Theor Appl Genet (1989) 77:421–455

Genetic diversity of wild emmer wheat in Israel and Turkey

Structure, evolution, and application in breeding

E. Nevo and A. Beiles

Institute of Evolution, University of Haifa, Mt. Carmel, Haifa 31999, Israel

Received June 28, 1988; Accepted July 5, 1988
Communicated by H.F. Linskens

Summary. Allozyme variation in the tetraploid wild emmer wheat, *Triticum dicoccoides*, the progenitor of all cultivated wheats, was studied for the proteins encoded by 42 gene loci in 1815 plants representing 37 populations – 33 from Israel and 4 from Turkey – sampled in 33 localities from 1979 to 1987. The results showed that: (a) 6 loci (14%) were monomorphic in all populations, 15 loci (36%) were locally polymorphic, and 21 loci (50%) were regionally polymorphic. These results are similar to those obtained earlier on 12 Israeli populations. All polymorphic loci (except 4) displayed high local levels of polymorphism ($\geq 10\%$). (b) The mean number of alleles per locus, A, was 1.252 (range: 1.050–1.634); the proportion of polymorphic loci per population averaged 0.220 (range: 0.050–0.415); genic diversity, He, averaged 0.059 (range: 0.002–0.119). (c) Altogether there were 119 alleles at the 42 putative loci tested, 114 of these in Israel. (d) Genetic differentiation was primarily regional and local, not clinal; 70% of the variant alleles were common ($\geq 10\%$) and not widespread, but rather localized or sporadic, displaying an "archipelago" population genetics and ecology structure. The coefficients of genetic distance between populations were high and averaged $D = 0.134$; range: 0.018–0.297, an indication of sharp genetic differentiation over short distances. (e) Discriminant analyses differentiated Israeli from Turkish populations, and within Israel, between central and 3 marginal regions, as well as between different soil-type populations. (f) Allozymic variation comprised 40% within and 60% between populations. (g) Gametic phase disequilibria were abundant, their number being positively correlated ($r_s = 0.60$, $P < 0.01$) with the humidity. (h) Multilocus organization was substantive, also positively correlated with humidity. (i) Allozyme diversity, overall and at single loci, was significantly correlated with, and partly predictable by, climatic and edaphic factors. (j) The distribution of the significant positive and negative values and the absence of autocorrelations in the correlogram revealed no similar geographic patterns across loci, eliminating migration as a prime factor of population genetic differentiation. These results suggest: (I) during the evolutionary history of wild emmer, diversifying natural selection, through climatic and edaphic factors, was a major agent of genetic structure and differentiation at both the single and multilocus levels; (II) wild emmer harbors large amounts of genetic diversity exploitable as genetic markers in sampling and abundant genetic resources utilizable for wheat improvement.

Key words: Genetic polymorphisms – Environmental selection – Genetic resources

Introduction

Modern evolutionary genetics derives its strength from the spectacular progress made during the last two decades in understanding molecular evolution and variation at the protein and DNA levels. This progress has, to a great extent, been due to the new biochemical techniques of protein electrophoresis and recombinant DNA (Nei 1987). Consequently, the genetic structure and differentiation of natural populations of plants and animals is now explicable at the molecular level, primarily in a dynamic, ecological context over space and time. Evidence of protein variation was critically reviewed for 1111 species of plants and animals by Nevo et al. (1984a), though the representation of inbreeders was small. The results indicated that genetic polymorphism and heterozygosity in nature are structured on a massive

scale and are primarily determined by diverse ecological factors, physical and biotic, interacting with stochastic processes.

Genetic diversity in time and in space is the basis for survival, adaptation and evolution. Understanding its nature, organization, geographical structure and differentiation is the core of evolutionary theory. Its preservation in nature and its wise application is the central aspect of biological conservation and genetic crop improvement. Regretably, modern plant breeding practices have eroded the genetic diversity of cultivated plants, including that of wheats, the prime food of man. This has made crops increasingly vulnerable to pathogens and climatic vagaries (Plucknett et al. 1983). The best hope for future crop improvements lies in exploiting wisely the abundant gene pools of the plant's wild relatives (Feldman and Sears 1981; Plucknett et al. 1987). Yet, the geographic structuring of genetic diversity across its range is known only in a few progenitor species of cultivated plants.

Our previous population genetic studies of wild emmer wheat, based on 42–50 electrophoretically tested gene loci, involved macrogeographic analyses of 12 populations of wild emmer wheat *Triticum dicoccoides* in Israel (Nevo et al. 1982) and 4 populations in Turkey (Nevo et al. 1988a), as well as a series of microgeographical studies in Israel (Golenberg 1986, 1987; Golenberg and Nevo 1987; Nevo et al. 1988b, c). The present study re-analyzes, integrates, compares and contrasts, the new results of 17 additional populations of wild emmer in Israel, both central and ecologically marginal, with those previously described in Israel and Turkey. Our objective in the present paper is to give an overview of genetic population structure and differentiation of wild emmer in the Near East, in an ecological context, combining the new with the earlier results. The evidence presented could enhance understanding of genetic differentiation and evolution across large parts of the origin and range of wild emmer wheat, the progenitor of all cultivated wheats in the Near East Fertile Crescent and advance potential application of the wild genetic resources in wheat improvement.

Materials and methods

Ecological background

Wild emmer wheat, *T. dicoccoides* (*T. turgidum* var. 'dicoccoides' in Kimber and Feldman 1987; genomic constitution AB), is the tetraploid, predominantly self-pollinated, wild progenitor from which modern tetraploid and hexaploid cultivated wheats were derived (Zohary 1970; Feldman 1976; Kimber and Feldman 1987), and with which they make fertile hybrids. Wild emmer is distributed over the Near East Fertile Crescent, in Israel, Jordan, Lebanon, Syria, east Turkey, north Iraq, and west Iran (Harlan and Zohary 1966; Kimber and Feldman 1987). The center of distribution of *T. dicoccoides* is found in the catchment area of the upper Jordan Valley in Israel and vicinity. In this area, wild emmer grows as a highly selfing, annual grass in several steppe-like herbaceous formations and in the open oak park forest belts of *Quercus ithaburensis* or *Q. brantii* (Zohary 1973). It occurs in primary habitats, growing together with wild barley and wild oats, but it also grows in secondary habitats such as agricultural and grazing fields. It grows mainly on basaltic and terra rossa soil types, but occupies also, though rarely, rendzina soils.

Wild emmer ranges over a wide altitudinal amplitude. Robust, early maturing phenotypes 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 and cooler elevations, reaching 1400 m on Mount Hermon (Zohary 1970). Earliness is also soil dependent (Nevo et al. 1988b). The populations of wild emmer are dense and lush in the catchment area of the upper Jordan Valley (Golan Heights, upper eastern Galilee Mts., etc.). However, towards their marginal and peripheral areas, both in Israel, as well as in Turkey, they become semi-isolated and isolated, and smaller in size. This distributional pattern has a dramatic effect on their population genetic structure and differentiation, as will be detailed later.

Sampling

This study of wild emmer, *T. dicoccoides*, comprises 37 populations, 33 from Israel and 4 from Turkey, sampled in 33 localities (the Tabigha population in Israel is represented by a sample from 1979 and 2 samples from 1984 and 1985, subdivided locally into basalt and terra rossa soil types). Altogether, we analyzed 1815 plants. Field collections were made between 1979 and 1987, and seeds were stored at the Institute of Evolution, University of Haifa for further studies. Locations of all tested populations appear in Fig. 1 and their ecological background is given in Table 1. Israeli climatic data is from the Atlas of Israel (1970), and publications of the Meteorological Service of Israel.

Electrophoresis

Tissue preparative procedures and starch gel horizontal electrophoresis techniques were similar to those used for wild barley (Brown et al. 1978). Locus and allele designations are as for the Israeli *T. dicoccoides* (Nevo et al. 1982), with some changes that appear next to the original designations in parentheses in the Appendix. The 42 loci coding for the soluble proteins and their abbreviations are given below. Several loci reported earlier have been omitted due to unreliability in scoring and/or missing data. The electrophoretic variants (electromorphs), 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 as 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), two loci (*Acph*-3; *Acph*-x); alcohol dehydrogenases (E.C. 1.1.1.1), four loci (*Adh*-1A, B; *Adh*-2A, B); catalases (E.C. 1.11.1.6), two loci (*Cat*-A, B); esterases (E.C. 3.1.1.2), four loci (*Est*-4A, B; *Est*-5A, B); glutamate dehydrogenases (E.C. 1.2.1.2), two loci (*Gdh*-A, B); glucosidase (E.C. 3.2.1.21), one locus (*Gluc*-B); aspartate aminotransferase (E.C. 2.6.1.1), six loci (*Aat*-1A, B; *Aat*-2A, B; *Aat*-3A, B; previously *Got*); hexokinase (E.C. 2.7.1.1), one locus (*Hk*); indophenol oxidases (E.C. 1.10.3.1), three loci (*Ipol*; *Ipor*-A, B); malate dehydrogenases (E.C. 1.1.1.37), three loci (*Mdh*-1A, B, *Mdh*-2); lipoamide diaphorases (E.C. 1.6.4.3), three loci (*Nadhd*-1A, B; *Nadhd*-2A);

Table 1. Geographical and climatological data for 37 populations of *Triticum dicoccoides* in Israel and Turkey

No.[a]	Population	N	Ln	Lt	Al	Tm	Ta	Tj	Td	Tdd	Rn	Rd	Hu14	Huan	Dw	Sh	Th	Trd	Ev	Sz	Ma	So	Rv	Rr
1.	(1) Mt. Hermon	40	35.73	33.30	1300	11	21	3	18	6	1400	66	48	60	60	80	–	0	150	2	1	1	30	20
2.	Andarta	30	35.63	33.01	100	20	28	11	17	11	400	43	48	58	45	50	−25	110	145	3	5	5	36	24
3.	Tsomet	30	35.67	33.02	380	19	27	11	16	12	470	50	43	58	58	50	–	60	155	3	5	5	39	26
4.	Kedmot Zvi	30	35.69	33.02	400	19	26	11	16	12	520	50	43	58	58	50	–	60	155	3	5	5	39	26
5.	(2) Qazrin	40	35.67	32.99	350	18	26	10	16	12	530	50	43	58	58	50	–	60	155	3	5	5	39	26
6.	Aniam	30	35.74	32.96	425	18	26	9	17	12	685	50	43	58	58	50	–	60	155	3	5	5	39	26
7.	(3) Yehudiyya	39	35.70	32.93	200	19	27	11	16	12	550	47	42	58	58	50	–	100	160	3	5	5	38	25
8.	Gamla	30	35.74	32.88	200	19	26	9	17	12	470	50	43	58	58	50	–	60	155	3	5	5	39	26
9.	(4) Rosh-Pinna	40	35.52	32.95	700	18	25	9	16	10	697	50	48	58	50	75	−10	35	150	3	5	1	35	22
10.	Ammiad	232	35.30	32.54	270	19	26	10	16	10	700	48	48	58	50	70	−10	50	150	3	5	1	38	25
11.	(5) Tabigha	40	35.53	32.90	0	24	32	15	17	10	436	45	45	57	58	60	−30	120	160	3	5	5	39	25
12.	Tabigha, basalt, 84	92	35.53	32.90	0	24	32	15	17	10	436	45	45	57	58	60	−30	120	160	3	5	5	39	25
13.	Tabigha, basalt, 85	90	35.53	32.90	0	24	32	15	17	10	436	45	45	57	58	60	−30	120	160	3	5	5	39	25
14.	Tabigha, t.r., 84	78	35.53	32.90	0	24	32	15	17	10	436	45	45	57	58	60	−30	120	160	3	5	1	39	25
15.	Tabigha, t.r., 85	96	35.53	32.90	0	24	32	15	17	10	436	45	45	57	58	60	−30	120	160	3	5	1	39	25
16.	(7) Mt. Gilboa	32	35.42	32.50	150	21	28	12	16	12	400	44	43	58	40	60	−30	160	165	2	3	1	34	24
17.	(8) Mt. Gerizim	25	35.28	32.20	800	17	23	8	15	9	700	47	45	60	42	–	10	0	155	2	3	1	38	25
18.	Gitit	48	35.40	32.10	300	21	29	13	16	12	360	39	39	55	25	–	−25	100	170	2	3	1	38	24
19.	(9) Kokhav Hashahar	40	35.34	31.95	600	20	28	12	16	12	400	40	45	59	30	80	−20	25	165	2	3	1	38	22
20.	(10) Taiyiba	41	35.30	31.95	450	19	26	10	16	12	400	40	44	58	30	80	−10	25	165	2	3	1	38	22
21.	(11) Sanhedriyya	40	35.22	31.80	800	17	24	9	15	9	548	44	51	62	44	102	−10	0	155	2	3	1	30	21
22.	(12) Bet-Meir	40	35.03	31.80	500	19	26	11	15	9	582	44	47	60	61	70	−10	100	160	2	3	1	33	25
23.	J'aba	50	35.08	31.67	660	17	25	9	15	9	500	41	49	62	57	90	−20	30	155	2	3	1	35	21
24.	Amirim	37	35.45	32.93	600	15	24	8	16	8	850	61	48	60	53	85	0	13	153	2	2	1	35	23
25.	Nahef	44	35.32	32.93	275	15	24	8	15	9	670	54	49	62	57	62	10	3	155	1	2	1	33	22
26.	Achihood	53	35.17	32.91	25	19	26	11	15	10	590	49	53	65	62	40	− 5	20	148	1	2	1	30	21
27.	Nesher	40	35.05	32.75	200	19	26	12	14	8	680	55	57	68	82	40	0	5	140	1	2	1	27	19
28.	Beit-Oren	40	35.03	32.73	400	17	24	11	13	8	700	55	59	69	80	41	5	0	142	1	2	1	25	19
29.	Daliyya	37	35.06	32.59	200	19	26	12	14	11	670	55	57	67	78	50	−10	100	160	1	2	2	25	20
30.	(6) Bat-Shelomo	40	35.02	32.60	75	20	26	13	13	10	650	55	58	68	77	40	−10	30	150	2	2	2	24	20
31.	Kabara	30	34.94	32.57	100	19	25	13	12	9	540	50	60	70	75	33	−10	53	138	1	2	1	27	21
32.	Yabad	44	35.15	32.44	375	19	25	11	14	11	550	50	48	63	65	52	−15	160	165	2	2	2	33	22
33.	Givat-Koach	40	34.92	32.03	75	20	26	12	14	12	540	46	50	64	65	42	−20	105	160	1	2	1	32	26
34.	West Siverek, 9 km	39	39.25	37.70	620	17	31	4	27	–	449	62	–	33	–	–	20	–	–	1	4	5	–	–
35.	East Siverek, 20 km	45	39.44	37.91	950	12	25	1	24	–	588	68	–	51	–	–	10	–	–	1	4	5	–	–
36.	W. Diyarbakir, 22 km	48	39.63	37.89	850	13	27	2	25	–	546	65	–	46	–	–	20	–	–	1	4	5	–	–
37.	N. Diyarbakir, 20 km	25	40.06	38.13	720	15	28	3	25	–	516	75	–	42	–	–	25	–	–	1	4	5	–	–

[a] Population number according to Nevo et al. (1982) in parenthesis

Symbols of variables:

Geographical: Ln = longitude (decimals); Lt = latitude (decimals); Al = Altitude (m)

Temperature: Tm = mean annual temperature; Ta = mean August temperature; Tj = mean January temperature; Td = seasonal temperature difference; Tdd = day-night temperature difference; Trd = mean number of tropical days; Sh = mean number of Sharav days, i.e., hot and dry days

Water availabilty: Rn = mean annual rainfall (mm); Rd = mean number of rainy days; Huan = mean annual humidity; Hu 14 = mean humidity at 14:00; Dw = mean number of dew nights in summer; Th = Thornthwaite's moisture index; Ev = mean annual evaporation; Rv = mean interannual variability of rainfall; Rr = mean relative variability of rainfall

Edaphic: So = soil type: 1 = terra rossa (= t.r.); 2 = rendzina; 5 = basalt

Biotic: Ma = marginality: 1 = north margin; 2 = west margin; 3 = south-east margin; 4 = Turkey; 5 = central population; Sz = estimate of population size: 1 = small, (from a dozen to few hundred plants); 2 = intermediate, 3 = large

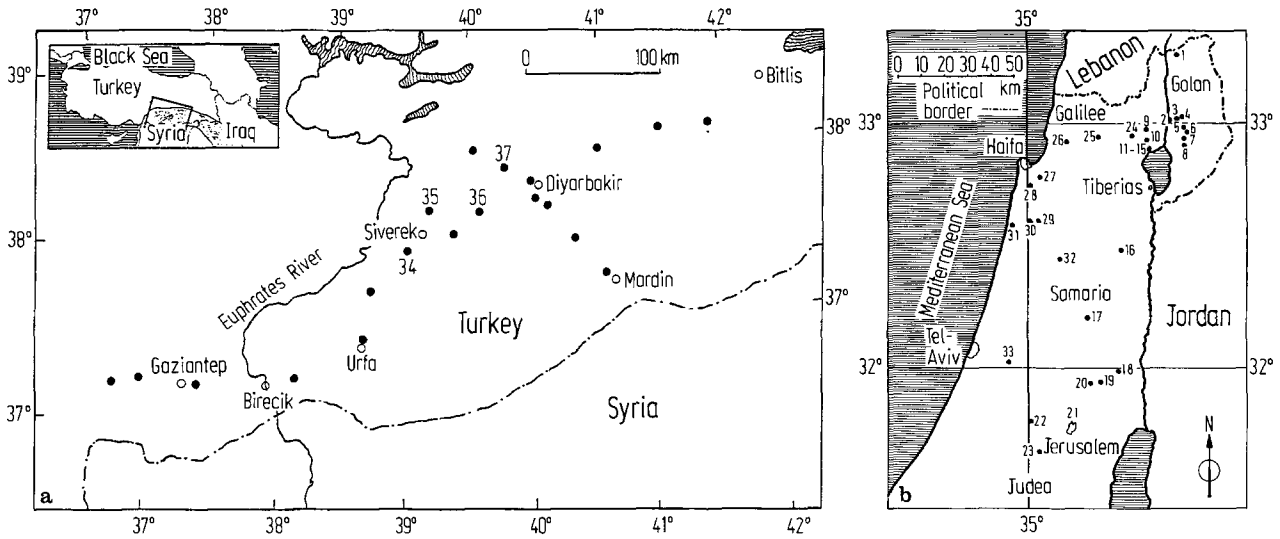

Fig. 1 a–b. Geographic distributions of 37 tested populations of wild emmer wheat in the Fertile Crescent: **a** 4 populations at 4 sites in Turkish Kurdistan, and **b** 33 populations at 29 sites in Israel; for names of numbered populations see list in Table 1. The black unnumbered solid circles in Turkey indicate sites in which wild barley was collected but wild emmer was not found

phosphoenol pyruvate carboxylase (E.C. 4.1.1.31), one locus (*Pepc*); peptidases (E.C. 3.4.13.11), three loci (*Pept*-1A, 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 6-phosphogluconate dehydrogenases (E.C. 1.1.1.44), three loci (*6Pgd*-1A, B; *6Pgd*-2).

Statistical analysis

We used SPSS-x (1986) and SAS (1985) statistical packages for conducting uni- and multivariate analyses, as well as the Spatial Autocorrelation Analysis Program (SAAP) (Sokal and Oden 1978a, b; Sokal and Wartenberg 1983), and genome organization (Brown et al. 1980). Levels of significance for all statistical analyses are as follows: $^{a}=p<0.10$; $*=p<0.05$; $**=p<0.01$; $***=p<0.001$; ns $=p>0.10$.

Results

Pattern of variation

Allele frequencies for 37 polymorphic loci (88%), of the 42 loci tested, appear in the Appendix. Eighteen systems exhibited contributions from both genomes *A* and *B* (34 loci) (*Gluc*-A and *Nadhd*-2B are not recorded) (81%), whereas 8 loci (*Acph*-3, *Acph*-x, *Hk*, *Ipol*, *Mdh*-2, *Pepc*, *Pept*-2, and *6Pgd*-2) displayed only one genome. Activity of the homeologous locus was indistinguishable in these cases. Our computed genetic values are based on the assumption of 26 enzymatic systems, presumably encoded by 42 gene loci. Although the variation we scored is real, some of its interpretation should be considered tentative until resolved by genetic crosses.

Out of 42 loci, 6 loci (14%) were monomorphic for the same allele in all 33 populations, considering the 5 subpopulations of Tabigha as one population (*Aat*-2B, *Aat*-3B, *Cat*-A, B, *Pept*-1A, *Pgm*-B). Fifteen loci (36%) were locally polymorphic ($\geq 1\%$ polymorphism in 1–5 populations out of 33), and 21 loci (50%) were regionally polymorphic (polymorphism in 6–21 populations).

The variation can be classified on the basis of genomes represented and degree of polymorphism as follows:

(A) Only one genome is represented or scored. Two groups which were progressively more polymorphic were recognized: (I) Locally polymorphic, 2 loci or 5% (*Mdh*-2, *Pepc*). (II) Regionally polymorphic, 8 loci or 19% (*Acph*-3, *Acph*-x, *Gluc*-B, *Hk*, *Ipol*, *Nadhd*-2A, *Pept*-2, *6Pgd*-2).

(B) Both genomes are represented: Six groups, progressively more polymorphic, were recognized: (I) Monomorphic in both genomes, 2 loci or 5% (*Cat*-A, B). (II) Monomorphic in one genome and locally polymorphic in the second genome, 4 loci or 10% (*Aat*-3A, B; *Pgm*-A, B). (III) Monomorphic in one genome and regionally polymorphic in the second genome, 4 loci or 10% (*Aat*-2A, B; *Pept*-1A, B). (IV) Locally polymorphic in both genomes, 6 loci or 14% (*Aat*-1A, B; *Adh*-2A, B; *6Pgd*-1A, B). (V) Locally polymorphic in one genome and regionally polymorphic in the second genome, 10 loci or 24% (*Adh*-1A, B; *Gdh*-A, B; *Ipor*-A, B; *Nadhd*-1A, B; *Mdh*-1A, B). (VI) Regionally polymorphic in both genomes, 6 loci or 14% (*Est*-4A, B; *Est*-5A, B; *Pgi*-A, B).

In the monomorphic and locally polymorphic groups (Ai; Bi, ii, iv), the same allele was either fixed or predominant ($>50\%$) in most populations. In contrast, the pattern of the regionally polymorphic groups (Aii; Biii, v, vi) chiefly displayed either sharp geographic differentiation over short distances, or shifts in the predominant allele between populations. In 22 out of the 42 loci (52%), the same allele was predominant throughout the range in at

least 32 out of the 33 tested populations, (including *Nadhd*-2A in all its 29 tested populations). In contrast, sharp geographic differentiation in 20 loci (48%) characterized the northern populations in the Golan, Jordan Valley and Mt. Carmel regions. Generally, the categorization of polymorphism and loci included in each category is slightly different than in our limited account of 12 Israeli populations in Nevo et al. (1982).

In the northern region, but chiefly in Mt. Hermon and the Golan, near or total alternative fixation occurred in 11 loci between several closely related populations. For example, (population numbers appear in parentheses): (i) *Est*-5A^{a-d} (3–5); (ii) *Gluc*-B^{a-b} (5–7); (iii) *Hk*$^{b-c}$ (5–7); (iv) *Ipol*$^{b-c}$ (1–5); (v) *Mdh*-1A^{a-b} (5–7); (vi) *Pept*-1B^{a-b} (5–7); (vii) *6Pgd*-2^{a-c} (5–7). The Qazrin-Yehudiyya populations (5–7), 10 km apart, were markedly differentiated at 6 loci (see Golenberg 1986; Golenberg and Nevo 1987 for detailed analysis), and the Hermon-Qazrin populations (1–5), 15 km apart, at 2 loci.

Genetic summary

A summary of the genetic data for each of the 37 populations of *T. dicoccoides* is given in Table 2, followed by means, for a series of different ecogeographical and demographic subdivisions. The following results were indicated:

(a) Mean levels of the number of alleles per locus, A; polymorphism P-1%, P-5%; and genic diversity, He, of all 37 populations of wild emmer were 1.252, 0.220, 0.176 and 0.059, respectively. The estimates derived here for wild emmer were also slightly lower than those reported earlier for 12 populations in Israel (Nevo et al. 1982, p 247) and 4 populations from Turkish Kurdistan (Nevo et al. 1988 a). The reason for the lower estimates reported here, as compared with our earlier wild emmer study, derives primarily from the lower values of some very small marginal populations in Israel (e.g., populations nos. 25, 26, 28, 29, 31, 33), and secondarily, from a lower number of loci tested here, 42 as against 50 earlier, excluding some highly polymorphic loci which were uncomparable with earlier results. Excluding these small marginal populations, the levels of polymorphism and genic diversity of wild emmer are similar to the mean estimates for plants, reported by Nevo et al. (1984 a).

(b) The estimates of genetic diversity of A, P-1%, P-5% and He showed the following patterns for the different categories (Table 2): (I) central > marginal ($P<0.05$); (II) basalt > terra rossa > rendzina ($P<0.05$); (III) large > medium > small ($P<0.01$). Note that central (= large) populations, and basalt soil populations had larger estimates of genetic diversity.

The overall numbers of alleles detected in the 42 loci in the 4 categories mentioned above were: (I) 119 (whole data set, 37 populations); (II) 93 (14 central populations); (III) 96 (19 marginal populations, Israel); and (IV) 61 (4 Turkish populations). The mean number of alleles per locus for the 119 alleles and 37 populations was 2.83, range 1–6.

Geographic patterns of allele distribution

The major pattern of allelic distribution was regional and local, and not clinal. A regional distribution of alleles (appearance in 2 or more regions) was exemplified, among others, by: *Mdh*-1A^{b}, *Pgi*-A^{d}, *Nadhd*-1A^{c}; local distribution (appearance in only one region) was exemplified, among others, by: *6Pgd*-1A^{b}, *Gdh*-A^{null}, *Adh*-2B^{null}.

To assess the various kinds of allele distributions, we followed the classification proposed by Marshall and Brown (1975). For this classification, we defined 9 regions, 8 in Israel and 1 in Turkey: (I) central populations of eastern Galilee; (II) central populations of Golan Heights; (III) marginal populations on Mt. Hermon; (IV) marginal populations of western and central Galilee; (V) marginal populations of Mt. Carmel; (VI) marginal populations of coastal plain; (VII) marginal populations of Samaria; (VIII) marginal populations of Judea; and (IX) marginal populations of Turkey. Each of the 119 alleles found in the 37 populations of *T. dicoccoides* in Israel and Turkey were classified into one of the following classes: *common*, at least one sample with frequency $\geq 10\%$: (a) *widespread*, common occurrence in more than two regions (64 alleles or 28.6% of the variants); (b) *sporadic*, common occurrence in two regions (12 alleles, or 15.6%); (c) *localized*, common occurrence in only one region (28 alleles, or 36.4%). (II) *Rare*, never occurs with frequency $\geq 10\%$; (d) *widespread*, in more than one region (1 allele, or 1.3%); and (e) *localized*, in only one region (14 alleles, or 18.2%). 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 70.1% of the variant alleles were not widespread (76% in our previous study of 12 Israeli populations in Nevo et al. 1982), but rather localized or sporadic. These figures suggest that populations of wild emmer wheat in the Near East Fertile Crescent differ considerably in their allelic content.

Genetic distance

Coefficients of genetic distance, D, were calculated for paired comparisons of all 37 populations, based on the normalized identity of all loci between each of the populations (Nei 1972). The results are given in Table 3. The mean value of D was 0.134, range 0.018–0.297. Standard error range was between 0.001 and 0.008. The estimates

Table 2. Summary of genetic variation, based on 42 allozyme loci, and genome organization, X(2), based on 29 polymorphic allozyme loci, in 37 populations of *Triticum dicoccoides* in Israel and Turkey

Locality	Sample size (*N*)	Mean no. of alleles per locus (A)	Mean proportion of loci				Genetic diversity (He)	Multi-locus organi-zation [X(2)]	No. of	
			Polymorphic per population (P)		Heterozygous per individual (H)				PL[b]	D
			(1%)	(5%)	Mean	S.E.				
1. Mt. Hermon	40	1.262	0.238	0.214	0.001	0.001	0.060	0.498*	9	32
2. Andarta	30	1.410	0.359	0.308	0.0	0.0	0.095	2.539*	13	68
3. Tsomet	30	1.359	0.308	0.256	0.0	0.0	0.089	1.239*	11	55
4. Kedmot Zvi	30	1.231	0.231	0.179	0.0	0.0	0.055	1.006*	9	36
5. Qazrin	40	1.310	0.286	0.167	0.004	0.002	0.032	0.568	10	43
6. Aniam	30	1.231	0.231	0.231	0.0	0.0	0.065	0.905*	9	36
7. Yehudiyya	39	1.167	0.167	0.119	0.001	0.001	0.047	0.382ns	7	20
8. Gamla	30	1.333	0.308	0.308	0.0	0.0	0.102	1.238*	12	66
9. Rosh-Pinna	40	1.333	0.286	0.238	0.001	0.001	0.093	0.901*	12	63
10. Ammiad	232	1.634	0.366	0.293	0.000	0.000	0.091	1.366*	18	135
11. Tabigha 1979	40	1.262	0.262	0.167	0.005	0.002	0.054	0.347ns	11	53
12. Tabigha, basalt 1984	92	1.452	0.357	0.286	0.002	0.001	0.119	1.015*	13	72
13. Tabigha, basalt 1985	90	1.262	0.238	0.238	0.0	0.0	0.077	0.322	9	34
14. Tabigha, t.r., 1874	78	1.452	0.357	0.262	0.005	0.002	0.089	0.409	13	62
15. Tabigha, t.r., 1985	96	1.310	0.310	0.238	0.0	0.0	0.073	0.910*	13	64
11–15 Tabigha[a]	396	1.643	0.381	0.310	0.002	0.001	0.113	0.475*	18	136
16. Mt. Gilboa	32	1.167	0.167	0.143	0.0	0.0	0.044	0.323ns	6	15
17. Mt. Gerizim	25	1.214	0.190	0.167	0.007	0.003	0.059	0.405ns	8	27
18. Gitit	48	1.512	0.415	0.293	0.013	0.005	0.116	0.490	15	93
19. Kokhav Hashahar	40	1.238	0.190	0.190	0.004	0.003	0.058	0.277ns	8	28
20. Taiyiba	41	1.238	0.214	0.190	0.0	0.0	0.051	0.905*	9	36
21. Sanhedriyya	40	1.143	0.143	0.143	0.0	0.0	0.048	1.960*	6	15
22. Bet-Meir	40	1.095	0.095	0.048	0.001	0.001	0.023	0.221ns	4	6
23. J'aba	50	1.463	0.366	0.244	0.003	0.001	0.072	2.021*	11	51
24. Amirim	37	1.366	0.293	0.268	0.002	0.002	0.102	0.883*	11	55
25. Nahef	44	1.171	0.146	0.098	0.001	0.001	0.039	0.179ns	5	9
26. Achihood	53	1.073	0.073	0.073	0.0	0.0	0.024	1.579*	3	3
27. Nesher	40	1.122	0.122	0.122	0.0	0.0	0.053	1.113*	3	3
28. Beit-Oren	40	1.050	0.050	0.0	0.0	0.0	0.002	–	1	0
29. Daliyya	37	1.098	0.073	0.049	0.004	0.004	0.009	−0.023ns	3	1
30. Bat-Shelomo	40	1.333	0.310	0.214	0.003	0.002	0.085	0.622*	13	78
31. Kabara	30	1.075	0.075	0.050	0.0	0.0	0.015	0.164ns	3	3
32. Yabad	44	1.073	0.073	0.049	0.001	0.001	0.010	−0.073ns	2	1
33. Givat-Koach	40	1.100	0.100	0.100	0.0	0.0	0.026	3.010*	4	6
34. West Siverek, 9 km	39	1.190	0.190	0.143	0.001	0.001	0.058	1.040*	7	21
35. East Siverek, 20 km	45	1.167	0.167	0.167	0.001	0.001	0.047	0.007ns	6	15
36. W. Diyarbakir, 22 km	48	1.238	0.214	0.167	0.001	0.001	0.055	0.988*	8	26
37. N. Diyarbakir, 20 km	25	1.189	0.162	0.108	0.0	0.0	0.048	1.131*	6	12
Means:										
Total (37 populations)	1815	1.252	0.220	0.176	0.002	0.000	0.059	0.857		
Range		1.050–1.634	0.050–0.415	0.0–0.308	0.0–0.013	0.0–0.005	0.002–0.119	−0.073–3.010		
Israel (33 pop.)	1658	1.259	0.224	0.180	0.002	0.001	0.060	0.866		
Range		1.050–1.634	0.050–0.415	0.0–0.308	0.0–0.013	0.0–0.005	0.002–0.119	−0.073–3.010		
Israel (29 pop.[a])	1658	1.257	0.213	0.175	0.002	0.001	0.057	0.899		
Range		1.050–1.643	0.050–0.415	0.0–0.308	0.0–0.013	0.0–0.005	0.002–0.116	−0.073–3.010		
Central (14 pop.),	897	1.339	0.290	0.235	0.001	0.00	0.077	0.939		
(=Large) Range		1.167–1.634	0.167–0.366	0.119–0.308	0.0–0.005	0.0–0.002	0.032–0.119	0.322–2.539		
Central (10 pop.[a])	897	1.365	0.292	0.241	0.001	0.000	0.078	1.062		
(=Large) Range		1.167–1.643	0.167–0.381	0.119–0.310	0.0–0.004	0.0–0.002	0.032–0.113	0.322–2.539		
Margins (23 pop.)	918	1.199	0.177	0.141	0.002	0.000	0.048	0.805		
(+Turkey) Range		1.050–1.512	0.050–0.415	0.0–0.293	0.0–0.013	0.0–0.005	0.002–0.116	−0.073–3.010		
Margins (19 pop.)	761	1.199	0.175	0.140	0.002	0.001	0.047	0.809		
(Israel) Range		1.050–1.512	0.050–0.415	0.0–0.293	0.0–0.013	0.0–0.005	0.002–0.116	−0.073–3.010		
North margins (1 pop.)	40	1.262	0.238	0.214	0.001	0.001	0.060	0.498		

Table 2. (continued)

Locality	Sample size (*N*)	Mean no. of alleles per locus (A)	Mean proportion of loci				Genetic diversity (He)	Multi-locus organi-zation [X(2)]	No. of
			Polymorphic per population (P)		Heterozygous per individual (H)				PL[b] D
			(1%)	(5%)	Mean	S.E.			
West margins (10 pop.)	405	1.146	0.132	0.102	0.001	0.001	0.037	0.828	
Range		1.050–1.366	0.050–0.310	0.0–0.268	0.0–0.004	0.0–0.004	0.002–0.102	−0.073–3.010	
S.E. margins (8 pop.)	311	1.259	0.223	0.177	0.004	0.001	0.059	0.825	
Range		1.095–1.512	0.095–0.415	0.048–0.293	0.0–0.013	0.0–0.005	0.023–0.116	0.221–2.021	
Turkey (4 pop.)	157	1.196	0.183	0.146	0.001	0.000	0.052	0.792	
Range		1.167–1.238	0.162–0.214	0.108–0.167	0.0–0.001	0.0–0.001	0.047–0.058	0.007–1.131	
Terra rossa (20 pop.)	1086	1.250	0.209	0.169	0.002	0.000	0.057	0.927	
Range		1.050–1.634	0.050–0.415	0.0–0.293	0.0–0.013	0.0–0.005	0.002–0.116	0.164–3.010	
Rendzina (3 pop.)	121	1.168	0.152	0.104	0.002	0.001	0.035	0.175	
Range		1.073–1.333	0.073–0.310	0.049–0.214	0.001–0.004	0.001–0.004	0.009–0.085	−0.073–0.622	
Basalt (14 pop.)	608	1.271	0.254	0.198	0.001	0.000	0.067	0.910	
(+Turkey) Range		1.167–1.452	0.162–0.359	0.108–0.308	0.0–0.005	0.0–0.002	0.032–0.119	0.007–2.539	
Basalt (10 pop.)	451	1.302	0.282	0.219	0.001	0.000	0.073	0.957	
(Israel) Range		1.167–1.452	0.167–0.359	0.119–0.308	0.0–0.005	0.0–0.002	0.032–0.119	0.322–2.539	
Large pop. (14 pop.)	897	1.339	0.290	0.235	0.001	0.000	0.077	0.939	
(=Central) Range		1.167–1.634	0.167–0.366	0.119–0.308	0.0–0.005	0.0–0.002	0.032–0.119	0.322–2.539	
Large pop. (10 pop.[a])	897	1.365	0.292	0.241	0.001	0.000	0.078	1.062	
(=Central) Range		1.167–1.643	0.167–0.381	0.119–0.310	0.0–0.004	0.0–0.002	0.032–0.113	0.322–2.539	
Medium pop. size (12 pop.)	477	1.259	0.224	0.180	0.003	0.001	0.061	0.711	
Range		1.073–1.512	0.073–0.415	0.048–0.293	0.0–0.013	0.0–0.005	0.010–0.116	−0.073–2.021	
Small pop. size (11 pop.)	441	1.132	0.123	0.098	0.001	0.000	0.034	0.919	
(+Turkey) Range		1.050–1.238	0.050–0.214	0.0–0.167	0.0–0.004	0.0–004	0.002–0.058	−0.023–3.010	
Small pop. size (7 pop.)	284	1.095	0.088	0.070	0.001	0.001	0.024	1.004	
(Israel) Range		1.050–1.171	0.050–0.146	0.0–0.122	0.0–0.004	0.0–0.004	0.002–0.053	−0.023–3.010	

[a] The 5 Tabigha subpopulations are considered to be one population
[b] PL = Number of polymorphic loci out of the 29 loci, included in the X(2) analysis, followed by the number of D's
* $P < 0.05$; ns = $P > 0.01$

of D were geographically independent. They displayed large D's, i.e., sharp genetic differentiation over very short geographic distances, against low D's between geographically distant populations. An extreme example was that of localities 5 and 7, separated by only 10 km, for which D was very high, 0.242. By contrast, for populations 30 and 36, separated by 750 km, D was only 0.056. Many other such drastic contrasts occur and are given in Table 3. We have also averaged genetic distances between regions with the following results: D (Israel–Turkey) = 0.148; D (Israel, central–marginal populations) = 0.147; D (Israel, western marginal and south-eastern marginal populations) = 0.108.

Discriminant analysis

We conducted several stepwise discriminant analyses (SPSS-x 1986) maximizing the overall multivariate F ratio between categories in each test. The tests were based on multilocus analyses involving a maximum of 22 polymorphic loci and 34 alleles. The results are given in Table 4 and Fig. 2, first for the 37 populations of Israel and Turkey (3 diagrams) and then for the 29 (excluding Turkey and the 4 microgeographical "populations" at Tabighia) populations of Israel (3 diagrams) for ecology, soil type, and population size, respectively. The program chose, in the ecogeographical analyses, 6 loci and 10 alleles, as the best differentiating factors. The alleles chosen were: *Pepc*[b], *Pept*-1B[a], *6Pgd*-2[c], *Adh*1A[b], *Est*-5A[a], *Est*-5A[e], *6Pgd*-2[a], *Nadhd*-1A[b], *Nadhd*-1A[c], *Est*-5A[d] (Table 4).

The analyses succeeded to differentiate significantly, on the basis of allele frequencies between the following categories: (I) wild emmer in Turkey from that in Israel; and in Israel, between central, northern, western, eastern and southern marginal populations; (II) wild emmer growing on different soil types (basalt, terra rossa and rendzina; (III) small, medium, and large populations of

Table 3. Coefficients of genetic distance (D) between 37 populations of *Triticum dicoccoides* in Israel and Turkey

Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 Mt. Hermon		0.192	0.126	0.111	0.090	0.192	0.178	0.124	0.063	0.073	0.154	0.107	0.132	0.142	0.110	0.034	0.062	0.091
2 Andarta			0.077	0.093	0.245	0.172	0.087	0.104	0.192	0.162	0.078	0.116	0.133	0.085	0.100	0.160	0.187	0.142
3 Tsomet				0.020	0.130	0.081	0.156	0.018	0.095	0.081	0.120	0.125	0.173	0.127	0.143	0.093	0.077	0.095
4 Kedmot Zvi					0.140	0.083	0.183	0.037	0.095	0.081	0.144	0.131	0.176	0.139	0.153	0.080	0.087	0.074
5 Qazrin						0.162	0.242	0.134	0.088	0.113	0.203	0.163	0.224	0.201	0.210	0.081	0.074	0.138
6 Aniam							0.257	0.104	0.129	0.158	0.224	0.189	0.242	0.208	0.233	0.166	0.155	0.160
7 Yehudiyya								0.191	0.172	0.187	0.018	0.062	0.082	0.028	0.061	0.161	0.180	0.196
8 Gamla									0.117	0.077	0.152	0.153	0.193	0.163	0.156	0.110	0.096	0.120
9 Rosh Pinna										0.065	0.142	0.108	0.150	0.140	0.137	0.040	0.032	0.092
10 Ammiad											0.155	0.122	0.171	0.145	0.159	0.052	0.058	0.071
11 Tabigha 1979												0.068	0.095	0.035	0.073	0.138	0.147	0.173
12 Tabigha, basalt 1984													0.021	0.020	0.040	0.099	0.104	0.114
13 Tabigha, basalt 1985														0.038	0.020	0.147	0.148	0.157
14 Tabigha, terra rossa 1984															0.037	0.119	0.135	0.137
15 Tabigha, terra rossa 1985																0.119	0.135	0.143
16 Mt. Gilboa																	0.036	0.051
17 Mt. Gerizim																		0.076
18 Gitit																		
19 Kohhav Hashahar																		
20 Taiyiba																		
21 Sanhedriyya																		
22 Bet Meir																		
23 Ja'ba																		
24 Amirim																		
25 Nahef																		
26 Achihood																		
27 Nesher																		
28 Beit Oren																		
29 Daliyya																		
30 Bat Shelomo																		
31 Kabara																		
32 Yabad																		
33 Givat Koach																		
34 West Siverek																		
35 East Siverek																		
36 West Diyarbakir																		
37 North Diyarbakir																		

D: Mean 0.134 Range 0.018–0.297

wild emmer. All categorizations (I–III) are differentiated, both in the overall analysis (37 populations) and in Israel (29 populations; see details in Table 4 and Fig. 2). The correct classification of plant populations into their respective categories was 84%–100%.

Environmental correlates with allozyme polymorphisms

Correlation among environmental variables, and among genetic indices. The environmental variables we used included the following: *geographical:* longitude (Ln), latitude (Lt), altitude (Al), and *climatic* means: *temperature,* annual, (Tm); January, (Tj); August, (Ta); seasonal temperature difference, (Td); daily temperature difference, (Tdd); Sharav, number of hot and dry days, (Sh); number of tropical days, (Trd); evaporation, (Ev); *moisture,* annual rainfall, (Rn); number of rainy days, (Rd); number of dewy nights in summer, (Dw); annual humidity, (Huan); humidity at 14:00, (Hu14); Thornthwaite moisture index, (Th); interannual variation in rainfall, (Rv); coefficient of variation in rainfall (Rr) and one *edaphic* dummy variable, basalt soil type. Among the environmental variables, water and temperature variables were significantly negatively correlated (Rn – Tm, $r_s = -0.58$). Temperature means in January and August, and the annual mean displayed high correlations ($r_s = 0.54–0.92$).

19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	
0.068	0.043	0.069	0.064	0.117	0.102	0.134	0.113	0.140	0.182	0.119	0.057	0.209	0.059	0.112	0.134	0.108	0.075	0.153	1
0.200	0.169	0.188	0.206	0.181	0.191	0.272	0.221	0.297	0.278	0.202	0.136	0.197	0.145	0.233	0.193	0.199	0.178	0.250	2
0.130	0.093	0.130	0.114	0.090	0.101	0.192	0.110	0.172	0.160	0.125	0.083	0.144	0.069	0.128	0.131	0.138	0.116	0.191	3
0.120	0.084	0.107	0.083	0.075	0.077	0.145	0.107	0.197	0.179	0.110	0.076	0.155	0.061	0.143	0.122	0.112	0.097	0.189	4
0.110	0.062	0.057	0.087	0.158	0.112	0.132	0.111	0.062	0.142	0.128	0.060	0.215	0.095	0.082	0.175	0.151	0.121	0.198	5
0.214	0.168	0.180	0.168	0.151	0.164	0.209	0.144	0.184	0.256	0.206	0.152	0.225	0.149	0.217	0.186	0.167	0.157	0.231	6
0.203	0.176	0.221	0.204	0.222	0.214	0.250	0.214	0.267	0.283	0.219	0.147	0.287	0.152	0.227	0.198	0.170	0.135	0.232	7
0.149	0.110	0.140	0.133	0.114	0.100	0.170	0.120	0.169	0.155	0.136	0.100	0.167	0.091	0.135	0.157	0.167	0.142	0.212	8
0.067	0.033	0.068	0.060	0.083	0.090	0.142	0.123	0.115	0.123	0.111	0.049	0.162	0.053	0.087	0.126	0.105	0.073	0.185	9
0.072	0.063	0.098	0.082	0.072	0.052	0.111	0.124	0.153	0.162	0.093	0.070	0.161	0.046	0.108	0.147	0.122	0.091	0.153	10
0.169	0.140	0.181	0.164	0.187	0.177	0.234	0.193	0.234	0.218	0.188	0.115	0.259	0.125	0.182	0.192	0.166	0.134	0.223	11
0.135	0.113	0.155	0.126	0.117	0.129	0.167	0.116	0.202	0.225	0.159	0.089	0.201	0.094	0.171	0.139	0.103	0.078	0.169	12
0.185	0.163	0.202	0.176	0.146	0.178	0.221	0.162	0.269	0.283	0.214	0.134	0.242	0.146	0.234	0.173	0.145	0.128	0.229	13
0.163	0.139	0.175	0.155	0.146	0.163	0.203	0.139	0.228	0.253	0.183	0.106	0.216	0.117	0.191	0.140	0.115	0.093	0.182	14
0.168	0.141	0.177	0.169	0.146	0.179	0.229	0.153	0.250	0.263	0.193	0.108	0.219	0.126	0.210	0.140	0.137	0.122	0.228	15
0.037	0.021	0.051	0.048	0.083	0.084	0.124	0.085	0.127	0.159	0.095	0.032	0.158	0.035	0.090	0.092	0.075	0.046	0.143	16
0.059	0.029	0.068	0.055	0.070	0.079	0.152	0.091	0.119	0.121	0.101	0.040	0.147	0.044	0.074	0.103	0.091	0.062	0.147	17
0.061	0.069	0.090	0.086	0.041	0.063	0.112	0.109	0.200	0.217	0.099	0.064	0.140	0.042	0.150	0.116	0.102	0.094	0.177	18
	0.044	0.088	0.074	0.096	0.094	0.160	0.137	0.166	0.170	0.123	0.060	0.184	0.067	0.088	0.147	0.119	0.090	0.178	19
		0.030	0.031	0.087	0.079	0.137	0.104	0.123	0.128	0.094	0.023	0.137	0.037	0.057	0.113	0.092	0.060	0.155	20
			0.056	0.118	0.094	0.114	0.125	0.117	0.154	0.112	0.040	0.168	0.073	0.072	0.139	0.119	0.096	0.195	21
				0.091	0.080	0.128	0.097	0.159	0.157	0.115	0.045	0.187	0.058	0.089	0.130	0.090	0.067	0.154	22
					0.057	0.120	0.101	0.203	0.196	0.111	0.082	0.115	0.056	0.130	0.124	0.102	0.107	0.202	23
						0.068	0.128	0.167	0.171	0.056	0.076	0.188	0.038	0.125	0.157	0.119	0.096	0.202	24
							0.152	0.154	0.229	0.143	0.137	0.277	0.110	0.193	0.213	0.145	0.136	0.248	25
								0.125	0.190	0.174	0.101	0.143	0.114	0.116	0.134	0.098	0.094	0.144	26
									0.151	0.187	0.133	0.239	0.150	0.116	0.232	0.199	0.168	0.237	27
										0.198	0.120	0.234	0.168	0.099	0.259	0.235	0.201	0.252	28
											0.087	0.220	0.051	0.133	0.176	0.159	0.125	0.216	29
												0.160	0.041	0.067	0.085	0.080	0.056	0.145	30
													0.160	0.142	0.209	0.203	0.202	0.240	31
														0.101	0.113	0.095	0.065	0.166	32
															0.184	0.160	0.129	0.170	33
																0.053	0.063	0.152	34
																	0.032	0.084	35
																		0.100	36
																			37

By contrast, Td−Tm, for example, displayed low $r_s = -0.10$. Among the genetic indices, the highest Spearman rank correlations were between P−1% and A, $r_s = 0.98$, and the lowest was between P−1% and He, $r_s = 0.89$.

Correlations between genetic indices, allele frequencies and ecogeographical variables in Israel. The Spearman rank correlation matrix between allozymes (strictly local alleles were excluded) and climate appear in Table 5, only for Israel, since most climatic parameters in Turkey are missing. Out of a matrix of 880 entries, 175 correlations were significant ($P < 0.05$). Thus, a substantial number of alleles displayed significant ecogeographical correlates much above that expected by chance.

Autocorrelation

Spatial autocorrelation analysis is a statistical approach for quantifying spatial relations among a set of univariate data observations. It gives a measure of the level of correlation of the observed values (in our case gene frequencies) at each locality with values of the same variables at other geographic sections. The method was extended in biology to include the computation of correlograms for spatial autocorrelation. These show the auto-

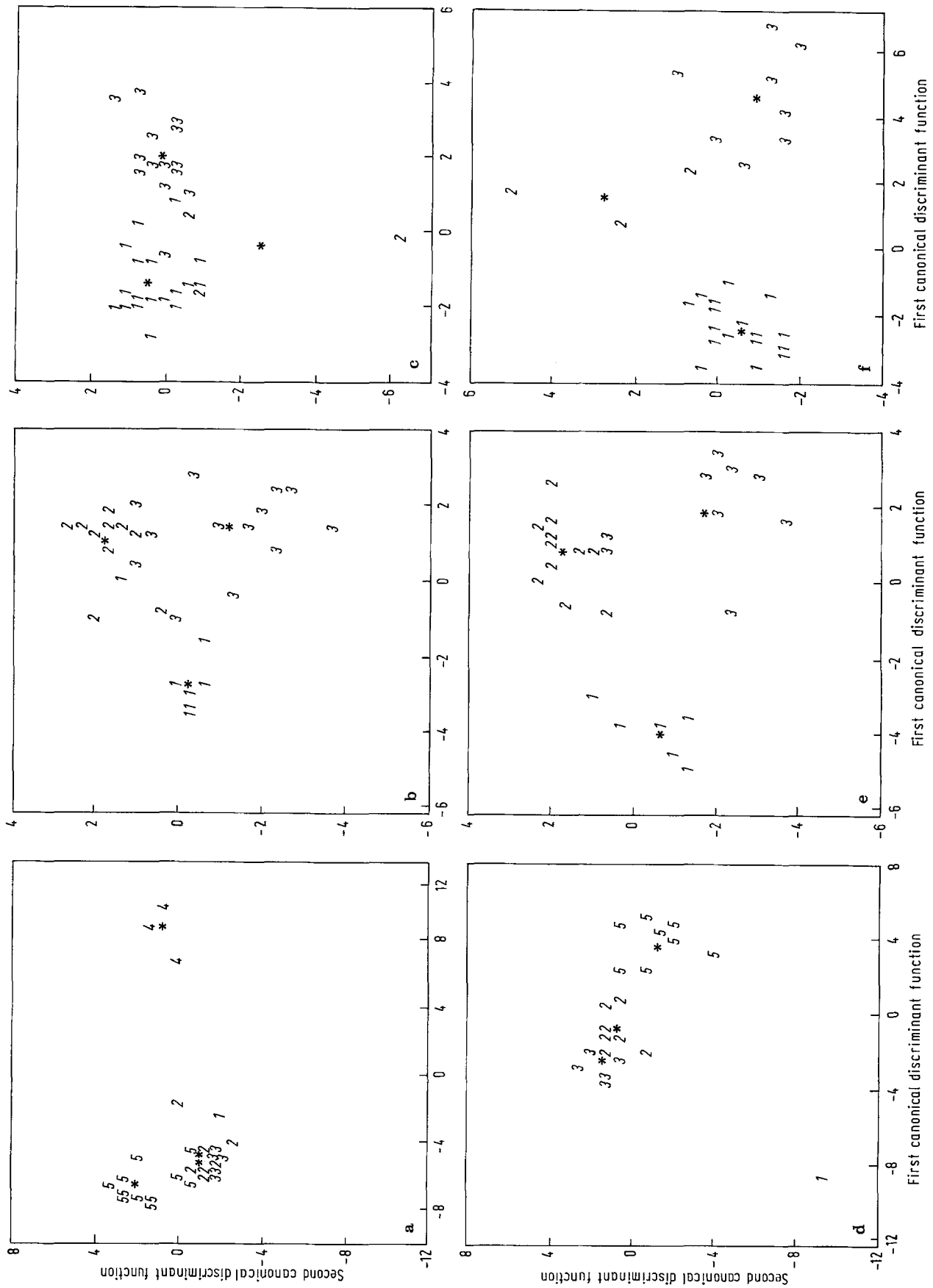

Fig. 2 a–f. Discriminant analysis between ecogeographical, edaphic, and population size categories in *Triticum dicoccoides* in Israel and Turkey (see Table 4 for details); figures **a–c** display the pattern of 37 populations in Israel and Turkey; figures **d–f** display the pattern of 29 populations from Israel (excluding the 4 micropopulations of Tabigha). On the left hand side, figures **a** and **d** discriminate between four types of marginal and one type of central populations: *1* cold steppe, *2* west margin, *3* east and south margin, *4* Turkey, *5* central population, * centroid. The middle figures **b** and **e** discriminate between small-, medium-, and large-size populations: population size: *1* small, *2* medium, *3* large, * group centroid. On the right hand side, figures **c** and **f** discriminate between populations growing on three soil types: *1* terra rossa. *2* rendzina, and *3* basalt; * group centroid

Table 4. Stepwise discriminant analysis of allele frequencies of *Triticum dicoccoides* in 37 populations, between marginal – central populations in Israel and Turkey, based on 22 loci and 34 alleles. The analysis includes: 1 cold steppic, 10 west marginal, 8 east and south marginal, 4 Turkish and 14 central populations

A. Pairwise comparisons

	1 Cold steppe	2 West margins	3 East and south margins	4 Turkey
2. West margins	$F=$ 3.0736			
	$P=$ 0.0125			
3. East and south margins	$F=$ 2.5059	2.5349		
	$P=$ 0.0332	0.0315		
4. Turkey	$F=$ 9.0382	38.640	38.476	
	$P=$ < 0.00005	< 0.00005	< 0.00005	
5. Central	$F=$ 3.9067	5.6761	4.6068	50.814
	$P=$ 0.0033	0.0003	0.0012	< 0.00005

Each F statistic has 10 and 23 degrees of freedom

B. Summary table (chosen alleles)

Alleles	Vars.	Wilk's lambda	Significance
1 *Pepc* b	1	0.23472	< 0.00005
2 *Pept*-1B a	2	0.11320	< 0.00005
3 *6Pgd*-2 c	3	0.04355	< 0.00005
4 *Adh*-1A b	4	0.02125	< 0.00005
5 *Est*-5A a	5	0.01406	< 0.00005
6 *Est*-5A e	6	0.01087	< 0.00005
7 *6Pgd*-2 a	7	0.00858	< 0.00005
8 *Nadhd*-1A b	8	0.00656	< 0.00005
9 *Nadhd*-1A c	9	0.00414	< 0.00005
10 *Est*-5A d	10	0.00299	< 0.00005

C. Canonical discriminant functions

No.	Eigenvalue	Percent of var.	Canonical correl.	After function	Wilks' lambda	Chi-squared	*d.f.*	Significance
				0	0.00299	165.63	40	0.0000
1	23.240	83.78	0.97916	1	0.07255	74.768	27	0.0000
2	2.423	8.73	0.84133	2	0.24833	39.700	16	0.0009
3	1.398	5.04	0.76355	3	0.59554	14.771	7	0.0390
4	0.679	2.45	0.63598					

D. Classification

Actual group	No. of cases	Predicted group membership				
		1	2	3	4	5
1. Cold steppe	1	1	0	0	0	0
		100.0%	0.0%	0.0%	0.0%	0.0%
2. West margins	10	0	8	2	0	0
		0.0%	80.0%	20.0%	0.0%	0.0%
3. East and south margins	8	0	1	7	0	0
		0.0%	12.5%	87.5%	0.0%	0.0%
4. Turkey	4	0	0	0	4	0
		0.0%	0.0%	0.0%	100.0%	0.0%
5. Central populations	14	0	1	2	0	11
		0.0%	7.1%	14.3%	0.0%	78.6%

83.78% of cases correctly classified

E. Classification results for:

Population size (11 small, 12 medium, 14 large): 83.78% of cases correctly classified
Soil type (20 terra rossa, 3 rendzina, 14 basalt): 89.19% of cases correctly classified

In 29 Israeli populations, based on 23 loci, 38 alleles for:
Marginality (1 cold steppic, 10 west marginal, 8 east and south marginal and 10 central populations): 93.10% of cases correctly classified
Population size (7 small, 12 medium, 10 large): 93.10% of cases correctly classified
Soil type (18 terra rossa, 3 rendzina, 8 basalt): 100.00% of cases correctly classified

Table 5. Spearman rank correlations (r_s) of genetic indices and allele frequencies of wild wheat (*T. dicoccoides*) with ecogeographical variables, in Israel

	Ln	Lt	Al	Tm	Ta	Tj	Td	Tdd	Rn	Rd
A	0.467**	0.213 ns	−0.058 ns	0.195 ns	0.384*	0.045 ns	0.600***	0.082 ns	−0.296@	−0.237 ns
P-1%	0.483**	0.218 ns	−0.119 ns	0.248 ns	0.435*	0.102 ns	0.611***	0.105 ns	−0.340@	−0.274 ns
P-5%	0.558***	0.253 ns	−0.065 ns	0.200 ns	0.392*	0.014 ns	0.683***	0.153 ns	−0.319@	−0.239 ns
He	0.507**	0.263 ns	−0.054 ns	0.189 ns	0.353*	0.030 ns	0.629***	0.055 ns	−0.220 ns	−0.169 ns
Aat-2A a	0.247 ns	0.119 ns	−0.243 ns	0.203 ns	0.349*	0.186 ns	0.325@	−0.038 ns	−0.216 ns	−0.266 ns
Acph-3 b	−0.306 ns	−0.408*	0.409*	−0.301 ns	−0.300 ns	−0.420*	−0.220 ns	0.037 ns	0.043 ns	−0.168 ns
Adh-1A b	0.421*	0.314@	−0.436*	0.346*	0.362*	0.243 ns	0.595***	−0.106 ns	−0.215 ns	−0.112 ns
Est-4A a	−0.140 ns	−0.084 ns	−0.462**	0.424*	0.371*	0.452**	−0.056 ns	0.250 ns	−0.357*	−0.056 ns
Est-4B c	0.179 ns	0.137 ns	−0.470**	0.511**	0.458**	0.400*	0.344*	−0.059 ns	−0.292@	−0.236 ns
Est-5A a	0.280 ns	−0.059 ns	−0.098 ns	0.407*	0.386*	0.293@	0.424*	0.126 ns	−0.429*	−0.483**
Est-5B e	0.276 ns	0.167 ns	−0.378*	0.403*	0.405*	0.322@	0.536***	−0.221 ns	−0.094 ns	−0.095 ns
Gluc-B b	−0.569**	−0.465*	0.461*	−0.509**	−0.692***	−0.423*	−0.659***	−0.154 ns	0.319 ns	0.128 ns
Hk b	−0.609***	−0.390*	0.542**	−0.423*	−0.619***	−0.390*	−0.568**	−0.343@	0.331@	0.117 ns
Mdh-1A a	0.734***	0.508**	−0.405*	0.329@	0.586***	0.268 ns	0.734***	0.166 ns	−0.316@	−0.160 ns
Nadhd-1A b	−0.166 ns	−0.200 ns	−0.410*	0.489**	0.366*	0.471**	−0.098 ns	0.130 ns	−0.254 ns	−0.224 ns
Pept-1B a	0.567***	0.345*	−0.532***	0.523**	0.684***	0.444**	0.594***	0.266 ns	−0.384*	−0.246 ns
Pept-2 c	−0.083 ns	−0.225 ns	−0.061 ns	0.259 ns	0.269 ns	0.207 ns	0.048 ns	0.138 ns	−0.454**	−0.428*
Pgi-A e	−0.261 ns	−0.355*	0.027 ns	0.151 ns	0.087 ns	0.163 ns	−0.108 ns	0.152 ns	−0.391*	−0.418*
6Pgd-2 c	0.658***	0.493**	−0.471**	0.435*	0.657***	0.342@	0.685***	0.209 ns	−0.305@	−0.182 ns

	Hu 14	Huan	Dw	Sh ($n=31$)	Th ($n=26$)	Trd	Ev	Rv	Rr	Basalt
A	−0.375*	−0.636***	−0.498**	0.388*	−0.403*	0.148 ns	0.034 ns	0.554***	0.307@	0.253 ns
P-1%	−0.403*	−0.660***	−0.462**	0.312@	−0.439*	0.207 ns	0.030 ns	0.575***	0.345*	0.291@
P-5%	−0.418*	−0.652***	−0.509**	0.319@	−0.427*	0.149 ns	−0.005 ns	0.592***	0.355*	0.326@
He	−0.369*	−0.615***	−0.468**	0.306@	−0.342@	0.100 ns	−0.036 ns	0.526**	0.301@	0.284 ns
Aat-2A a	−0.261 ns	−0.527**	−0.277 ns	0.300 ns	−0.317 ns	0.259 ns	0.246 ns	0.386*	0.165 ns	0.145 ns
Acph-3 b	0.075 ns	0.284 ns	−0.207 ns	0.205 ns	0.260 ns	−0.351@	0.006 ns	−0.281 ns	−0.113 ns	−0.437*
Adh-1A b	−0.168 ns	−0.405*	0.082 ns	0.085 ns	−0.399*	0.277 ns	0.057 ns	0.291 ns	0.138 ns	0.308@
Est-4A a	0.053 ns	−0.028 ns	0.178 ns	−0.299 ns	−0.216 ns	0.297@	0.145 ns	0.053 ns	0.118 ns	0.094 ns
Est-4B c	−0.127 ns	−0.369*	−0.079 ns	0.115 ns	−0.479*	0.296@	0.280 ns	0.171 ns	−0.147 ns	−0.039 ns
Est-5A a	−0.498**	−0.531***	−0.243 ns	0.245 ns	−0.570**	0.462**	0.468**	0.420*	0.264 ns	0.138 ns
Est-5B e	−0.086 ns	−0.471**	0.016 ns	0.248 ns	−0.476*	0.288 ns	0.101 ns	0.359*	0.166 ns	0.072 ns
Gluc-B b	0.379@	0.722***	0.163 ns	−0.119 ns	0.634**	−0.532**	−0.251 ns	−0.625***	−0.351@	−0.593***
Hk b	0.459*	0.628***	−0.095 ns	0.459*	0.532*	−0.450*	0.014 ns	−0.629***	−0.599***	−0.604***
Mdh-1A a	−0.477**	−0.682***	−0.056 ns	0.008 ns	−0.585**	0.452**	0.095 ns	0.698***	0.563***	0.742***
Nadhd-1A b	0.060 ns	−0.017 ns	0.245 ns	−0.260 ns	−0.357@	0.390*	0.133 ns	0.116 ns	0.180 ns	0.132 ns
Pept-1B a	−0.517**	−0.676***	−0.136 ns	−0.165 ns	−0.576**	0.537***	0.183 ns	0.636***	0.534***	0.622***
Pept-2 c	−0.069 ns	−0.114 ns	−0.463**	0.199 ns	−0.333 ns	0.093 ns	0.217 ns	−0.047 ns	−0.176 ns	−0.106 ns
Pgi-A e	0.107 ns	0.068 ns	−0.270 ns	0.124 ns	−0.209 ns	−0.004 ns	0.117 ns	−0.068 ns	−0.097 ns	−0.150 ns
6Pgd-2 c	−0.457**	−0.711***	−0.084 ns	−0.038 ns	−0.581**	0.536***	0.097 ns	0.704***	0.565***	0.687***

Abbreviations as in Table 1

Significance: @ = $p<0.010$; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$; ns = $p>0.10$

Table 6. Spatial autocorrelation analysis of allele frequencies in 37 populations of *Triticum dicoccoides* in Israel and Turkey. Moran's I coefficients for each allele in ten distance classes are given. The expected I is −0.028

	Distance classes (km)									
Allele *N:*	0–18 71	18–29 63	29–43 70	43–58 64	58–72 67	72–85 67	85–104 67	105–572 67	573–666 68	666–795 61
Aat-2A a	−0.12	0.20*	−0.15	−0.11	−0.12	0.27**	−0.20	0.04	−0.09	0.04
Adh-1A a	0.18*	−0.06	0.33***	−0.05	−0.16	−0.04	−0.20	−0.31**	−0.12	0.14
Adh-1B a	0.24***	0.01	−0.05	−0.09	−0.06	−0.06	−0.26**	0.00	0.05	−0.08
Adh-2B a	0.01	0.00	0.00	0.00	−0.02	−0.03	0.00	−0.22**	0.03	−0.04
Est-4A a	−0.07	−0.05	0.05	−0.12	−0.14	0.15	0.00	0.02	−0.01	−0.14
Est-4A b	−0.12	−0.03	0.05	−0.17	−0.20	0.19*	0.03	0.04	−0.07	0.01
Est-4B a	0.13	0.10	0.11	−0.04	−0.04	0.09	−0.05	−0.44***	0.05	−0.20*
Est-4B b	0.04	0.08	0.22**	0.15*	0.06	0.06	0.07	0.07	−0.38***	−0.70***
Est-4B c	0.24*	−0.16	0.17	0.18	−0.40***	0.00	0.09	−0.36**	0.14	−0.15
Est-4B d	0.13**	0.09*	−0.04	−0.13	−0.16*	−0.05	−0.15*	0.00	0.05	−0.04
Est-4B null	−0.11	−0.31*	0.01	−0.04	0.00	−0.10	0.29**	−0.17	−0.09	0.04
Est-5A a	0.11	−0.10	0.15	−0.18	−0.14	−0.03	0.01	−0.02	0.01	−0.14
Est-5A b	0.05	0.02	0.18*	0.00	−0.11	0.10	−0.12	−0.38***	0.07	−0.11
Est-5A c	−0.10	−0.02	−0.07	0.19**	−0.16	−0.13	0.00	0.02	0.01	−0.02
Est-5A d	−0.20*	0.06	0.00	−0.10	−0.01	0.15*	−0.09	−0.03	−0.05	0.02
Est-5A null	0.09	−0.20	0.22**	−0.20	−0.03	−0.05	−0.13	0.02	−0.02	−0.01
Est-5B a	0.10	−0.08	−0.19	−0.05	−0.02	0.20*	−0.22	0.12	0.02	−0.21*
Est-5B b	0.00	0.02	−0.04	0.14**	−0.06	−0.18**	−0.07	−0.07	0.03	−0.04
Est-5B c	0.26**	−0.23	−0.26*	−0.05	0.15	−0.05	−0.09	0.08	0.09	−0.23*
Est-5B d	0.00	−0.02	0.00	−0.04	−0.13*	−0.02	−0.08	0.01	0.01	−0.02
Est-5B e	0.22**	−0.26*	−0.04	0.02	−0.19	0.09	−0.05	−0.04	−0.08	0.03
Gdh-A a	0.06	0.02	0.06	0.30***	0.06	0.06	0.04	0.02	−0.60***	−0.29**
Gdh-A b	−0.04	−0.01	0.01	0.12	0.06	0.06	0.01	−0.01	−0.19*	−0.30**
Gdh-B b	−0.08	−0.07	0.08	−0.02	0.07	0.02	0.02	−0.03	−0.18	−0.10
Gdh-B c	−0.15	0.00	0.08	−0.14	0.09	−0.03	0.03	−0.11	−0.09	0.05
Gdh-B null	0.06	0.02	0.06	0.30***	0.06	0.06	0.04	0.02	−0.60***	−0.29**
Ipor-B a	−0.09	−0.01	0.01	−0.04	−0.03	0.00	0.02	−0.09	0.05	−0.10
Mdh-1A a	0.61***	0.23*	−0.13	−0.05	−0.30**	−0.13	−0.22	−0.23*	−0.21*	0.15
Mdh-2 a	0.04	0.02	−0.04	0.10*	0.04	0.04	0.03	0.03	−0.34***	−0.29**
Mdh-2 b	−0.03	0.04	−0.03	0.08	−0.17	−0.13	0.02	0.04	−0.06	−0.02
Mdh-2 c	−0.04	0.01	−0.03	0.00	−0.13*	−0.11	0.01	0.03	0.01	−0.02
Mdh-2 d	0.04	0.04	0.02	−0.01	0.00	0.04	−0.01	0.00	−0.08	−0.33***
Nadhd-1A a	−0.11	0.08	−0.01	−0.01	−0.02	−0.05	−0.08	−0.07	−0.03	0.04
Nadhd-1A b	−0.14	−0.14	0.07	0.03	−0.01	0.01	0.01	−0.09	−0.05	0.03
Nadhd-1A c	−0.14	−0.09	0.07	−0.15	0.02	−0.04	0.16	−0.09	−0.02	−0.01
Nadhd-1B a	−0.02	0.00	−0.02	−0.12*	−0.02	−0.09	−0.03	0.03	0.01	−0.02
Nadhd-1B b	−0.16	0.01	−0.04	0.00	−0.03	0.08	−0.09	−0.03	−0.01	0.01
Nadhd-1B c	−0.15	0.11	−0.05	0.01	0.01	−0.06	−0.09	−0.04	−0.03	0.04
Pept-1B a	0.13	0.25*	0.02	0.18	0.02	0.05	−0.01	−0.08	0.05	−0.94***
Pgi-A c	0.02	−0.22	−0.13	0.41***	−0.05	−0.16	−0.03	0.00	−0.06	−0.04
Pgi-A d	−0.10	−0.05	0.06	0.14	0.01	0.08	−0.09	−0.19	0.11	−0.24*
Pgi-A e	0.07	−0.02	0.22**	0.18*	−0.03	0.09	−0.47***	−0.32**	0.07	−0.08
Pgi-B a	0.03	−0.22	−0.01	0.06	−0.04	−0.03	−0.06	0.02	−0.07	0.04
Pgm-A b	0.13*	−0.07	−0.06	−0.01	−0.10	−0.02	−0.07	−0.07	−0.06	0.05
Pgm-A null	0.15	−0.13	−0.06	−0.01	−0.09	0.02	−0.03	−0.03	−0.03	0.02
6Pgd-1B a	−0.02	0.00	−0.02	−0.12*	−0.02	−0.09	−0.03	0.03	0.01	−0.02
6Pgd-1B b	0.01	−0.02	−0.16	−0.13	−0.02	−0.08	0.20**	−0.06	0.01	−0.02
6Pgd-1B c	0.05	−0.03	−0.24**	−0.14	0.02	0.24***	−0.05	−0.13	−0.02	0.03
6Pgd-2 a	0.52***	0.09	−0.18	−0.12	−0.05	−0.14	−0.05	−0.27*	−0.22*	0.13
6Pgd-2 b	−0.04	−0.06	−0.01	−0.05	−0.14	0.13**	−0.11	0.00	0.01	−0.03
6Pgd-2 c	0.66***	0.26**	−0.16	−0.05	−0.31**	−0.14	−0.22	−0.26*	0.22*	0.16*
Average	0.046	−0.018	−0.001	0.001	−0.060	0.005	−0.046	−0.071	−0.054	−0.083
SE	0.025	0.017	0.017	0.019	0.015	0.015	0.017	0.018	0.022	0.027

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Table 7. Coefficient of multiple regressions (R^2) of genic diversity (He) and allele frequencies as the dependent variables and climatic and edaphic variables in 33 populations of *Triticum dicoccoides* in Israel as independent variables, and in the two subsets of 14 central and 19 marginal populations

Stepwise model									
	Over all (33 populations)			Central (14 populations)			Marginal (19 populations)		
Genetic indices									
A	Huan 0.353***	Huan Ev 0.424***	Huan Ev Ren 0.481***	Hu14 0.418*	Hu14 Rr 0.659**	Hu14 Rr Tr 0.718**	Huan 0.285*	Huan Rr 0.352*	
P-1%	Huan 0.433***	Huan Ev 0.504***	Huan Ev Ren 0.568***	Hu14 0.368*	Hu14 Rr 0.563**		Huan 0.284*	Huan Rr 0.349*	
P-5%	Td 0.496***			Hu14 0.279@	Hu14 Rr 0.435*	Hu14 Rr Td 0.517@	Huan 0.367**	Huan Trd 0.478**	Huan Trd Tr 0.528**
He	Huan 0.368***	Huan Ev 0.453***	Huan Ev Ren 0.491***	Hu14 0.246@	Hu14 Td 0.338 ns		Huan 0.285*	Huan Trd 0.399*	Huan Trd Tj 0.465*
Alleles									
Aat-1A b	Tdd 0.063 ns	Tdd Rv 0.140 ns		Huan 0.275@			Rv 0.078 ns	Rv Rd 0.260@	Rv Rd Rn 0.347@
Aat-1B a	Tdd 0.048 ns	Tdd Ev 0.106 ns		Huan 0.298*					
Aat-2A a	Hu14 0.069 ns	Hu14 Rr 0.128 ns	Hu14 Rr Al 0.207@	Rr 0.150 ns	Rr Hu14 0.549*	Rr Hu14 Al 0.657*	Hu14 0.093 ns		
Acph-3 a	Ba 0.353***			Ev 0.189 ns			Tr 0.414**		
Acph-x a	Tj 0.112@	Tj Tr 0.207@		Td 0.482*	Td Tr 0.617@		Rd 0.086 ns	Rd Ev 0.352*	
Adh-1A b	Td 0.295***	Td Huan 0.444***	Td Huan Tm 0.523***	Tm 0.422*			Rn 0.675***	Rn Rd 0.791***	Rn Rd Ta 0.850***
Adh-1B a	Dw 0.298***	Dw Huan 0.382***	Dw Huan Ta 0.430***				Dw 0.345**	Dw Ta 0.455**	Dw Ta Al 0.559**
Est-4A a	Al 0.203**			Rr 0.508**	Rr Hu14 0.842***	Rr Hu14 Rn 0.942***	Al 0.232*	Al Rr 0.317*	Al Rr Ta 0.421*
Est-4B c	Ta 0.334***	Ta Rn 0.487***	Ta Rn Rr 0.529***	Huan 0.653***	Huan Rr 0.702***	Huan Rr Ev 0.868***	Td 0.112 ns	Td Al 0.339*	Td Al Ev 0.603**
Est-5A a	Huan 0.277**	Huan Rd 0.341**	Huan Rd Rn 0.390**	Tm 0.241@			Hu14 0.274*		
Est-5 B e	Ta 0.402***	Ta Tdd 0.505***		Huan 0.512**			–		
Gdh-A b	Rd 0.151*	Rd Dw 0.268**	Rd Dw Rn 0.375**	Td 0.222@	Td Rr 0.379@	Td Rr Rn 0.476@	–		
Gdh-B b	Rd 0.101@	Rd Rr 0.244*	Rd Rr Dw 0.328**	Tdd 0.237@			Rr 0.161@	Rr Rd 0.460**	Rr Rd Trd 0.570**
Gluc-B b	Ta 0.634***	Ta Tr 0.705***	Ta Tr Tdd 0.781***	Trd 0.925***	Trd Rv 0.947***	Trd Rv Td 0.960***	Tr 0.817***	Tr Td 0.868***	
Hk b	Ba 0.361***	Ba Al 0.429***	Ba Al Td 0.486***	Rn 0.190 ns			Hu14 0.258@	Hu14 Ta 0.376@	Hu14 Ta Rv 0.465@
Ipol b	Ev 0.202*	Ev Tdd 0.347**		Tdd 0.314*			Ev 0.443**	Ev Tdd 0.753***	Ev Tdd Hu14 0.844***
Ipor-B b	Rd 0.073 ns	Rd Ev 0.280**	Rd Ev Rv 0.344**	Dw 0.531**	Dw Rn 0.798***	Dw Rn Hu14 0.908***	Rn 0.096 ns	Rn Ev 0.187 ns	Rn Ev Dw 0.306 ns
Mdh-1A a	Ta 0.545***	Ta Ba 0.608***	Ta Ba Tdd 0.690***	Trd 0.834***	Trd Td 0.859***		Al 0.469***	Al Rv 0.614***	Al Rv Dw 0.773***
Mdh-2 b	Ren 0.299***			–			Tr 0.278*		
Nadhd-1A b	Tm 0.166*	Tm Ta 0.217*	Tm Ta Trd 0.253*	Rn 0.295*	Rn Tr 0.401@		Trd 0.165@		
Nadhd-1B b	Ev 0.105@			Rn 0.532**	Rn Td 0.769***	Rn Td Al 0.896***	Ev 0.167@	Ev Ta 0.275@	Ev Ta Tdd 0.348@

Table 7. (continued)

Stepwise model	Over all (33 populations)			Central (14 populations)			Marginal (19 populations)		
Nadhd-2A c	Huan 0.089 ns	Huan Ev 0.198@	Huan Ev Td 0.383**	Al 0.899***	Al Tdd 0.991***	Al Tdd Rn 0.999***	Hu14 0.229*	Hu14 Tj 0.360*	Hu14 Tj Tdd 0.543**
Pept-1B a	Ta 0.477***	Ta Ba 0.578***	Ta Ba Rn 0.637***	Trd 0.735***	Trd Tj 0.828***	Trd Tj Rn 0.894***	Tr 0.234*	Tr Trd 0.308@	Tr Trd Rr 0.401*
Pept-2 c	Dw 0.358***	Dw Rv 0.447***	Dw Rv Ta 0.542***	Dw 0.698***	Dw Rv 0.934***	Dw Rv Hu14 0.951***	Ta 0.469***	Ta Al 0.702***	Ta Al Tm 0.736***
Pgi-A d	Td 0.140*	Td Ren 0.372***		Rr 0.339*			Td 0.169@	Td Tr 0.467**	Td Tr Al 0.561**
Pgi-A e	Td 0.158*	Td Ren 0.271**	Td Ren Rd 0.330**	Dw 0.452**	Dw Rn 0.758***	Dw Rn Tr 0.852***	Rd 0.106 ns	Rd Huan 0.243 ns	Rd Huan Rv 0.382@
Pgi-B b	Tj 0.094@	Tj Al 0.299**	Tj Al Rv 0.350**	Trd 0.175 ns	Trd Al 0.813***	Trd Al Rr 0.925***	Tm 0.181@	Tm Al 0.408*	Tm Al Rv 0.692***
Pgm-A b	Ba 0.217**	Ba Ta 0.302**	Ba Ta Tdd 0.364**	Huan 0.171 ns	Huan Tr 0.335 ns		–		
6Pgd-1B c	Rn 0.384***	Rn Td 0.478***	Rn Td Rv 0.559***	–			Rn 0.409**	Rn Td 0.605***	Rn Td Trd 0.679***
6Pgd-2 a	Ta 0.401***	Ta Ev 0.533***	Ta Ev Trd 0.570***	Trd 0.754***	Trd Rr 0.879***	Trd Rr Hu14 0.921***	Ev 0.200@	Ev Tdd 0.319*	

Level of significance: *** = $P<0.001$; ** = $P<0.01$; * = $P<0.05$; @ = $P<0.10$; ns = $P>0.10$
Abbreviations: Ba = basaltic soil; Ren = rendzina soil; Tr = terra rossa soil
For other abbreviations see Table 1

correlation coefficients (and their significance levels) as a function of distance between pairs of localities being considered, and summarize the patterns of geographic variation exhibited by the response surface of any given variable (Sokal and Oden 1978a, b).

We calculated Moran's I autocorrelations coefficient of alleles across the entire geographic range given in our study including all 37 populations (33 Israeli and 4 Turkish populations). We partitioned the space into 10 distance classes, so that each class contained equal numbers of locality pairs. The results appear in Table 6. The following are the main points:

1. Average coefficients. All the average autocorrelation coefficients over all tested alleles in all 10 distance groups were very low and nonsignificant. Note that in each column in Table 6, positive and negative values of low, medium, and sometimes high estimates sum up into low averages. This pattern indicates that there is no similar pattern across loci.

2. Low order: short distance (0–18 km) autocorrelations. Positive, negative, and no autocorrelations were intermixed across loci.

(2.1) Significant positive autocorrelations were displayed by 10 alleles comprising 7 loci (e.g., *6Pgd*-2, *Mdh*-1A and *Est*-5B).

(2.2) Negative autocorrelations (≥ -0.10) were displayed by 12 alleles comprising 8 loci, (e.g., *Nadhd*-1A, *Nadhd*-1B, *Pgi*-A, *Est*-5A). Although only one of these was significant (*Est*-5A[d]), their abundance suggests the existence of an opposite pattern to that of 2.1.

(2.3) Absence of autocorrelations was predominant at most alleles and loci, although they did demonstrate significant correlations in further distant groups (e.g., *6Pgd*-1B, *Pgi*-A, *Gdh*-A, *Pept*-1B, *Aat*-2A).

3. Scattered positive autocorrelations at:

(3.1) Low, medium and high order distances. Some alleles displayed positive autocorrelation in several distant groups while the autocorrelation in the first, low order (0–18 km) group was lacking (e.g., *6Pgd*-1B around 85 km; *Pgi*-A around 45 km, etc). *6Pgd*-2[e] showed alternate autocorrelation across a different distance group, culminating in a positive autocorrelation in the last distant group.

(3.2) Generally, positive correlations were more frequent at low and medium order distance groups, whereas negative autocorrelations were more frequent at high order distance groups.

Multiple regression analysis

Several tests of multiple regression (MR) were conducted to find out the best predictors of A, P, He, and represen-

tative allele frequencies at various polymorphic loci. The tests involved: (I) 33 Israeli populations; (II) 14 central Israeli populations; (III) 19 marginal Israeli populations, and for the 4 Turkish populations see Nevo et al. (1988a). The results are given in Table 7, first for all factors (not given in the Table), then for climatic factors, including altitude and edaphic factors (see Table entries). Clearly, a substantial amount of the genetic variation encountered, for both overall genetic indices and for specific alleles, is significantly explained by (a) water factors, Hu, Rn, (e.g., *Est*-5A^a, *Gdh*-A^b, *Gdh*-B^b; (b) temperature factors (e.g., *6Pgd*-2^a); (c) water and temperature (*6Pgd*-1B^c, *Est*-4B^c, *Adh*-1A^b); (d) soil type (*Acph*-3^a, *Mdh*-2^b); (e) soil and climate (e.g., *Hk*^{b}, *Pept*-1B^a, *Pgi*-A^d, *Gluc*-B^b).

In general, the levels of explanation in the central populations are higher than that of the marginal ones. Likewise, the number of explained genetic variances is, by far, above that expected by chance, many involving high levels of significance ($P<0.001$). Randomization tests were less frequently significant at a lower level, indicating that the results are generally not spurious. Thus, the MR analysis generated for all four genetic indices, in the real data, R^2s at $P<0.001$, while none was produced in three randomization tests. Likewise, the MR generated R^2s at $P<0.001$ for 19 of 52 alleles in the real data, and only for 3.7 alleles in the randomization tests.

We also compared the present analyses (i.e., overall central and marginal populations) with our preliminary analysis of 12 populations (Nevo et al. 1982). For comparison we ran MR on the same six climatic and soil factors that we used in our previous analysis. In general, for the genetic indices (P−1%, He), we found that humidity was the first and foremost explanatory factor in the previous and present analyses. Similarly, for the explained variation of most alleles, common factors were involved in both overall analyses. We also compared the two partial analyses (central and marginal populations) with the overall analysis in the present study, involving all 19 environmental variables. We found consistency in the explanatory variable for all genetic indices and for many alleles. We interpret this repetitive consistency in the previous, present, and partial analyses as reinforcing our conclusion that environmental factors, primarily humidity, are substantial factors in the genetic differentiation of wild emmer populations.

Genetic differentiation within and among populations

Gene diversity of a subdivided population (Ht) can be analyzed into its components: measures of the average (Dst) and the relative (Gst) degree of gene differentiation among subpopulations, where Hs is the mean gene diversity in a population, and Ht is the total diversity, and Ht = Hs + Dst (Nei 1973). Table 8 summarizes the estimates of the diversity (Ht) and the proportion expressed between populations (Gst) for each locus. The average total genic diversity across all 42 loci of *T. dicoccoides* in the 37 populations in Israel and Turkey was Ht = 0.16 (ranging from 0.0 to 0.68). Sixteen loci were markedly variable, 4 loci were near and below average, and 22 loci were weakly polymorphic, including 5 monomorphic loci. It should be noted that the Ht values were distributed discontinuously.

The average relative differentiation among the 37 populations among 37 polymorphic loci was Gst = 0.60 (ranging from 0.034 to 0.95). In other words, 40% of the allozymic variation was within populations and 60% was between populations. The highest interpopulation differentiation Dst was displayed by the following loci: *Est*-4B, *Gluc*-B, *6Pgd*-2, *Pept*-1B, *Est*-5B, *Mdh*-1A, *Est*-5A and *Acph*-x. We ran a second Gst analysis, considering Israel and Turkey each as a megapopulation, and obtained a Gst of 5%. We added at the bottom of the table, the means of parallel analyses conducted on partial data sets. This generally indicates that Gst, i.e., the relative genetic differentiation between populations, increases for small, and west marginal populations. These populations are more geographically isolated than the others.

Genetic differentiation at the two-locus level: gametic phase disequilibria

Examples of gametic phase disequilibria (D) based on 55 pairs of 11 alleles belonging to 11 widely distributed polymorphic loci in 37 populations are given in Table 9. Notably, a considerable amount of significant gametic phase disequilibria occurs within populations across the geographic range studied, above that which might be expected by chance. Out of 2035 entries, we found 390 Ds distributed in an archipelago structure. Of these 390 Ds, 69 were significant in being equally subdivided between the three significant levels of $P<0.05$; $P<0.01$; $P<0.001$. Of the 321 nonsignificant Ds, 173 were complete, i.e., reached their maximal D in the given allele frequencies. Out of the 4 pairs each displaying 4 significant Ds, 2 had a consistent sign: *6Pgd*-2^c × *Gluc*-B^b(+), and *6Pgd*-2^c × *Pept*-1B^a(−) in most central populations.

Using climatic factors, we ran Spearman rank correlations on the number of significant Ds in each of the 37 populations, and found a highly significant negative correlation between the number of Ds and evaporation, $r_s = -0.64^{***}$. By running a partial correlation analysis, thereby controlling each of the genetic indices, we found that the negative correlation, with evaporation remained the same ($r = -0.56^{**}$). In addition, a similar negative correlation with relative rainfall, Rv, and a positive correlation with humidity ($r = 0.60^{**}$) was revealed. This environmental association is the same as that for the multilocus organization described below. We take these environmental correlates as demonstrating selection.

Table 8. Partition of genetic diversity of *Triticum dicoccoides* within and between 37 populations in Israel and Turkey, based on 42 polymorphic loci (*Gst* analysis; Nei 1973)

Locus	Alleles	Sample	Ht	Hs	Dst	Gst	Dm	Rst
Aat-1A	4	1,754	0.0136	0.0129	0.0007	0.0526	0.0007	0.0570
Aat-1B	3	1,795	0.0155	0.0146	0.0009	0.0559	0.0009	0.0609
Aat-2A	2	1,788	0.1179	0.0895	0.0284	0.2407	0.0292	0.3257
Aat-2B	1	1,799	0.0	0.0000	0.0000	–	0.0000	–
Aat-3A	2	1,756	0.0445	0.0022	0.0423	0.9496	0.0435	19.3587
Aat-3B	1	1,796	0.0	0.0000	0.0000	–	0.0000	–
Acph-3	3	1,561	0.2505	0.1362	0.1143	0.4561	0.1179	0.8656
Acph-x	2	1,169	0.3744	0.1604	0.2139	0.5715	0.2208	1.3767
Adh-1A	2	1,295	0.2644	0.0813	0.1830	0.6924	0.1881	2.3130
Adh-1B	2	1,298	0.0840	0.0307	0.0532	0.6338	0.0547	1.7791
Adh-2A	2	1,607	0.0124	0.0092	0.0032	0.2585	0.0033	0.3584
Adh-2B	2	1,608	0.0318	0.0096	0.0222	0.6978	0.0228	2.3734
Cat-A	1	1,424	0.0	0.0000	0.0000	–	0.0000	–
Cat-B	1	1,425	0.0	0.0000	0.0000	–	0.0000	–
Est-4A	3	1,426	0.0373	0.0315	0.0058	0.1557	0.0060	0.1896
Est-4B	5	1,426	0.6803	0.1995	0.4807	0.7067	0.4945	2.4780
Est-5A	6	1,747	0.3996	0.1475	0.2521	0.6309	0.2591	1.7564
Est-5B	6	1,689	0.5353	0.2632	0.2722	0.5084	0.2797	1.0628
Gdh-A	4	1,790	0.0385	0.0288	0.0097	0.2524	0.0100	0.3469
Gdh-B	4	1,790	0.0644	0.0525	0.0119	0.1847	0.0122	0.2328
Gluc-B	4	1,405	0.4572	0.1391	0.3180	0.6956	0.3286	2.3617
Hk	4	1,135	0.3587	0.1680	0.1906	0.5315	0.1970	1.1723
Ipol	4	1,180	0.2985	0.1103	0.1882	0.6306	0.1941	1.7604
Ipor-A	3	1,780	0.0090	0.0079	0.0010	0.1123	0.0010	0.1301
Ipor-B	2	1,789	0.1295	0.0572	0.0723	0.5580	0.0743	1.2974
Mdh-1A	2	1,735	0.3545	0.0941	0.2603	0.7344	0.2676	2.8420
Mdh-1B	2	1,736	0.0012	0.0011	0.0000	0.0339	0.0000	0.0361
Mdh-2	4	1,778	0.0679	0.0180	0.0499	0.7352	0.0513	2.8533
Nadhd-1A	3	1,539	0.2224	0.0677	0.1547	0.6954	0.1589	2.3468
Nadhd-1B	3	1,540	0.1016	0.0309	0.0707	0.6956	0.0727	2.3483
Nadhd-2A	3	1,576	0.0553	0.0438	0.0115	0.2072	0.0118	0.2698
Pepc	3	1,502	0.1281	0.0117	0.1165	0.9088	0.1197	10.2471
Pept-1A	2	1,719	0.0023	0.0022	0.0001	0.0389	0.0001	0.0416
Pept-1B	2	1,717	0.4123	0.1363	0.2760	0.6695	0.2837	2.0816
Pept-2	3	969	0.2126	0.0979	0.1147	0.5397	0.1181	1.2068
Pgi-A	5	1,782	0.4254	0.2492	0.1763	0.4143	0.1811	0.7270
Pgi-B	2	1,784	0.2426	0.0853	0.1573	0.6482	0.1616	1.8939
Pgm-A	3	1,779	0.0316	0.0273	0.0043	0.1350	0.0044	0.1605
Pgm-B	1	1,779	0.0	0.0000	0.0000	–	0.0000	–
6Pgdh-1A	2	1,766	0.0113	0.0085	0.0028	0.2457	0.0028	0.3348
6Pgdh-1B	3	1,766	0.0202	0.0166	0.0036	0.1788	0.0037	0.2237
6Pgdh-2	3	1,605	0.4174	0.1265	0.2909	0.6969	0.2990	2.3627
Mean			0.1649	0.0659	0.0989	0.6000	0.1018	1.5434
Central populations ($n=14$):								
Mean			0.1600	0.0811	0.0789	0.4931	0.0853	1.0516
Israeli marginal populations ($n=19$):								
Mean			0.1298	0.0487	0.0811	0.6250	0.0857	1.7613
West marginal populations ($n=10$):								
Mean			0.1363	0.0377	0.0987	0.7238	0.1103	2.9300
South-east marginal populations ($n=8$):								
Mean			0.1078	0.0604	0.0474	0.4400	0.0542	0.8983
Terra rossa populations ($n=20$):								
Mean			0.1575	0.0658	0.0918	0.5825	0.0968	1.4712
Israeli basalt populations ($n=10$):								
Mean			0.1577	0.0777	0.0800	0.5074	0.0899	1.1575
Large populations ($n=14$):								
Mean			0.1600	0.0811	0.0789	0.4931	0.0853	1.0516
Medium populations ($n=12$):								
Mean			0.1111	0.0623	0.0487	0.4388	0.0532	0.8537
Israeli small populations ($n=7$):								
Mean			0.1414	0.0244	0.1169	0.8271	0.1384	5.6607

Abbreviations: *Ht* – Total gene diversity; *Hs* – Average gene diversity within populations; *Dst* – Average gene diversity between populations; *Dm* – Average of interpopulational diversity only; *Gst* – Gene diversity between populations, relative to *Ht*; *Rst* – Interpopulational diversity, relative to *Hs*

Table 9. Examples of gametic phase disequilibria (D) between pairs of 11 loci of *Triticum dicoccoides* in each of the 37 populations in Israel and Turkey (All values of D are ×1000)

Locus and Allele	Population																														
	Hermon	Central populations														South East margins								West margins $				Turkey $		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	26	30	33	34	35	37
Adh-1A b		c						c			c	c	c	c*								c		c						
× *Est*-5B a	42	94	.	.	.	.	.	27	.	.	−25	−15	30	112	.	.	.	.	.	.	.	24	.	22	.	.	.	.	.	41
Adh-1A b		a																												
× *Est*-4B null	.	250	.	.	.	.	.	.	.	.	.	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Adh-1A b							c							c						c				c		c				
× *Pgi*-A d	.	.	.	.	.	.	6	−55	.	.	−27	67	23	42	7	.	.	.	.	9	.	.	.	−24	.	1	.	.	.	.
Adh-1A b		c																						c	c***	c				
× *Est*-5A a	.	−188	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	−7	−151	−15	.	.	.	.
Adh-1A b							*				c		**	c										c		c				
× *Acph*-3 b	.	.	.	.	.	.	92	.	.	.	23	63	52	−31	8	.	.	.	.	.	.	.	.	−44	.	8	.	.	.	.
Adh-1A b												c*		c											c***	c				
× *Acph*-x a	.	.	.	.	.	.	.	.	.	.	.	−142	20	−14	.	.	.	.	.	.	.	.	.	.	−145	15	.	.	.	.
Adh-1A b	c**	a						c																		c				
× *Gluc*-B b	79	188	.	.	.	.	.	24	.	.	.	.	.	.	−9	.	.	.	.	.	.	.	.	.	.	−15	.	.	.	.
Adh-1A b		c						c					c													c				
× *Pept*-1B a	.	−63	.	.	.	.	.	−24	.	.	−8	88	15	.	4	.	.	.	.	.	.	.	.	.	.	16	.	.	.	.
Pept-1B a		c*	c					c						c																
× *Est*-5B a	.	89	27	6	.	−60	.	8	.	−11	9	−11	21	22	12	.	.	0	.	.	.	.	.	.	.	.	.	.	.	.
Pept-1B a										c								c												
× *Est*-4B null	.	−19	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	18	.	.	.	.	.	.	.	.	.	.	.	.
Pept-1B a		c				c		c			c		***		*		c									c				
× *Pgi*-A d	.	11	33	.	.	−31	.	27	.	4	15	32	78	1	46	.	−39	.	.	.	.	.	.	.	.	10	.	.	.	.
Pept-1B a				c		c		c																		*				
× *Est*-5A a	.	35	.	12	.	−31	.	−66	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	−85	.	.	.	.
Pept-1B a										**	c							c												
× *Acph*-3 b	.	.	.	.	.	.	.	.	.	−13	8	19	−14	0	−19	.	.	7	.	.	.	.	.	.	.	32	.	.	.	.
Pept-1B a										c		*			**	c	c									***				
× *Acph*-x a	.	.	.	.	.	.	.	.	.	−1	.	−95	55	−5	96	−8	−14	−24	.	.	.	.	.	.	.	163	.	.	.	.
Pept-1B a		c	**	c*				c**						c			c													
× *Cluc*-B b	.	−58	−121	−57	.	8	.	−87	.	−3	.	.	.	4	2	.	4	.	.	.	.	.	.	.	.	−74	.	.	.	.
Pgi-A d		c	c		c	c		c			c	*		c*				c	c				c					c		
× *Est*-5B a	.	−8	−44	.	−1	20	.	−16	.	−16	−5	50	−7	43	4	.	.	24	32	.	.	.	.	17	51	.	.	.	.	35	.
Pgi-A d		c								**		c						c					c							
× *Est*-4B null	.	−17	.	.	.	.	.	.	.	30	.	4	.	.	.	.	.	−10	.	.	.	.	−28	.	.	.	.	.	.	.
Pgi-A d		c			c	c			c	**													c	c		c	a***			
× *Est*-5A a	.	−10	.	.	2	−4	.	−53	−54	48	.	.	.	.	.	.	.	.	−19	.	.	.	0	63	.	−11	130	.	.	.
Pgi-A d					c		c				c	**	*	**	c**			c					c			c				
× *Acph*-3 b	.	.	.	.	−1	.	10	.	9	−3	5	81	42	64	−51	.	.	9	.	.	.	.	−22	25		−7	.	.	.	.
Pgi-A d									c					c	***			c								c		c**		
× *Acph*-x a	.	.	.	.	.	.	.	.	19	−10	.	−54	45	57	136	.	48	−21	.	.	.	.	.	.	.	10	.	.	−86	.
Pgi-A d		c			c	c		c	c					c	c*											c		c		
× *Gluc*-B b	.	5	−80	.	−2	−12	.	−36	15	3	.	.	.	−14	35	.	−5	.	−3	.	.	.	.	.	.	15	.	.	−18	.

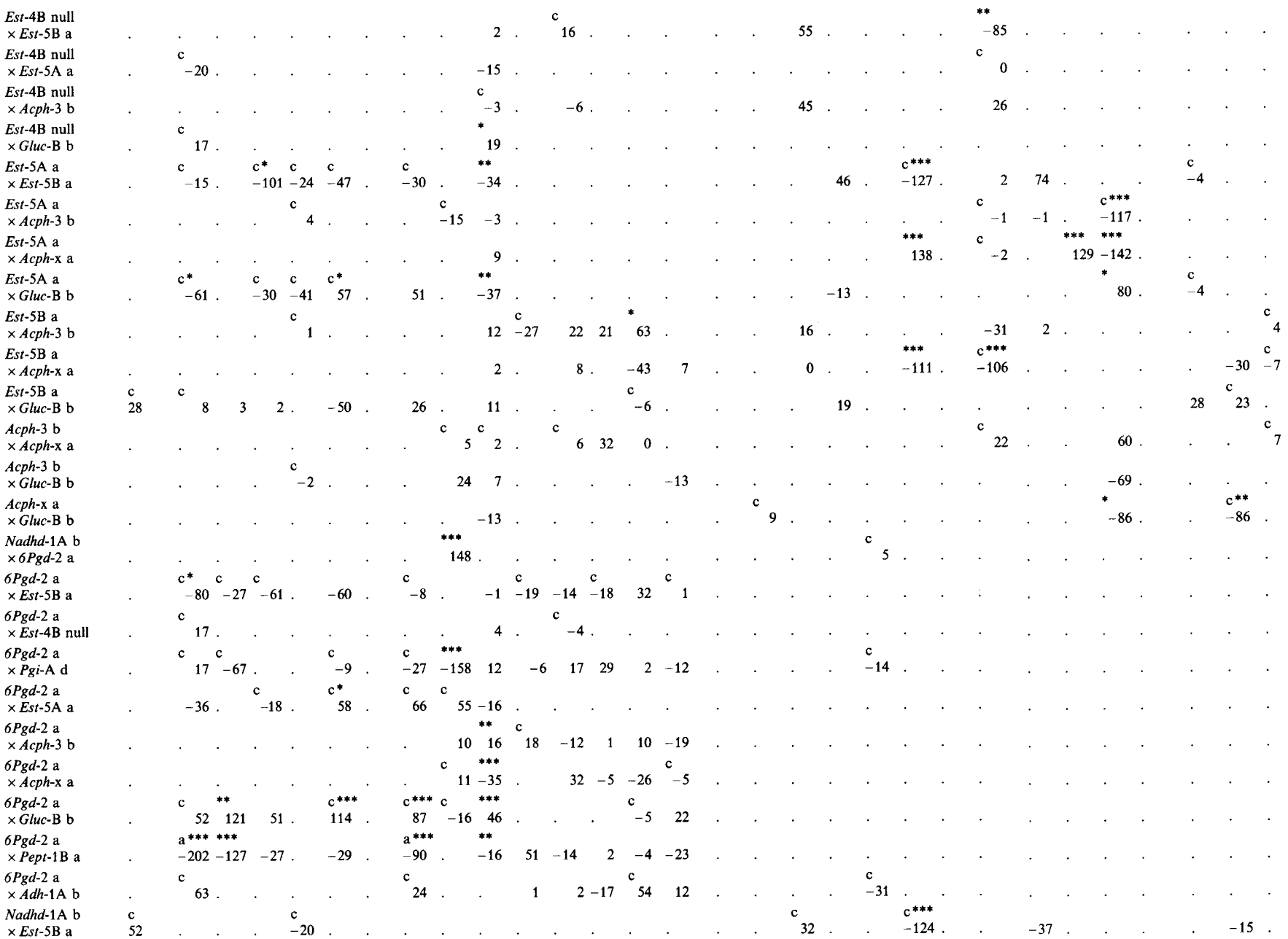
Est-4B null × Est-5B a
Est-4B null × Est-5A a
Est-4B null × Acph-3 b
Est-4B null × Gluc-B b
Est-5A a × Est-5B a
Est-5A a × Acph-3 b
Est-5A a × Acph-x a
Est-5A a × Gluc-B b
Est-5B a × Acph-3 b
Est-5B a × Acph-x a
Est-5B a × Gluc-B b
Acph-3 b × Acph-x a
Acph-3 b × Gluc-B b
Acph-x a × Gluc-B b
Nadhd-1A b × 6Pgd-2 a
6Pgd-2 a × Est-5B a
6Pgd-2 a × Est-4B null
6Pgd-2 a × Pgi-A d
6Pgd-2 a × Est-5A a
6Pgd-2 a × Acph-3 b
6Pgd-2 a × Acph-x a
6Pgd-2 a × Gluc-B b
6Pgd-2 a × Pept-1B a
6Pgd-2 a × Adh-1A b
Nadhd-1A b × Est-5B a

Table 9. (continued)

Locus and Allele	Population																													
	Hermon	Central populations														South East margins								West margins $				Turkey $		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	26	30	33	34	35	37
Nadhd-1A b × *Est*-4B null	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	c* 76	.	.	.	.	.	.	.	.	.	.	.	.
Nadhd-A b × *Pgi*-A d	.	.	.	.	c 6	.	.	.	** −111	.	.	.	.	.	.	.	.	20	.	1	.	.	.	c −40	.	.	.	.	c −15	.
Nadhd-1A b × *Est*-5A a	.	.	.	.	22	.	.	.	c 50	.	.	.	.	.	.	.	.	.	.	.	*** 170	.	.	** −86	.	.	.	.	.	.
Nadhd-1A b × *Acph*-3 b	.	.	.	.	−14	.	.	.	12	.	.	.	.	.	.	.	.	18	.	.	.	.	.	−9	.	.	.	.	.	.
Nadhd-1A b × *Acph*-x a	.	.	.	.	.	.	.	.	c 10	.	.	.	.	.	.	−48	.	c −34	.	.	*** 134	.	.	.	.	.	.	.	c* −72	.
Nadhd-1A b × *Gluc*-B b	33	.	.	.	c 4	.	.	.	c −17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	c −15	.
Nadhd-1A b × *Pept*-1B a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	c 3	.	c 8	.	.	.	.	.	.	.	.	.	.	.	.
Nadhd-1A b × *Adh*-1A b	* 78	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	c 3	.	.	.	c 3	.	.	.	.	.	.

$ Populations 27, 28, and 29 had no D with these 11 loci; in population 25, the only D is *Est*-4B null × *Acph*-3 b = 0.002; in population 31, the only one is *Est*-5B a × *Acph*-3 b = 0.008 c; in population 32, the only one is *Est*-4B null × *Acph*-3 b = −0.012 c; and in population 36, the only one is *Est*-5B a × *Acph*-x a = −0.013 c. These 7 populations are omitted from the table

Significance: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; P by chi square with Yates correction, or by Fisher's exact test

c = complete association: one gametic type is missing (Clegg et al. 1976);

a = absolute association: only two gametic types are present (Clegg et al. 1976).

. = one or both alleles of the pair were not in a polymorphic state, or missing data

Multilocus organization

The multilocus organization index, related to the single-locus Simpson Index, and based on the observed distribution of the number of heterozygous loci (K) in two randomly chosen gametes, was proposed by Brown et al. (1980). It measures multilocus associations when multiple alleles and many loci are analyzed by combining all paired-loci gametic-phase-disequilibria. We calculated multilocus organization indices for each of the 37 populations and averaged the estimates for each ecogeographical subdivision separately. The results are given in Table 2. The levels of significance between the expected and observed variances of K for each population are given in the table. The observed variance of K in 24 populations was significantly above the expected. The average measure of intensity of multilocus association X(2) was 0.86, and the range was $-0.07-3.01$. X(2) was correlated with all genetic indices (A, P−1%, He), $r_s = 0.32-0.38$ ($P < 0.05$). X(2) was also significantly and negatively correlated with evaporation across the range ($r_s = -0.40$, $P < 0.05$), increasing substantially to $r_s = -0.66$, $P = 0.01$ in 14 central populations in Israel. Notably, the trends of correlation are displayed also, though nonsignificantly, with humidity. In other words X(2) is larger with increasing humidity.

Discussion

The evidence of genetic diversity found in natural populations of *T. dicoccoides,* the wild progenitor of all cultivated wheats, is important for two major reasons. First, theoretically, for understanding the evolutionary history of this unique progenitor of wheats, and second, practically, for evaluating the potential genetic resources for conservation and utilization for crop improvement. Modern genetic techniques permit the transference of genetic material between the ancestors and their derived domesticates. Very few ancestors have been studied across their geographical range at the interface of population genetics and ecology. This interface is important in unraveling the actual genetic differentiation of the progenitor and its ecological determinants, thereby obtaining clues of the potential genetic resources it harbors for breeding (Nevo 1987). We have previously analyzed, in a similar way, the genetic differentiation of wild barley, *Hordeum spontaneum,* in the Near East (Nevo et al. 1986b), and attempt here, though on a smaller scale, (Iran's wild emmer is not represented) to do the same for wild emmer wheat.

Population genetic structure of wild emmer wheat

"Archipelago" population genetics structure. Wild emmer grows in lush and extensive stands in the catchment area of the Upper Jordan Valley (in Israel, in the eastern upper Galilee Mts. and the Golan Heights). However, elsewhere in the Fertile Crescent (Fig. 1a, b), populations of wild emmer are semi-isolated and isolated, and largely display a patchy structure. At least in Israel, but possibly also elsewhere across the range of wild emmer in the Fertile Crescent, populations are subdivided into demes or clumps of varying sizes, including large, medium, and small patches. This has been previously described for a smaller sample of wild emmer in Israel (Nevo et al. 1982) and Turkey (Nevo et al. 1988a), and for wild barley, *Hordeum spontaneum,* in the Near East (Nevo et al. 1986b).

The highly subdivided "archipelago"-type ecological population structure of wild emmer is even more distinct than that of wild barley and is matched by its genetic population structure. We have found substantially more gene differentiation within and between populations sometimes geographically very close in Israel than between wild emmer in Israel and Turkey (Table 3). Of the total genetic diversity of *T. dicoccoides,* 40% exists within populations, 60% between populations, whereas only 5%, between Israel and Turkey as megapopulations (see Gst analysis in Table 8). This conclusion is reinforced by the microgeographic analysis based on edaphic, topographic, and temporal differentiation (Nevo et al. 1988b), and on microclimatic local differentiation (Nevo et al. 1988c), as well as on the extreme case of local differentiation in the Golan Heights (Nevo et al. 1982; Golenberg and Nevo 1987).

The high genetic differentiation within and between populations of *T. dicoccoides* is also reflected by the analysis of allele distribution. The latter reveals sharp local and regional differentiation in overall genetic indices (Table 2) as well as in individual allele frequencies (Appendix). Out of the 119 alleles, 61 occurred in Turkey, and 114 were found in Israel. Of the 61 alleles at 42 shared loci across Israel and Turkey, 5 alleles (8.2%) were unique for Turkey. Likewise, allele uniqueness was also found for the ecogeographical subdivisions in Israel as follows: (I) out of 93 alleles occurring in *central* populations, 17 alleles (18.3%) were unique; in *marginal* populations: (II) the southeastern margins had 84 alleles, 6 unique (7.1%); (III) the western margins had 79 alleles, 6 unique (7.6%); (IV) the northeast (Mt. Hermon) had 53 alleles, 1 unique (1.9%); *soil types* (V) basalt had 89 alleles, 11 unique (12.4%); and finally, (VI) *population size,* "large" populations had 93 alleles, 17 unique (18.3%); "medium" had 78 alleles, 11 unique (14.1%); and "small" had 82 alleles, 10 unique (12.2%).

Moreover, 70% of all variant alleles were not widespread, but revealed localized and sporadic distribution. Likewise, the analysis of genetic distances between populations supports the conclusion, based on genetic differentiation and allele distribution, that sharp local differ-

entiation over short geographic distances is the rule, and the frequency of some common alleles (>10%) is localized and high. The population genetic structure of wild emmer is mosaic. This genetic mosaicism appears to reflect the underlying ecological heterogeneity which derives from local and regional geological, edaphic, climatic, and biotic differentiations. The resulting structure is, like in wild barley, an ecological–genetic "archipelago", where the genetic structures are in accordance with the ecological ones.

Autocorrelation

The autocorrelation analysis predicts that migration will cause high positive correlations (similarity) in the low order distant groups (i.e., between neighbors), starting from the first ones. Migration is expected to cause similarity between loci and alleles. This prediction is not realized in our results. In contrast, loci and alleles of wild emmer differ drastically in their autocorrelation pattern between loci. In addition, positive autocorrelations emerge at intermediate distance groups, thus negating migration as an important evolutionary factor.

The autocorrelation analysis also predicts that genetic drift will not create any autocorrelative pattern. Our data is structured, hence negates randomness. Despite the between loci variation, a general tendency of more positive correlations on the left-hand side of the table, and more negative correlations on the right-hand side are evident.

Environmental selection is also partly autocorrelated and affects loci differentially. This is supported by our data because of the following three reasons: (I) variation among loci; (II) positive correlation in different distant groups, and not necessarily the first one; (III) the predominance of negative correlations in the larger distant groups is expected due to decreasing ecological similarity often with increasing distance.

Genome organization

The multilocus genome organization estimates expressed by X(2) in the last columns of Table 2 need elucidation. The measure was first suggested by Brown et al. (1980) as an estimate of multilocus associations for summing up multiple gametic phase disequilibria. The behavior of this statistic, including its strength and drawbacks, were discussed by Brown et al. 1980. The merit of this estimate, in comparison with a set of two locus linkages disequilibrium, is that it effectively summarizes multilocus association to a few values for comparative studies of populations and species. This measure is an inverse function of two locus gametic frequencies in inverse analogy with the single locus Simpson diversity measure. The drawbacks include, first, a severe loss of information and ignorance of the behavior of particular allelic combinations. Second, it assumes that all loci are of equal interest, which is biologically unjustified. Third, in some cases, the summation combines positive and negative contributions, thus it may obscure existing multilocus organizations. Finally, this measure is partially dependent on the single loci diversity and/or the number of loci scored, which is important in comparing estimates that are based on radically different single-locus data bases.

We acknowledge all the above-mentioned four drawbacks. In our present case, there is no one locus that is polymorphic across all 37 populations (Appendix). Therefore, we based our analysis on 29 loci which were polymorphic to different degrees, in different populations. This explains the wide variation in the number of polymorphic loci and the number of pairwise Ds on which X(2) is based in each population (last two columns of Table 2). We ran several analyses of X(2), some excluding very small populations, but, nevertheless, obtained similar average estimates for the different subdivisions in Table 2, as well as similar correlations as described below. Our results indicated a significant negative Spearman rank correlation of X(2) with evaporation across the range ($r_s = -0.40$, $P < 0.05$), reinforced in the large highly polymorphic central populations. We speculate that the intensity of X(2) as a summary statistic may vary in content, though be similar in level – different *Ds* in different ecologies. In other words, the same level of intensity of genome organization may be caused by different ecological stresses.

Finally, we did obtain different estimates of X(2) here, as compared with our previous separate studies of wild emmer in Turkey and Tabigha, Israel. These differences are due to different data bases, based on different numbers of loci. Nevertheless, the general trends were similar.

The adaptive nature of allozyme polymorphisms in wild emmer

Multiple lines of evidence, presented in the results, support the hypothesis that allozyme polymorphisms are at least partly adaptive and are determined by natural diversifying selection. The evidence includes: (I) the association of single loci and multilocus structures with climatic and soil parameters (Tables 5–7 and 9). Genetic differentiation appears to match, to a large extent, the ecological heterogeneous background. (II) Genetic differentiation is not correlated with geographic distance, but rather with local ecological conditions of soil and climate (Tables 1 and 3, and the autocorrelation in Table 6). (III) Macrogeographical genetic differentiation is partially paralleled by microgeographical soil, and topographical and yearly climatic fluctuations (compare with Nevo et al. 1988 b, c). (IV) The genetic differentiation of wild emmer is far from random. Significant phase dis-

equilibria abound, displaying allele association at the two locus level (Table 9). (V) Strong allele associations occur at the multilocus level, above that expected by chance (Table 2). (VI) Spatial autocorrelation analysis reveals different significant spatial patterns for different alleles and loci (Table 6), ruling out migration as a differentiating factor. Likewise, the general order of negative and positive correlations rules out random drift as a major agent of genetic differentiation in wild emmer.

Our overall results indicate that genetic diversity among localities and over time (see Appendix and Tables 2 and 3 for microsite spatial and temporal variation at Tabigha, and Table 6 for autocorrelation analysis) display weak correlations with geography and stronger ones with ecology, for single loci and for multilocus genome organization. This evidence permits us to eliminate genetic drift and migration as basic factors of genetic differentiation in wild emmer. By contrast, the structures described suggest that climatic and edaphic diversifying single loci and multilocus epistatic selection regimes operate at different spatial scales from the micro- to the macrogeographic ones. These results appear to largely match those found earlier in wild barley, locally (Nevo et al. 1981, 1983, 1986a) and regionally (Nevo et al. 1979, 1986b, e, f).

Stochastic factors certainly interact with natural selection in varying environments over space and time. Some of the very small populations of wild emmer described here (e.g., nos. 28, 29, 31, and 33) may have derived their low levels of P and He from either founder effects and/or genetic drift. The latter can be a potent force for removing variation, particularly in small populations and when the random environment tends to occasionally push alleles down to low frequencies (Nei 1980; Gillespie 1985). However, most of the populations described here are medium and large, and they appear to derive and maintain their genetic polymorphisms and structure from climatically and edaphically varying environments.

The maintenance of polymorphisms in wild emmer may be explicable by both spatial and temporal variation in selection. Theory indicates that selection, acting differentially in space, coupled with limited migration (which is typical to wild emmer, mean of 1.25 m per generation at Yehudiyya, Israel; Golenberg 1987), will maintain a substantial amount of polymorphism (Karlin and McGregor 1972; Hedrick 1986). Two niche models, that of Levene (1953) and that of Gillespie (1978), the SAS-CFF model, can explain genetic differentiation in wild emmer. Different homozygotes are favored in different climatic and edaphic niches. The latter operate on all scales, from regional to local to miniscule niches at a locality.

The limited migration of seeds between niches over many generations and the accumulated seed banks in the soil provide rich reservoirs of genetic diversity for natural selection to operate on. Such accumulated seed pools provide a memory of past selection regimes. These seed pools can greatly reduce the fitness uncertainty generated by cyclical or random environments and thus free the plant population from having to respond genetically to the fitness conditions realized in every year (Templeton and Levin 1979). We have exemplified the temporal differentiation in allele frequency, presumably realized by the richness of seed pools in our microsite emmer wheat study in Tabigha (Appendix and details in Nevo 1988b).

The wild gene pool of emmer wheat and future wheat breeding

The wild gene pool of emmer wheat can provide useful genetic resources for the improvement of the cultivated gene pools. This idea, which was suggested as early as the turn of the century, has been reviewed for its historical aspects and significance by Feldman (1979 and references therein), and in its more modern version by several authors (Avivi 1979a, b; Grama and Gerechter 1974, Grama et al. 1983, Gerechter-Amitai and Grama 1974; Feldman 1979; Feldman and Sears 1981; Nevo 1983; Nevo et al. 1982, 1988a–c; Zohary 1983).

The utilization of wild emmer in breeding began with the finding, in 1964, that Israeli populations harbor a valuable source of stripe rust resistance (Gerechter-Amitai and Stubbs 1970). In 1967 it was discovered that the grain protein content in several collections of wild emmer ranges from 20% to 24%, considerably higher than that found in cultivated wheat (Gerechter-Amitai and Grama 1977). Further extended research revealed protein values in wild emmer ranging from 13.9% to 28.9% (Grama et al. 1983). Similar results were reported by Avivi (1979a, b). The current breeding program in the Volcani Center of the Agricultural Research Organization (ARO) utilizes a selection of wild emmer, G-25, that is resistant to stripe rust, and has a protein content of 20.5% and a kernel weight of 31.5 mg. Thus, it combines several desirable traits in a donor. The hexaploid wild emmer wheat derivatives developed at the ARO were grown under New Zealand conditions and tested for a number of milling and baking quality parameters and for gliadin and high molecular weight (HMW) glutenin protein composition. Superior qualities of protein content, dough strength, and baking quality were found to be related to the presence of specific protein components (Grama et al. 1987a). Likewise, four wild emmer derivatives grown in New Zealand proved superior to standard bread wheats in total content of grain nitrogen and flour protein after foliar urea sprays at heading (Grama et al. 1987b).

The properties of high kernel weight and high grain protein have also been transferred from tetraploid *T. dicoccoides* accessions collected in Israel to hexaploid bread wheat (Kushnir and Halloran 1984). They pro-

duced high kernel weight and high grain protein hexaploid wheat lines from the cross of a high kernel weight and a high protein *T. dicoccoides* accession with 'Chinese Spring' and its two homologous pairing mutants, ph_{1b} and ph_2. Those pentaploids were then crossed with two cultivars to produce the stable hexaploid high kernel weight and high grain protein lines.

Studies conducted at the Institute of Evolution, University of Haifa

During recent years, we have also included in our research program of wild emmer wheat, at the Institute of Evolution, University of Haifa, Israel, surveys on phenotypic and genotypic variances of agronomically important traits within and between populations of wild emmer. In the course of these studies, we have found rich genetic resources which could be utilized in wheat amelioration. First, we compared the phenotypic performance of natural populations in two, relatively standardized and contrasting environments: mesic and xeric. We found striking genetic variation in 12 variables, including germination, growth rates, earliness, yield, and biomass (Nevo et al. 1984b). Next we investigated disease resistance to several pathogens in the same populations. We found in the wild gene pool of emmer wheat in Israel rich sources of resistance to powdery mildew, *Erysiphe graminis tritici* (Moseman et al. 1984), leaf rust incited by *Puccinia recondita* (Moseman et al. 1985), and rust incited by *Puccinia striiformis* (Nevo et al. 1986c). The resistant accessions to powdery mildew and leaf rust identified in our studies are currently being used to develop cultivated wheat germplast resistant to these pathogens. Following earlier findings by Grama, Gerechter-Amitai, Avivi, and Feldman (cited previously), we found geographically structured resources of high protein genotypes in our wild emmer populations (Nevo et al. 1986d). These findings were followed by the discovery that there are striking variations in the intergenic spacer of ribosomal DNA of wild emmer populations in Israel (Flavell et al. 1986). This rDNA diversity may have a regulatory function, and it is likely to play a special role in rDNA expression that involves protein binding. Finally, we found a rich diversity of HMW glutenin subunits in our wild emmer which are not present in bread wheat. This diversity could be utilized in breeding varieties with improved bread-making quality (Nevo and Payne 1987).

The rich genetic variation found in wild emmer wheat, especially the aforementioned traits, is geographically structured, primarily in accordance with macro- and microecological heterogeneity. This variation is largely neither random nor neutral. We developed a predictive methodology, based on allelic isozyme markers and ecology, for identifying elite genotypes resistant to powdery mildew and leaf rust (Nevo et al. 1985), stripe rust (Nevo et al. 1986c), high protein content (Nevo et al. 1986d), and HMW glutenin subunit diversity (Nevo and Payne 1987). Our predicitve methodology permits, in principle, the optimization of sampling strategies for diverse, agronomically important characters and for the screening and evaluation of elite populations and genotypes appropriate for breeding (reviewed in Nevo 1987).

Conclusions

Unanswered questions and future prospects

The evidence of genetic structure and differentiation of wild emmer wheat, *T. dicoccoides*, the progenitor of tetraploid and hexaploid cultivated wheats, suggests that genetic diversity is ecogeographically structured and is partly predictable by climatic and edaphic determinants. Wild emmer has a unique ecological-genetic structure. Its central populations in the catchment area of the upper Jordan Valley are massive and lush. However, both southward in Israel and northward into Turkey, it becomes fragmented into semi-isolated and isolated populations that are characterized by an "archipelago" genetic structure where alleles are built up locally in high frequency, but are often missing in neighbor localities.

The unique population structure of wild emmer is not random. Rather, it is intimately associated with the environment at both the macro- and microecological levels. Ecology appears to overdominate geography in affecting population differentiation. Natural selection, primarily diversifying, climatic and edaphic selection regimes, seems to be the major differentiator of single gene loci and multilocus structures of populations in accordance with the multiniche background structure of varying environments in space and in time. Selection rather than genetic drift and migration appears to be a major determinant of genetic differentiation except in very small populations where founder and drift phenomena may become prominent.

The center of origin and diversity of wild emmer and other progenitors of cultivated plants is the Near East Fertile Crescent (Zohary 1983). Particularly in Israel, with its extraordinary biotic and physical diversity (Nevo 1986), wild emmer developed, both within and between populations, a wide range of adaptive diversity to multiple diseases, pests, and ecological stress over a long evolutionary history. Most importantly, this variation is neither random nor neutral. By contrast, it displays at all levels, adaptive genetic diversity for biochemical, morphological, and immunological characteristics which contribute to its ability to adapt to widely diverse climatic and edaphic conditions. The long-lasting co-evolution with parasites and with the ecologically heterogeneous nature of Israel caused the development of single variable

genes in these wild cereals, as well as multilocus coadapted structures, locally and regionally, for both short and long-term survival. These include genetic resources for disease resistance, physiological adaptation for drought, heat and salt tolerance, and diverse morphological traits of economic importance. The latter include growth rates, ripening, and yield, in accordance with specific habitats, as well as grain size and protein quality and quantity.

In a series of population genetic and ecological studies conducted at the Institute of Evolution during the last decade, 1978–1988, we have discovered rich genetic diversity in the wild progenitors of wheat and barley. This diversity involves a variety of mostly untapped genes associated with elite agronomic traits, disease resistance, and protein quantity, as well as with adaptations to ecological stresses of heat, drought, and salinity. The genetic resources of those wild cereals, and most probably of other progenitors of many crops found in Israel and elsewhere, exhibit nonrandom, ecogeographical distribution. This distribution is correlated with and predicted by climatic and soil factors, as well as by allozyme markers. We have suggested a predictive methodology, based on ecology and genetic markers to optimize sampling strategies and maximize the screening and evaluation of those elite populations and genotypes of wild emmer appropriate for breeding cultivated wheats.

What next? Many theoretical evolutionary genetic and practical agronomic problems remain unresolved and should be explored in the future to elucidate the evolution of wild emmer. In particular, the revolutionary and powerful recombinant DNA technology could be used to unravel genetic differentiation in wild emmer, as elsewhere. The three separate but interacting genomes of plants, the chloroplast genome (cpDNA), the mitochondrial genome (mtDNA), and the nuclear genome are yet largely unexplored in wild emmer. They should be investigated in depth, at the restriction fragment length (RFLP) and sequence polymorphisms, as well as in genome organization and change, transposable elements, and gene expression. Their genetic transmission, genetic mapping, biochemical properties and evolutionary patterns, rates and differentiating forces within and between populations should and could be probed. These evolutionary genetics studies should be conducted in an ecological context and under environmental stresses. Only under environmental stresses can the potentially rapid genomic changes be tracked, and only by appropriate transplant experiments can fitness parameters be conclusively evaluated.

The use of isozyme markers and RFLPs in mapping plant genomes is dramatically progressing (e.g., Brown and Clegg 1983; Tanksley and Orton 1983; Beckman and Soler 1986; Nevo 1987). These techniques reveal the linkage of the genetic markers with agronomically important traits and are substantial to enhancing the conservation and utilization of wild emmer gene resources, as well as that of other progenitors. Transferring and expressing foreign genes is now also progressing speedily (e.g., Schell 1987). Clearly, both theoretically and practically, the challenges of exploring and utilizing wisely the genome of wild wheat for future reference, are wide open, exciting, and very promising.

Acknowledgements. We thank E. M. Golenberg for field work data and T. Krugman for laboratory work. These studies were supported by the Wolfson Foundation, the United States – Israel Binational Agricultural Research and Development Fund, BARD; the Israel Discount Bank Chair of Evolutionary Biology, the Ancell-Teicher Research Foundation for Genetics and Molecular Evolution established by F. and T. Baumritter, New York City, and the Humana Inc./KY.

References

Atlas of Israel (1970) Surveys of Israel ministry of labour. Jerusalem and Elsevier, Amsterdam

Avivi L (1979a) High grain protein content in wild tetraploid wheat *Triticum dicoccoides:* In: Ramanujam S (ed) Proc 5th Int Wheat Genet Symp Indian Soc Genet Plant Breed, Indian Agric Res Inst, New Delhi, pp 372–380

Avivi L (1979b) Utilization of *T. dicoccoides* for the improvement of grain quantity and quality of cultivated wheats. Monogr Genet 4:27–38

Beckmann JS, Soller M (1986) Restriction fragment length polymorphisms in plant genetic improvement. Oxford Surv Plant Mol Cell Biol 3:196–250

Brown AHD, Clegg MT (1983) Isozyme assessment of plant genetic resources. In: Rattazzi MC, Scandalios GJ, Whitt AR (eds) Isozymes: current topics in biological and medical research, vol. 11:medical and other applications. Alan R Liss, New York, pp 285–295

Brown AHD, Nevo E, Zohary D, Dagan O (1978) Genetic variation in natural populations of wild barley *Hordeum spontaneum.* Genetica 49:97–108

Brown AHD, Feldman MW, Nevo E (1980) Multilocus structures of natural populations of *Hordeum spontaneum.* Genetics 96:523–536

Clegg MT, Kidwell JF, Kidwell MG, Daniel NJ (1976) Dynamics of correlated genetic system. I. Selection in the region of the glued locus of *Drosophila melanogaster.* Genetics 83:793–810

Feldman M (1976) Wheats. In: Simmonds NW (ed) Evolution of crop plants. Longman, London, pp 120–128

Feldman M (1979) Genetic resources of wild wheats and their use in Breeding. Monogr Genet Agrar 4:9–26

Feldman M, Sears ER (1981) The wild gene resources of wheat. Sci Am 244:102–112

Flavell RB, O'Dell M, Sharp P, Nevo E, Beiles A (1986) Variation in the intergenic spacer of ribosomal DNA of wild wheat, *Triticum dicoccoides* in Israel. Mol Biol Evol 3:547–558

Gerechter-Amitai ZK, Grama A (1974) Inheritance of resistance to stripe rust (*Puccinia striiformis*) in crosses between wild emmer (*Triticum dicoccoides*) and cultivated tetraploid and hexaploid wheats. I. *Triticum durum.* Euphytica 23:387–392

Gerechter-Amitai ZK, Grama A (1977) Use of alien genes in wheat breeding. Annu Wheat Newsl 23:57–58

Gerechter-Amitai ZK, Stubbs RW (1970) A valuable source of yellow rust resistance of Israeli population of wild emmer, *Triticum dicoccoides*. Euphytica 19:12–21

Gillespie JH (1978) A general model to account for enzyme variation in natural populations. V. The SAS-CFF model. Theor Pop Biol 14:1–45

Gillespie JH (1985) The interaction of genetic drift and mutation with selection in a fluctuating environment. Theor Pop Biol 27:222–237

Golenberg EM (1986) Multilocus structures in Plant populations: Population and genetic dynamics of *Triticum dicoccoides*. PhD. Thesis, State University of New York at Stony Brook

Golenberg EM (1987) Estimation of gene flow and genetic neighborhood size by indirect methods in a selfing annual, *Triticum dicoccoides*. Evolution 41:1326–1334

Golenberg EM, Nevo E (1987) Multilocus differentiation and population structure in a selfer, wild emmer wheat, *Triticum dicoccoides*. Heredity 58:951–956

Grama A, Gerechter-Amitai ZK (1974) Inheritance of resistance to stripe rust (*Puccinia striiformis*) in crosses between wild emmer (*Triticum dicoccoides*) and cultivated tetraploid and hexaploid wheats. II. *Triticum aestivum*. Euphytica 23:393–398

Grama A, Gerechter Amitai ZK, Blum A (1983) Wild emmer as donor of genes for resistance to stripe rust and for high protein content. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp Plant Germ-Plasm Inst Facul Agr Kyoto Univ, Kyoto, pp 178–192

Grama A, Cressey PJ, Lindley T (1987a) Hexaploid wild emmer wheat derivatives grown under New Zealand conditions. 1. Relationship between protein composition and parameters. N Z Agric Res 30:35–43

Grama A, Porter NG, Wright DSC (1987b) Hexaploid wild emmer wheat derivatives grown under New Zealand conditions. 2. Effect of foliar urea sprays on plant and grain nitrogen and baking quality. N Z J Agric Res 30:45–51

Harlan JR, Zohary D (1966) Distribution of wild wheat and barley. Science 153:1074–1080

Hedrick PW (1986) Genetic polymorphism in heterogeneous environments: a decade later. Annu Rev Ecol Syst 17:535–566

Karlin S, McGregor JL (1972) Polymorphisms for genetics and ecological systems with weak coupling. Theor Pop Biol 3:210–238

Kimber G, Feldman M (1987) Wild wheats. An introduction. Special Report 353. College of Agriculture, Univ of Missouri, Columbia, pp 1–142

Kushnir U, Halloran GM (1984) Transfer of high kernel weight from wild tetraploid wheat (*Triticum turgidum dicoccoides*) to bread wheat (*T. aestivum*) using homologous and homoeologous recombination. Euphytica 33:249–255

Levene H (1953) Genetic equilibrium when more than one ecological niche is available. Am Nat 87:331–333

Marshall DR, Brown AHD (1975) Optimum sampling strategies in genetic conservation. In: Frankel OH, Hawles JG (eds) Crop genetic resources for today and tomorrow. Cambridge University Press, Cambridge, pp 53–70

Moseman JG, Nevo E, El-Morshidy MA, Zohary D (1984) Resistance of *Triticum dicoccoides* collected in Israel to infection with *Erysiphe gramminis tritici*. Euphytica 33:41–47

Moseman JG, Nevo E, Gerechter-Amitai ZK, El-Morshidy MA, Zohary D (1985) Resistance of *Triticum dicoccoides* collected in Israel to infection with *Puccinia recondita tritici*. Crop Sci 25:262–265

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

Nei M (1973) Analysis of gene diversity in subdivided populations. Proc Natl Acad Sci USA 70:3321–3323

Nei M (1980) Protein polymorphism and the SAS-CFF model. Genetics 94:1085–1087

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

Nevo E (1983) Genetic resources of wild emmer wheat: Structure, evolution and application in breeding. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp Plant Germ-Plasm Inst Facul Agr Kyoto Univ, Kyoto, pp 421–431

Nevo E (1986) Genetic resources of wild cereals and crop improvement: Israel, a natural laboratory. Isr J Bot 35:255–278

Nevo E (1987) Plant genetic resources: Prediction by isozyme markers and ecology. In: Rattazzi MC, Scandalios JG, Whitt GS (eds) Isozymes: current topics in biological and medical research, vol. 16:agriculture, physiology, and medicine. Alan R Liss, New York, pp 247–267

Nevo E, Payne PI (1987) Wheat storage proteins: Diversity of HMW glutenin subunits in wild emmer from Israel. Theor Appl Genet 74:827–836

Nevo E, Zohary D, Brown AHD, Haber M (1979) Genetic diversity and environmental associations of wild barley *Hordeum spontaneum* in Israel. Evolution 33:815–833

Nevo E, Brown ADH, Zohary D, Storch N, Beiles A (1981) Microgeographic edaphic differentiation of allozyme polymorphism of wild barley. Plant Syst Evol 138:287–292

Nevo E, Golenberg EM, Beiles A, Brown AHD, Zohary D (1982) Genetic diversity and environmental associations of wild wheat, *Triticum dicoccoides* in Israel. Theor Appl Genet 62:241–254

Nevo E, Beiles A, Storch N, Doll H, Anderson B (1983) Microgeographic edaphic differentiation in hordein polymorphisms of wild barley. Theor Appl Genet 64:123–132

Nevo E, Beiles A, Ben-Shlomo R (1984a). The evolutionary significance of genetic diversity: Ecological, demographic and life history correlates. In: Mani GS (ed) Evolutionary dynamics of genetic diversity. Proc Symp Manchester/UK, March 1983. Springer, Berlin Heidelberg New York, pp 13–213. Lecture notes in biomathematics, vol 53

Nevo E, Beiles A, Gutterman Y, Storch N, Kaplan D (1984b) Genetic resources of wild cereals in Israel and vicinity. I. Phenotypic variation within and between populations of wild wheat, *Triticum dicoccoides*. Euphytica 33:717–735

Nevo E, Moseman JG, Beiles A, Zohary D (1985) Patterns of resistance of Israeli wild emmer wheat to pathogens. I. Predictive method by ecology and allozyme genotypes for powdery mildew and leaf rust. Genetica 67:209–222

Nevo E, Beiles A, Kaplan D, Golenberg EM, Whittaker L, Naveh Z (1986a) Natural selection of allozyme polymorphisms: A test revealing ecological–genetic differentiation among microsites. Evolution 40:13–20

Nevo E, Beiles A, Zohary D (1986b) Genetic resources of wild barley in the Near East: Structure, evolution and application in breeding. Biol J Linn Soc 27:355–380

Nevo E, Gerechter-Amitai ZK, Beiles A, Golenberg EM (1986c) Resistance of wild wheat to stripe rust: Predictive method by ecology and allozyme genotypes. Plant Syst Evol 153:13–30

Nevo E, Grama A, Beiles A, Golenberg EM (1986d) Resources of high-protein genotypes in wild wheat, *Triticum dicoccoides* in Israel: Predictive method by ecology and allozyme markers. Genetica 68:215–227

Nevo E, Zohary D, Beiles A, Kaplan D, Storch N (1986e) Genetic diversity and environmental associations of wild barley, *Hordeum spontaneum* in Turkey. Genetica 68:203–213

Nevo E, Beiles A, Kaplan D, Storch N, Zohary D (1986f) Genetic diversity and environmental associations of wild barley, *Hordeum spontaneum (Poaceeae)*, in Iran. Plant Syst Evol 153:141–164

Nevo E, Beiles A, Kaplan D (1988a) Genetic diversity and environmental associations of wild emmer wheat, in Turkey. Heredity 61:31–45

Nevo E, Beiles A, Krugman T (1988b) Natural selection of allozyme polymorphisms: a microgeographical differentiation by edaphic, topographical, and temporal factors in wild emmer wheat (*Triticum dicoccoides*). Theor Appl Genet 76:737–752

Nevo E, Beiles A, Krugman T (1988c). Natural selection of allozyme polymorphisms: A microgeographic climatic differentiation in wild emmer wheat (*Triticum dicoccoides*). Theor Appl Genet 76:737–752

Plucknett DL, Smith NJH, Williams JT, Anishetty NM (1983) Crop germplasm conservation and developing countries. Science 220:163–169

Plucknett DL, Smith NJH, Williams JT, Anishetty NM (1987) Gene banks and the world's food. Princeton/NJ, Princeton University Press

SAS (1985) User's guide, 5th edn. SAS Institute, Cary/NC

Schell JSt (1987) Transgenic plants as tools to study the molecular organization of plant genes. Science 237:1176–1183

Sokal RR, Oden NL (1987a) Spatial autocorrelation in biology. I. Methodology. Biol J Linn Soc 10:229–249

Sokal RR, Oden NL (1987b) Spatial autocorrelation in biology. 2. Some biological implications and four applications of evolutionary and ecological interest. Biol J Linn Soc 10: 229–249

Sokal RR, Wartenberg DW (1983) A test of spatial autocorrelation using an isolation-by-distance model. Genetics 105: 219–237

SPSS-x (1986) User's guide, 2nd edn. McGraw-Hill, New York

Tanksley D, Orton TJ (1983) Isozymes in plant genetics and plant breeding, parts A and B. Elsevier, Amsterdam

Templeton AR, Levin DA (1979) Evolutionary consequences of seed pools. Am Nat 114:232–249

Zohary D (1970) Centers of diversity and centers of origin. In: Frankel OH, Bennett E (eds) Genetic resources in plants – their exploration and conservation. Blackwell, Oxford, pp 33–42

Zohary M (1973) Geobotanical foundations to the Middle East, vols 1 and 2. G Fischer, Stuttgart, and Swets and Zeitlinger, Amsterdam

Zohary D (1983) Wild genetic resources of crops in Israel. Isr J Bot 32:97–122

Appendix. Allele frequencies at 42 # loci of 37 populations of *Triticum dicoccoides* in Israel and Turkey

Locus	Population @																		
Allele $	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
N =	40	30	30	30	40	30	39	30	40	232	40	92	90	78	96	32	25	48	40
Aat-1A																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.013	0.0	0.0	0.0	0.0	0.0
(a) b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.978	1.000	0.961	1.000	1.000	1.000	0.978	1.000
c	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.022	0.0	0.026	0.0	0.0	0.0	0.0	0.0
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.022	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.044	0.0	0.076	0.0	0.0	0.0	0.043	0.0
Aat-1B																			
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.978	1.000	0.974	1.000	1.000	1.000	0.978	1.000
b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.022	0.0	0.026	0.0	0.0	0.0	0.022	0.0
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.044	0.0	0.051	0.0	0.0	0.0	0.043	0.0
Aat-2A																			
a	0.0	0.0	0.0	0.0	0.026	0.0	0.378	0.0	0.175	0.009	0.050	0.157	0.126	0.052	0.073	0.0	0.0	0.380	0.0
b	1.000	1.000	1.000	1.000	0.974	1.000	0.622	1.000	0.825	0.991	0.950	0.843	0.874	0.948	0.927	1.000	1.000	0.620	1.000
He	0.0	0.0	0.0	0.0	0.050	0.0	0.470	0.0	0.289	0.017	0.095	0.265	0.221	0.098	0.135	0.0	0.0	0.471	0.0
Aat-3A																			
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.996	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.004	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.009	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acph-3																			
a	0.0	–	–	–	0.026	–	0.590	–	0.0	0.022	0.975	0.136	0.0	0.265	0.0	0.0	0.0	0.0	0.0
b	1.000	–	–	–	0.949	–	0.410	–	0.821	0.957	0.025	0.755	0.852	0.720	0.765	1.000	1.000	0.894	1.000
c	0.0	–	–	–	0.026	–	0.0	–	0.179	0.022	0.0	0.109	0.148	0.015	0.235	0.0	0.0	0.106	0.0
He	0.0	–	–	–	0.099	–	0.484	–	0.295	0.084	0.049	0.400	0.252	0.412	0.360	0.0	0.0	0.190	0.0
Acph-x																			
a	0.0	–	–	–	0.0	–	0.0	–	0.028	0.035	0.0	0.242	0.536	0.432	0.778	0.214	0.217	0.635	0.0
b	1.000	–	–	–	1.000	–	1.000	–	0.972	0.965	1.000	0.758	0.464	0.568	0.222	0.786	0.783	0.365	1.000
He	0.0	–	–	–	0.0	–	0.0	–	0.054	0.068	0.0	0.367	0.497	0.491	0.346	0.337	0.340	0.463	0.0
Adh-1A																			
a	0.162	0.750	1.000	1.000	1.000	1.000	0.794	0.588	1.000	1.000	0.868	0.591	0.080	0.842	0.029	1.000	1.000	1.000	1.000
b	0.838	0.250	0.0	0.0	0.0	0.0	0.206	0.412	0.0	0.0	0.132	0.409	0.920	0.158	0.971	0.0	0.0	0.0	0.0
He	0.272	0.375	0.0	0.0	0.0	0.0	0.327	0.484	0.0	0.0	0.229	0.483	0.147	0.266	0.056	0.0	0.0	0.0	0.0
Adh-1B																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.008	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.500	0.889
b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.992	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.500	0.111
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.016	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.500	0.198
Adh-2A																			
a	1.000	1.000	1.000	1.000	1.000	1.000	0.737	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
b	0.0	0.0	0.0	0.0	0.0	0.0	0.263	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.388	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Adh-2B																			
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Est-4A																			
a	0.946	1.000	1.000	1.000	1.000	1.000	0.897	1.000	0.853	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.800	1.000	1.000
b	0.054	0.0	0.0	0.0	0.0	0.0	0.103	0.0	0.147	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.200	0.0	0.0
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.102	0.0	0.0	0.0	0.0	0.0	0.185	0.0	0.251	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.320	0.0	0.0
Est-4B																			
a	0.432	0.091	0.0	0.0	0.897	0.0	0.029	0.0	0.471	0.0	0.362	0.0	0.0	0.0	0.0	0.250	0.200	0.0	0.471
b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.118	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
c	0.568	0.091	0.0	0.0	0.103	0.0	0.971	0.0	0.412	0.081	0.637	0.982	1.000	1.000	1.000	0.750	0.080	0.162	0.382
d	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.720	0.132	0.147
null	0.0	0.818	1.000	1.000	0.0	1.000	0.0	1.000	0.0	0.919	0.0	0.018	0.0	0.0	0.0	0.0	0.0	0.706	0.0
He	0.491	0.314	0.0	0.0	0.184	0.0	0.057	0.0	0.595	0.149	0.462	0.036	0.0	0.0	0.0	0.375	0.435	0.458	0.611

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	Mean
41	40	40	50	37	44	53	40	40	37	40	30	44	40	39	45	48	25	1815
0.0	0.0	0.0	0.047	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.002
1.000	1.000	1.000	0.953	0.892	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.993
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.002
0.0	0.0	0.0	0.0	0.108	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.003
0.0	0.0	0.0	0.089	0.193	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.012
1.000	1.000	1.000	0.930	0.892	1.000	1.000	1.000	1.000	0.946	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.992
0.0	0.0	0.0	0.0	0.108	0.0	0.0	0.0	0.0	0.054	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.006
0.0	0.0	0.0	0.070	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.002
0.0	0.0	0.0	0.130	0.193	0.0	0.0	0.0	0.0	0.102	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.015
0.0	0.0	0.0	0.191	0.0	0.545	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.063
1.000	1.000	1.000	0.809	1.000	0.455	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.937
0.0	0.0	0.0	0.310	0.0	0.496	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.079
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.025	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.977
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.975	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.023
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.049	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.002
0.0	0.0	0.0	0.021	0.0	0.013	0.0	0.0	0.0	0.065	0.0	0.0	0.057	0.0	0.0	0.0	0.0	0.043	0.064
1.000	1.000	1.000	0.938	0.852	0.961	1.000	1.000	0.0	0.887	0.725	1.000	0.943	1.000	1.000	1.000	1.000	0.957	0.861
0.0	0.0	0.0	0.042	0.148	0.026	0.0	0.0	1.000	0.048	0.275	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.075
0.0	0.0	0.0	0.119	0.252	0.077	0.0	0.0	0.0	0.207	0.399	0.0	0.107	0.0	0.0	0.0	0.0	0.083	0.121
0.0	0.225	0.0	0.875	0.0	0.0	0.769	0.0	0.0	0.0	0.400	1.000	0.0	0.0	1.000	0.425	0.024	0.083	0.249
1.000	0.775	1.000	0.125	1.000	1.000	0.231	1.000	1.000	1.000	0.600	0.0	1.000	1.000	0.0	0.575	0.976	0.917	0.751
0.0	0.349	0.0	0.219	0.0	0.0	0.355	0.0	0.0	0.0	0.480	0.0	0.0	0.0	0.0	0.489	0.048	0.153	0.158
0.969	1.000	0.967	1.000	0.964	1.000	0.809	1.000	1.000	1.000	0.974	1.000	1.000	1.000	1.000	1.000	1.000	0.727	0.843
0.031	0.0	0.033	0.0	0.036	0.0	0.191	0.0	0.0	0.0	0.026	0.0	0.0	0.0	0.0	0.0	0.0	0.273	0.157
0.061	0.0	0.064	0.0	0.069	0.0	0.310	0.0	0.0	0.0	0.051	0.0	0.0	0.0	0.0	0.0	0.0	0.397	0.097
0.094	0.0	0.0	0.0	0.214	0.0	0.0	0.0	0.0	0.0	0.026	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.044
0.906	1.000	1.000	1.000	0.786	1.000	1.000	1.000	1.000	1.000	0.974	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.956
0.170	0.0	0.0	0.0	0.337	0.0	0.0	0.0	0.0	0.0	0.050	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.034
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.994
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.006
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.010
1.000	1.000	0.297	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.984
0.0	0.0	0.703	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.016
0.0	0.0	0.418	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.011
1.000	1.000	1.000	0.971	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.781	–	0.981
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.011
0.0	0.0	0.0	0.029	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.219	–	0.008
0.0	0.0	0.0	0.056	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.342	–	0.035
0.838	1.000	1.000	0.014	0.0	0.0	0.0	0.359	1.000	0.0	0.895	0.0	0.0	1.000	0.0	0.0	0.0	–	0.239
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.513	0.198	0.125	–	0.027
0.162	0.0	0.0	0.114	0.0	0.614	1.000	0.641	0.0	0.027	0.105	0.0	0.179	0.0	0.487	0.802	0.875	–	0.413
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.019
0.0	0.0	0.0	0.871	1.000	0.386	0.0	0.0	0.0	0.973	0.0	1.000	0.821	0.0	0.0	0.0	0.0	–	0.302
0.272	0.0	0.0	0.227	0.0	0.474	0.0	0.460	0.0	0.053	0.188	0.0	0.295	0.0	0.500	0.317	0.219	–	0.199

Appendix. (continued)

Locus	Population @																		
Allele $	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
N =	40	30	30	30	40	30	39	30	40	232	40	92	90	78	96	32	25	48	40
Est-5A $																			
a	1.000	0.857	1.000	0.828	0.077	0.933	1.000	0.593	0.921	0.724	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.870
b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.074
c	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.026	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
d	0.0	0.107	0.0	0.0	0.923	0.0	0.0	0.037	0.0	0.250	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.056
e	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.079	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
null	0.0	0.036	0.0	0.172	0.0	0.067	0.0	0.370	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.253	0.0	0.285	0.142	0.124	0.0	0.510	0.145	0.413	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.234
Est-5B $ (a = null)																			
a	0.921	0.893	0.867	0.414	0.974	0.300	1.000	0.926	1.000	0.777	0.972	0.193	0.218	0.396	0.936	1.000	1.000	0.340	0.926
b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.004	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.404	0.0
c	0.053	0.107	0.133	0.586	0.026	0.700	0.0	0.074	0.0	0.129	0.028	0.096	0.172	0.026	0.0	0.0	0.0	0.255	0.074
d	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
e	0.026	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.080	0.0	0.711	0.609	0.578	0.064	0.0	0.0	0.0	0.0
f	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.009	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.148	0.191	0.231	0.485	0.050	0.420	0.0	0.137	0.0	0.373	0.054	0.448	0.551	0.508	0.120	0.0	0.0	0.656	0.137
Gdh-A																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(a) b	1.000	1.000	0.967	0.967	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
c	0.0	0.0	0.033	0.033	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.064	0.064	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gdh-B																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(a) b	0.950	1.000	0.900	1.000	0.950	1.000	1.000	0.833	1.000	1.000	0.975	1.000	1.000	1.000	1.000	1.000	0.880	1.000	0.925
(b) c	0.050	0.0	1.000	0.0	0.050	0.0	0.0	0.167	0.0	0.0	0.025	0.0	0.0	0.0	0.0	0.0	0.120	0.0	0.075
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.095	0.0	0.180	0.0	0.095	0.0	0.0	0.278	0.0	0.0	0.049	0.0	0.0	0.0	0.0	0.0	0.211	0.0	0.139
Gluc-B $																			
a	0.088	0.931	0.192	0.172	0.043	0.172	1.000	0.133	0.050	0.194	1.000	1.000	1.000	0.984	0.844	0.0	0.040	–	0.175
b	0.912	0.069	0.692	0.828	0.957	0.828	0.0	0.867	0.950	0.806	0.0	0.0	0.0	0.016	0.156	1.000	0.960	–	0.825
c	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0
null	0.0	0.0	0.115	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0
He	0.161	0.128	0.470	0.285	0.083	0.285	0.0	0.231	0.095	0.313	0.0	0.0	0.0	0.031	0.263	0.0	0.077	–	0.289
Hk																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.137	0.0	0.191	0.0	0.250	0.0	0.0	0.0	0.0	0.0
(a) b	1.000	0.111	0.360	0.700	1.000	0.759	0.0	0.310	1.000	0.740	0.0	0.723	1.000	0.203	0.687	1.000	1.000	0.960	1.000
(b) c	0.0	0.889	0.640	0.300	0.0	0.241	1.000	0.690	0.0	0.123	1.000	0.085	0.0	0.547	0.313	0.0	0.0	0.0	0.0
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.040	0.0
He	0.0	0.198	0.461	0.420	0.0	0.366	0.0	0.428	0.0	0.419	0.0	0.433	0.0	0.597	0.430	0.0	0.0	0.077	0.0
Ipol																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
b	1.000	0.966	0.524	1.000	0.0	0.185	1.000	0.483	1.000	0.879	1.000	0.700	0.830	0.935	1.000	1.000	0.640	1.000	1.000
c	0.0	0.034	0.476	0.0	1.000	0.815	0.0	0.517	0.0	0.121	0.0	0.300	0.170	0.065	0.0	0.0	0.360	0.0	0.0
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.067	0.499	0.0	0.0	0.302	0.0	0.499	0.0	0.213	0.0	0.420	0.283	0.121	0.0	0.0	0.461	0.0	0.0
Ipor-A																			
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.977	1.000	1.000	1.000	1.000
b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.023	0.0	0.0	0.0	0.0
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.045	0.0	0.0	0.0	0.0
Ipor-B																			
a	1.000	0.233	1.000	0.967	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.969	0.813	1.000	0.602	1.000
b	0.0	0.767	0.0	0.033	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.031	0.188	0.0	0.398	0.0
He	0.0	0.358	0.0	0.064	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.061	0.305	0.0	0.479	0.0

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	Mean
41	40	40	50	37	44	53	40	40	37	40	30	44	40	39	45	48	25	1815
1.000	0.275	1.000	0.990	0.200	0.0	0.811	0.0	0.0	0.0	0.575	1.000	1.000	0.150	0.974	1.000	1.000	1.000	0.767
0.0	0.725	0.0	0.0	0.0	0.0	0.189	0.0	0.0	0.0	0.150	0.0	0.0	0.850	0.0	0.0	0.0	0.0	0.046
0.0	0.0	0.0	0.0	0.486	0.0	0.0	0.0	0.0	1.000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.034
0.0	0.0	0.0	0.0	0.143	0.0	0.0	0.425	0.025	0.0	0.275	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.076
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.002
0.0	0.0	0.0	0.010	0.171	1.000	0.0	0.575	0.975	0.0	0.0	0.0	0.0	0.0	0.026	0.0	0.0	0.0	0.075
0.0	0.399	0.0	0.020	0.674	0.0	0.306	0.489	0.049	0.0	0.571	0.0	0.0	0.255	0.050	0.0	0.0	0.0	0.133
1.000	0.825	0.325	0.200	0.343	0.0	0.0	1.000	1.000	1.000	1.000	0.276	1.000	1.000	0.846	0.216	0.405	0.080	0.634
0.0	0.0	0.0	0.120	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.015
0.0	0.175	0.675	0.680	0.657	1.000	1.000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.154	0.784	0.405	0.440	0.219
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.724	0.0	0.0	0.0	0.0	0.0	0.0	0.012
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.190	0.480	0.118
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001
0.0	0.289	0.439	0.483	0.451	0.0	0.0	0.0	0.0	0.0	0.0	0.400	0.0	0.0	0.260	0.339	0.636	0.570	0.226
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.308	0.0	0.229	0.0	0.013
1.000	1.000	1.000	1.000	0.706	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.692	1.000	0.771	1.000	0.980
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001
0.0	0.0	0.0	0.0	0.294	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.006
0.0	0.0	0.0	0.0	0.415	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.426	0.0	0.353	0.0	0.036
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.150	0.0	0.0	0.0	0.0	0.003
1.000	1.000	1.000	1.000	0.706	1.000	1.000	1.000	1.000	1.000	0.975	1.000	1.000	0.850	0.692	1.000	0.771	1.000	0.967
0.0	0.0	0.0	0.0	0.294	0.0	0.0	0.0	0.0	0.0	0.025	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.017
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.308	0.0	0.229	0.0	0.013
0.0	0.0	0.0	0.0	0.415	0.0	0.0	0.0	0.0	0.0	0.049	0.0	0.0	0.255	0.426	0.0	0.353	0.0	0.069
0.0	0.0	0.0	–	–	–	0.0	0.0	0.0	–	0.421	0.0	–	0.0	0.0	0.0	0.0	0.0	0.331
1.000	1.000	1.000	–	–	–	1.000	1.000	1.000	–	0.579	1.000	–	1.000	0.846	0.867	1.000	1.000	0.658
0.0	0.0	0.0	–	–	–	0.0	0.0	0.0	–	0.0	0.0	–	0.0	0.154	0.133	0.0	0.0	0.009
0.0	0.0	0.0	–	–	–	0.0	0.0	0.0	–	0.0	0.0	–	0.0	0.0	0.0	0.0	0.0	0.002
0.0	0.0	0.0	–	–	–	0.0	0.0	0.0	–	0.488	0.0	–	0.0	0.260	0.231	0.0	0.0	0.119
0.0	0.0	0.0	0.0	0.0	0.0	–	–	–	0.0	0.0	–	0.0	–	0.0	0.0	0.0	–	0.033
1.000	1.000	1.000	1.000	1.000	1.000	–	–	–	1.000	1.000	–	1.000	–	1.000	1.000	1.000	–	0.778
0.0	0.0	0.0	0.0	0.0	0.0	–	–	–	0.0	0.0	–	0.0	–	0.0	0.0	0.0	–	0.189
0.0	0.0	0.0	0.0	0.0	0.0	–	–	–	0.0	0.0	–	0.0	–	0.0	0.0	0.0	–	0.001
0.0	0.0	0.0	0.0	0.0	0.0	–	–	–	0.0	0.0	–	0.0	–	0.0	0.0	0.0	–	0.123
0.146	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	–	0.0	–	0.0	0.0	0.0	–	0.005
0.829	1.000	1.000	1.000	1.000	1.000	0.0	0.0	–	1.000	0.750	–	1.000	–	1.000	1.000	1.000	–	0.821
0.0	0.0	0.0	0.0	0.0	0.0	1.000	1.000	–	0.0	0.0	–	0.0	–	0.0	0.0	0.0	–	0.164
0.024	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.250	–	0.0	–	0.0	0.0	0.0	–	0.009
0.290	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.375	–	0.0	–	0.0	0.0	0.0	–	0.107
0.854	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.996
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001
0.146	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.003
0.250	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.008
0.634	0.359	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.862	0.069	0.989	1.000	1.000	1.000	1.000	0.960	0.930
0.366	0.641	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.137	0.931	0.011	0.0	0.0	0.0	0.0	0.040	0.070
0.464	0.460	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.237	0.128	0.022	0.0	0.0	0.0	0.0	0.077	0.072

Appendix. (continued)

Locus	Population @																		
Allele $	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
N =	40	30	30	30	40	30	39	30	40	232	40	92	90	78	96	32	25	48	40
Mdh-1A																			
a	0.057	0.759	0.167	0.138	0.014	0.100	1.000	0.100	0.0	0.085	0.947	0.460	1.000	0.897	0.851	0.0	0.0	0.0	0.0
b	0.943	0.241	0.833	0.862	0.986	0.900	0.0	0.900	1.000	0.915	0.053	0.540	0.0	0.103	0.149	1.000	1.000	1.000	1.000
He	0.108	0.366	0.278	0.238	0.027	0.180	0.0	0.180	0.0	0.155	0.100	0.497	0.0	0.185	0.254	0.0	0.0	0.0	0.0
Mdh-1B																			
a	1.000	0.966	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
null	0.0	0.034	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.067	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mdh-2																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(a) b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.996	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00
c	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.004	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
d	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.009	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nadhd-1A																			
a	0.0	0.0	0.0	0.0	0.0	1.000	0.0	0.0	0.350	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
b	0.625	1.000	1.000	1.000	0.218	0.0	1.000	1.000	0.650	1.000	1.000	1.000	1.000	1.000	1.000	0.906	1.000	0.897	1.000
c	0.375	0.0	0.0	0.0	0.782	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.094	0.0	0.103	0.0
He	0.469	0.0	0.0	0.0	0.341	0.0	0.0	0.0	0.455	0.0	0.0	0.0	0.0	0.0	0.0	0.170	0.0	0.184	0.0
Nadhd-1B																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(a) b	1.000	1.000	1.000	1.000	1.000	0.0	1.000	1.000	0.438	0.876	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
(b) c	0.0	0.0	0.0	0.0	0.0	1.000	0.0	0.0	0.563	0.124	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.492	0.217	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nadhd-2A																			
a	0.0	–	–	–	0.0	–	0.0	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.071	0.0
(a) b	1.000	–	–	–	0.950	–	1.000	–	0.825	0.947	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.857	1.000
(b) c	0.0	–	–	–	0.050	–	0.0	–	0.175	0.053	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.071	0.0
He	0.0	–	–	–	0.095	–	0.0	–	0.289	0.100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.255	0.0
Pepc																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(a) b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.961	1.000
c	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.039	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.076	0.0
Pept-1A																			
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.960	1.000	1.000	1.000	1.000	1.000
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.040	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.077	0.0	0.0	0.0	0.0	0.0
Pept-1B																			
a	0.0	0.720	0.200	0.069	0.0	0.533	1.000	0.100	0.0	0.038	0.679	0.639	0.651	0.850	0.632	0.031	0.100	0.064	0.0
b	1.000	0.280	0.800	0.931	1.000	0.467	0.0	0.900	1.000	0.962	0.321	0.361	0.349	0.150	0.368	0.969	0.900	0.936	1.000
He	0.0	0.403	0.320	0.128	0.0	0.498	0.0	0.180	0.0	0.074	0.436	0.461	0.455	0.255	0.465	0.061	0.180	0.120	0.0
Pept-2																			
a	0.692	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
b	0.308	0.583	1.000	1.000	1.000	1.000	1.000	1.000	1.000	–	0.975	1.000	1.000	1.000	1.000	0.469	1.000	0.444	0.225
c	0.0	0.417	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.025	0.0	0.0	0.0	0.0	0.531	0.0	0.556	0.775
He	0.426	0.486	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.049	0.0	0.0	0.0	0.0	0.498	0.0	0.494	0.349
Pgi-A																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.030	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
b	0.0	0.0	0.033	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(a) c	0.0	0.0	0.300	0.0	0.025	0.067	0.026	0.267	0.675	0.387	0.188	0.275	0.488	0.107	0.211	0.0	0.625	0.047	0.0
(b) d	1.000	0.933	0.667	1.000	0.975	0.933	0.974	0.733	0.325	0.583	0.813	0.703	0.512	0.893	0.789	1.000	0.375	0.919	0.412
(c) e	0.0	0.067	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.022	0.0	0.0	0.0	0.0	0.0	0.035	0.587
He	0.0	0.124	0.464	0.0	0.049	0.124	0.051	0.391	0.439	0.510	0.305	0.429	0.500	0.191	0.332	0.0	0.469	0.153	0.485

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	Mean
41	40	40	50	37	44	53	40	40	37	40	30	44	40	39	45	48	25	1815
0.0	0.059	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.230
1.000	0.941	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.770
0.0	0.111	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.072
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.999
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.002
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.013	0.0	0.073	0.0	0.002
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.0	1.000	1.000	1.000	0.850	0.987	1.000	0.927	0.440	0.965
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.021
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.150	0.0	0.0	0.0	0.560	0.011
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.255	0.025	0.0	0.135	0.493	0.025
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.011
0.902	0.308	1.000	1.000	0.865	0.0	1.000	0.0	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.889	1.000	1.000	0.874
0.098	0.692	0.0	0.0	0.135	1.000	0.0	1.000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.111	0.0	0.0	0.115
0.176	0.426	0.0	0.0	0.234	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.198	0.0	0.0	0.072
0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.000	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.026
1.000	1.000	1.000	0.868	1.000	1.000	1.000	0.0	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.947
0.0	0.0	0.0	0.132	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.027
0.0	0.0	0.0	0.229	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.025
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.436	0.0	0.042	0.0	0.014
1.000	1.000	0.975	0.988	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.564	1.000	0.958	1.000	0.972
0.0	0.0	0.025	0.012	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.014
0.0	0.0	0.049	0.024	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.492	0.0	0.080	0.0	0.043
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.000	0.105	0.0	0.0	0.025
1.000	1.000	1.000	1.000	1.000	0.977	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.0	0.0	0.925	0.0	0.932
0.0	0.0	0.0	0.0	0.0	0.023	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.895	0.075	1.000	0.043
0.0	0.0	0.0	0.0	0.0	0.044	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.188	0.139	0.0	0.012
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.999
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.002
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.385	0.0	0.0	0.0	1.000	1.000	1.000	1.000	0.291
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.615	1.000	1.000	1.000	0.0	0.0	0.0	0.0	0.709
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.473	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.122
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.028
1.000	1.000	1.000	0.860	1.000	0.875	1.000	1.000	1.000	1.000	0.900	1.000	1.000	1.000	1.000	1.000	1.000	–	0.882
0.0	0.0	0.0	0.140	0.0	0.125	0.0	0.0	0.0	0.0	0.100	0.0	0.0	0.0	0.0	0.0	0.0	–	0.090
0.0	0.0	0.0	0.240	0.0	0.219	0.0	0.0	0.0	0.0	0.180	0.0	0.0	0.0	0.0	0.0	0.0	–	0.084
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.004
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001
0.0	0.0	0.0	0.422	0.270	0.0	0.0	0.395	1.000	0.0	0.025	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.191
0.756	1.000	1.000	0.022	0.703	1.000	1.000	0.605	0.0	1.000	0.975	0.0	1.000	0.154	1.000	0.867	1.000	1.000	0.730
0.244	0.0	0.0	0.556	0.027	0.0	0.0	0.0	0.0	0.0	0.0	1.000	0.0	0.846	0.0	0.133	0.0	0.0	0.075
0.369	0.0	0.0	0.513	0.432	0.0	0.0	0.478	0.0	0.0	0.049	0.0	0.0	0.260	0.0	0.231	0.0	0.0	0.199

Appendix. (continued)

Locus	Population @																		
Allele $	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
N =	40	30	30	30	40	30	39	30	40	232	40	92	90	78	96	32	25	48	40
Pgi-B																			
a	1.000	1.000	0.933	1.000	1.000	1.000	1.000	0.433	1.000	0.252	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.953	1.000
b	0.0	0.0	0.067	0.0	0.0	0.0	0.0	0.567	0.0	0.748	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.047	0.0
He	0.0	0.0	0.124	0.0	0.0	0.0	0.0	0.491	0.0	0.377	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.089	0.0
Pgm-A																			
a	0.0	0.0	0.033	0.0	0.063	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
b	1.000	1.000	0.967	1.000	0.938	1.000	1.000	1.000	1.000	1.000	1.000	0.807	0.909	1.000	1.000	1.000	1.000	1.000	1.000
null	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.193	0.091	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.064	0.0	0.117	0.0	0.0	0.0	0.0	0.0	0.0	0.312	0.165	0.0	0.0	0.0	0.0	0.0	0.0
6*Pgd*-1 A																			
a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
He	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6*Pgd*-1 B																			
a	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(a) b	0.865	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.935	1.000	1.000	1.000
(b) c	0.135	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.065	0.0	0.0	0.0
He	0.234	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.121	0.0	0.0	0.0
6*Pgd*-2																			
a	1.000	0.241	0.800	0.897	1.000	0.867	0.0	0.900	0.629	0.890	0.329	0.222	0.081	0.263	0.101	1.000	1.000	1.000	1.000
b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.314	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
c	0.0	0.759	0.200	0.103	0.0	0.133	1.000	0.100	0.057	0.110	0.671	0.778	0.919	0.737	0.899	0.0	0.0	0.0	0.0
He	0.0	0.366	0.320	0.185	0.0	0.231	0.0	0.180	0.503	0.196	0.441	0.346	0.150	0.388	0.182	0.0	0.0	0.0	0.0

@ Population numbers refer to those listed in Table 1

List of the 5 monomorphic loci, and the designation of their alleles: *Aat*-3B a, *Aat*-2B a, *Cat*-A a, *Cat*-B a, *Pgm*-B a

$ Allele designation (in parenthesis) in Nevo et al. (1982). The designation of the alleles of *Est*-5A, B and *Gluc*-B is entirely new

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	Mean
41	40	40	50	37	44	53	40	40	37	40	30	44	40	39	45	48	25	1815
1.000	1.000	1.000	0.844	0.541	0.186	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.859
0.0	0.0	0.0	0.156	0.459	0.814	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.141
0.0	0.0	0.0	0.263	0.497	0.303	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.058
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.002
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.984
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.014
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.018
1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.750	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.994
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.250	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.006
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.375	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.010
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.250	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.006
1.000	1.000	1.000	0.974	1.000	1.000	1.000	0.750	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.990
0.0	0.0	0.0	0.026	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.005
0.0	0.0	0.0	0.051	0.0	0.0	0.0	0.375	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.021
0.941	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.0	1.000	1.000	1.000	1.000	1.000	1.000	0.719
0.059	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.000	0.0	0.0	0.0	0.0	0.0	0.0	0.027
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.254
0.111	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.097