAlLn	0.32	0.50	0.80***	0.89***	HuTaSoRn	0.32	0.50	0.63	0.74
Glume length			SoLnRnEv	0.63***	0.70***	0.80***	0.83**	SoEvHuTa	0.63***	0.70***	0.70*	0.71
Grain weight			LnTaEvLt	0.66***	0.86****	0.90****	0.92***	HuRnTaSo	0.50**	0.64**	0.71*	0.73

[a] Only loci polymorphic at least in 2 populations were considered
[b] The Bat Shelomo population was excluded because it is the only tested population growing on rendzina as well as being a peripheral population (see in text)
[c] Abbreviations of environmental variables: Ln = longitude, Lt = latitude, Al = altitude, Ta = mean temperature in August, Rn = mean annual rainfall, Hu = mean mid-day relative humidity, Ev = mean annual evaporation, So = soil type
* $P<0.05$; ** $P<0.025$; *** $P<0.01$; **** $P<0.001$

Ta), (ii) Moisture (mean annual rainfall, Rn, mean mid-day relative humidity, Hu, mean annual evaporation, Ev), (c) Soil type, So, (d) Plant formation, Pl. The plant formations were ordered from the most xeric to the most mesic one, and therefore the correlation with the formation rank represents a real trend.

Of the environmental variables in our study the following were correlated, where r is the Pearsonian correlation for all 12 populations. Sometimes an additional correlation for only 11 populations (r_{11}), excluding the exceptional Bat Shelomo population, is also listed separately (Table 1, Materials and Methods). Lt-Ln

(r=0.77, r_{11}=0.93), Rn-Ta (r=−0.67), Hu-Tm (r=−0.33, r_{11}=−0.55) Hu-Ev (r=−0.66, r_{11}=−0.34), Tm-Tj (r=0.94), Tm-Ta (r=0.91), Ta-Tj (r=0.92, r_{11}=0.97). Since all temperature variables are highly intercorrelated we ran our multiple regression analysis with only one temperature variable (Ta).

Pearsonian Correlations

The allozyme variants displayed some morphological and environmental correlates. Henceforward, * P<0.05; ** P<0.01; *** P<0.001.

Allozyme Variation vs. Spikelet Variation. First, morphological and allozymic variation was partly correlated. Thirty three out of the 156 correlations (=21%) between the character means and allozymic variation were significant. In particular, the following loci showed significant correlations with several spikelet characters: *Acph-3, Est-1* B, *Hk*, *Mdh-1* A, *Pept-1* B, *6Pgd-2* (in each locus at least one r=0.74**). Likewise, the lengths of the awns and the glumes displayed significant correlations with 9 alleles, grain weight with 6 alleles and color with 2 alleles. In contrast, grain length showed only low, nonsignificant, correlations.

Environmental Correlations of Spikelet Variation. Slender ecotypes were correlated with altitude, Al, as reflected by the following correlations: 1st awn, r=−0.64*; seed lenght, r=−0.52; glume length, r=−0.61*. Seed weight was significantly correlated with Lt,Ln, (r=0.75**, 0.74**, r_{11}=0.60*, respectively). Finally, glume length was also correlated with basalt (r_{11}=0.79**).

Environmental Correlates of Polymorphism and Allozymic Variation. Polymorphism, P, increased with latitude, Lt, (r=0.52, r_{11}=0.66*) and decreased with humidity (r_{11}=0.61*), and with increasing plant over (r=−0.56). Water factors (Rn, Hu, Ev) were significantly correlated with *Acph-*x^b, *Adh-1* A^a, *Est-1* A^c, *Est- 2* A^c, *Est-2* B^a, and *Lap*^{null} (at least one r=0.61* to 0.90***). Temperature variables were primarily associated with *Adh-1* A^a, *Lap*^{a} (r=0.73**, 0.77**). Basalt was associated with *Est-1* B^b, *Mdh-1* A^a, *Pept-1* B^a (r=0.74** to 0.77**), and terra rossa with *Acph-*3^b *Gluc*^{b}, *Hk*^{a}, and *6Pgd-*2^a (r=0.68* to 0.77**). Plant formation was associated with *Lap*^{null} (steppic plant formation).

Multiple Regression Analysis

A test of the best predictors of P, H_e, and representative allele frequencies at 17 polymorphic loci and five spikelet variables in 11 populations was conducted by stepwise multiple linear regression analysis (Nie et al. 1975), employing these characters as dependent variables and geographic, climatic and edaphic factors as independent variables. The results are given in Table 6, first for all factors, then only for climatic and edaphic factors.

Water, soil and temperature factors, singly or in combination, explained significant proportion of the variation in polymorphism and allozymes. Polymorphism, P, is primarily predicted by water factors. The best two climatic variable-predictor of P explaining significantly 0.60* of its variance was HuRn (humidity and rainfall). A four variable combination involving both geographic (latitude) and climatic (evaporation and humidity) and soil factors, LtEvHuSo, accounted significantly for 0.84* of the variance in polymorphism.

Alleles and spikelet characters can be classified into several categories in term of their prime ecological predictors: (a) water factors (Rn,Hu,Ev) (*Acph-*x^b, *Adh-1* A^a, *Est-1* A^c, *Est-2* A^c, *Est-2* B^a, *Est-5* B^b, *Lap*^{a}, and grain weight); (b) water+temperature (*Est-2* A^d, grain length); (c) soil type (*Acph-*3^a, *Gluc*^{null}, *Hk*^{b}, *Mdh-1*^{a}, *Pept-1* B^a, *6pgd-*2^c), all associated with basalt; (d) soil+temperature (*Est-1* B^c); (e) soil+water (glume length); (f) temperature (*Acph-1* A^a, first awn). In some cases one of the two putative genomes was related with one factor (water in *Est-1* A), whereas the second genome with another factor (soil and temperature in *Est-1* B). The direction of the correlation, i.e., xeric or mesic is given by the Pearsonian correlations.

Discussion

The pattern of genetic diversity found in natural populations of *T. dicoccoides*, the wild progenitor of cultivated wheats, is important both for evolutionary theory and breeding programs. We will dwell in turn on both aspects.

(i) The Adaptive Nature of Genetic Variation in Wild Wheat

The debate whether allozyme variation in natural populations is selectively meaningful or adaptively neutral (Lewontin 1974) is still going on. This problem has both theoretical and practical implications. If neutral, then the abundant allozyme polymorphisms found in natural populations of plant and animals are predominantly of interest only as genetic markers. If this variation is largely adaptive, it may be of use in plant breeding programs.

The electrophoretic evidence in 243 species, in which more than 14 loci were tested, has suggested that the amounts of genetic polymorphism and heterozygosity vary nonrandomly between loci, populations,

species, habitats, and life zones, and are correlated with ecological heterogeneity (Nevo 1978). Natural selection, in some form, may often be the major determinant of population genetic structure and population differentiation. Our studies in wild barley, *Hordeum spontaneum* (Nevo et al. 1979), wild oat, *Avena barbata* (Kahler et al. 1980) and now wild wheat, *T. dicoccoides*, in Israel, are in line with a selectionist viewpoint for at least part of the allozymic variation in these wild cereals (Table 6). Natural selection may be operating either directly on the observed variants of the marker loci and/or any block of genes with which they are associated.

Allozymic variation in *T. dicoccoides* appears to be at least partly adaptive because of the following considerations: (a) Strong regional and local differentiation over short distances in values of A, P, H_e, and D (Tables 3, 5); (b) This geographic differentiation in the overall levels of diversity, P, and in allele frequencies of polymorphic systems is associated with, and predictable in part by, climatic regimes (water and temperature factors) and soil type (Table 6); (c) The variation in specific loci in the *T. dicoccoides* tested shows environmental associations. For example, about 85% of the variance in the *Adh-1* A locus of *T. dicoccoides* in Israel is predicted by the two variable combination of rainfall and evaporation, RnEv (Table 6). Noteworthy, *Adh* has already been shown to differentiate according to soil moisture gradients (in wild sunflower, Torres et al. 1977).

The aforementioned genetic patterns suggest that they are in part due to natural selection. In other words, these patterns are unlikely to result purely from non-selective factors: migration and genetic drift. Though gene flow in *T. dicoccoides* is limited per generation, restricted by the diaspors (Zohary 1969) and by high inbreeding rates, sufficient time has elapsed for appreciable gene migration to take place. If migration was the predominant force, clinal patterns should have been more distinct. Furthermore, *T. dicoccoides* distribution in Israel is characterized by an abundance of discontinuities and by "patchy" or "island" structure. If allozymes were neutral, such a spatial pattern is expected to result in marked differentiation between populations, independent of the climate and soil. Neither the first nor the second expectation is realized in *T. dicoccoides* in Israel, as the population structures are both regional and local rather than clinal, and alternative fixations due to soil type are restricted to a small northern area. In 73% of the loci studied, the same allele is either fixed or predominant across the range in at least 11 populations. Likewise, sporadic and localized alleles amount to 76%. These genetic patterns and their climatic and soil associations (Table 6), independent of the island population structure, suggest distinct local adaptations through diversifying selection, rather than drift.

(ii) The Genetic Strategy of Wild Tetraploid Wheats

It is instructive to compare and contrast the genetic patterns of the three wild cereals sharing the same habitats in Israel, one diploid (wild barley, *H. spontaneum*, Nevo et al. 1979) and two tetraploids (wild oat, *Avena barbata*, Kahler et al. 1980, and wild wheat, *T. dicoccoides*, reported herein). The comparison of the amount of variation depends on the total number of loci studied and particularly on the proportion of the monomorphic loci involved. The 32 systems resolved in the present study might correspond to 64 genes, but we recognized only 50 gene loci. The problem of assessment relates to the interpretation of the single-banded systems. There are essentially two possibilities for monomorphic, and apparently only one for polymorphic situations: (a) Monomorphic systems: (i) both homoeologous loci produce a band, hence in these cases (i.e., *Cat, Aat-1, 3*) one monomorphic band is assumed to be the product of two identical monomorphic genes (as we assumend in this study), or (ii) that a monomorphic band is the product of one gene only, and the homoeologous gene is silent and therefore can not be counted (as we assumed in this study for *Hk, Mdh-2, Pepc,* and *G-6pd*). The only evidence at present for choosing between these two possibilites is the electrophoretic band pattern of the putative diploid progenitors of tetraploid emmer wheat. (b) Polymorphic systems: if the single-banded system is polymorphic, assumption (i) becomes highly unlikely. This was the case in 8 systems in our study: *Acph-3, Acph-x, Aat-2, Ipol, Lap, Nadhd-2, Pept-2,* and *6Pgd.*

The average levels of polymorphism, P, in the aforementioned three progenitors in natural populations sampled along a similar southward transect of increasing aridity in Israel are 0.30, 0.25, and 0.25, respectively. Since the number of populations and loci tested vary among the three species, it remains to be seen whether a comparison of the shared loci and localities gives the same result, or suggests a differential genetic pattern between the diploid and tetraploids. We are currently testing this hypothesis within the wheat group.

Finally, it is noteworthy that 6 systems (*Gdh, Mdh-1, Pept-1, Pgi, Pgm,* and *6Pgd-1*) are monomorphic in one genome and polymorphic in the second genome. This may suggest a genetic strategy of conservatism in one genome and active experimentation in the second genome.

(iii) Sampling Strategies and Conservation

The present study established that *T. dicoccoides* in Israel stores a considerable amount of genetic variation at least partly correlated with ecological factors. The patterns detected can suggest some rules of sampling for maximizing the genetic variation collected per unit of cost and effort.

First, there is no single region rich in diversity within Israel but rather local, sporadic and regional patterns of differentiation involving different population sizes and degrees of isolation. Second, several alleles in *T. dicoccoides* are restricted to one or two populations or areas, but occuring there in appreciable frequency (≧ 10%). The proportion of the common sporadic and localized alleles in *T. dicoccoides* in Israel amount to a staggering 68%, and only 8% are rare across the entire range (Table 2, Results). Therefore, collection of smaller samples in as many localities as possible is desirable in wild emmer. In this species the chance of finding new variants which are locally common in new regions is indeed very high. Marshall and Brown (1975) have already argued that localized alleles deserve priority in sampling procedures. Third, since differentiation is partly adaptive and ecologically meaningful, sampling sites should be chosen on maximized environmental diversity, involving varied geographical altitude, latitude, longitude), climatic (humidity and temperature), edaphic (soil type and structure) and biotic (plant formation and population size) determinants.

(iv) The Use of T. dicoccoides in Breeding

The need to increase the genetic variation of cultivated wheats stems from the reduction in their genetic diversity due to past pure-line selection which has depleted the genetic material available for future breeding (Frankel and Bennett 1970; Feldman 1979; Feldman and Sears 1981). The idea of using wild gene resources in the improvement of cultivated wheats has been repeatedly advocated since Aaronshon discovered the wild progenitor of cultivated wheats *Triticum dicoccoides* in Rosh Pinna, Upper Galilee, Israel in 1906 (see Feldman 1977, 1979 and his references for historical and genetical discussion of wild wheats and their use in breeding).

Wild emmer, *T. dicoccoides* (genome AB) is the immediate progenitor of all cultivated forms of tetraploid wheat, *T. turgidum,* and hexaploid wheat *T. aestivum.* It is conspecific, and cytogenetically close to cultivated tetraploid wheats with which it is fully interfertile. It is partly fertile with hexaploid wheats, as well. The chromosome homology of genome AB to those of the A and B genomes of tetraploid and hexaploid cultivated wheats permits regular and complete pairing. Thus genes can be transferred from the wild to the cultivated gene pool easily. *T. dicoccoides* is therefore a convenient source of germplasm for improving cultivated wheats. Examples of the agronomically important characters already found in *T. dicoccoides* are large grain size and high protein content (Avivi 1979a, b) and yellow-rust resistance (Gerechter-Amitai and Stubbs 1970). Yet there has only been limited exploitation of this germplasm resource to date. Our finding of 110 allozyme alleles in 50 gene loci in 12 populations of *T. dicoccoides* in Israel, some of which are adaptively associated with ecological variables, indicates that substantial genetic resources of potential significance to wheat improvement exist in the wild gene pool.

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