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Photosynthetic performance in wild emmer wheat, *Triticum dicoccoides*: ecological and genetic predictability

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Summary. In a twin study, we have shown that wild emmer wheat, *Triticum dicoccoides*, the progenitor of all cultivated wheats, harbours important genetic variation (Vg) in photosynthetic characteristics. This Vg resides within and between populations and ecogeographical regions in Israel, which is the center of origin and diversity of wild emmer wheat. Here we analyzed, by univariate and multivariate methods, the significant differentiation of variation in photosynthetic characteristics of 107 genotypes from 27 populations of wild emmer in Israel, distributed in three ecogeographical regions including central, xeric (northern cold and eastern warm) marginal, and mesic (western) marginal populations. The highest photosynthetic efficiency was displayed by populations of the xeric marginal region, but most variation for photosynthetic capacity occurs between accessions within ecogeographical regions and populations. Genotypes and populations of *T. dicoccoides* having high photosynthetic capacity can be identified by climatic factors and isozyme markers. The identification by genetic markers, if substantiated by testcrosses, can facilitate the maximization of conservation, in situ or ex situ, and utilization of these photosynthetic genetic resources for improvement of hexaploid wheat (*T. aestivum*).

Key words: Photosynthesis – Genetic resources – *Triticum dicoccoides* – Allozyme polymorphisms – Natural selection

Introduction

Genetic improvement of crops is essential in view of the general genetic homogenization of cultivars. Remarkably, while crop yields have generally been increasing recently, due in part to improved agrotechniques (e.g., Avery 1985), the genetic base of most of the important food crops has been rapidly narrowing (Plucknett et al. 1983). This is due to the global extension of modern pure breeding practices, which increase genetic homogeneity (Frankel and Bennett 1970; Frankel and Hawkes 1975; Frankel and Soulé 1980; Harlan 1975, 1976). Amelioriation of this trend lies in the utilization of genetic resources from the wild progenitors of cultivars (e.g., Feldman and Sears 1981). A global network of gene banks has been established to provide plant breeders with the genetic resources for crop improvement (Plucknett et al. 1983). However, the conservation of diverse germ plasm, either ex or in situ, is insufficient. To achieve more efficient and comprehensive utilization of the conserved gene pool, it is essential to predict, screen, and evaluate promising genetic resources in wild populations (Marshall and Brown 1981; Nevo 1987).

The Near East Fertile Crescent is very rich in wild relatives of cultivated plants, and represents a major source of plant cultivation. Old World wild wheat, barley, oats, and rye are the traditional cereal crops of the Old World belt of Mediterranean agriculture (Zohary 1983). The Near East Fertile Crescent, and Israel in particular (Nevo 1986), represent the major center of origin and diversity of wheat, barley, and oats. Here, these crops built up a wealth of genetic diversity throughout their evolutionary history, as a result of selective pressures by parasites and environmental heterogeneity and stresses. This variation is neither random nor neutral. On the contrary, it displays at all levels adaptive genetic diversity for biochemical, morphological, and immunological characteristics, which contribute to its adaptive nature to mountaintops and lowlands, mesic and xeric habitats, and different soil types (Nevo and Beiles 1989).

Genetic resources of wild emmer wheat, *T. dicoccoides* (reviewed in Nevo 1983, 1988 a) across the Fertile Crescent, have been studied at the Institute of Evolution, University of Haifa. Wild emmer wheat, genomic constitution AB, is the tetraploid wild progenitor from which all wheats originated (Zohary 1970; Kimber and Feldman 1987). It hybridizes with cultivated tetraploid wheats, and gene transfer from wild to hexaploid cultivated wheats is possible through a partially fertile, pentaploid bridge (Grama and Gerechter-Amitai 1974). Wild emmer is distributed throughout the Near East Fertile Crescent (Harlan and Zohary 1966), but its center of distribution is in the catchment area of the upper Jordan River in Israel. For its ecology see Nevo et al. (1982), and for its population genetic structure, differentiation, and evolution see Nevo and Beiles (1989).

Multidisciplinary studies of wild emmer wheat were conducted from 1982 to 1987 at the Institute of Evolution, University of Haifa, and have been reviewed by Nevo (1988 a). The following aspects were discussed: (i) population genetics and ecology at the micro- and macrogeographical levels in Israel and Turkey; (ii) genetic resources of disease resistances; (iii) wheat storage proteins; (a) protein content; (b) diversity of HMW glutenin subunits; (iv) rDNA diversity; and (v) plant genetic resources: predictability by isozyme markers and ecology. It was concluded that the rich genetic diversity of wild emmer for multiple disease resistances, elite agronomic traits, and environmental adaptations is geographically structured and predictable by ecology, and by allozyme and DNA markers. Consequently, sampling strategies in nature could be optimized by following ecological and genetic factors as guidelines for conservation and utilization in wheat improvement (Nevo 1987). We have recently added variation in photosynthetic capacity to our research program of wild emmer.

Genetic diveristy of photosynthetic characters in 107 accessions from 27 populations of wild emmer wheat from Israel were summarized by Carver and Nevo (1990). Accessions sampled in the center of wild emmer distribution (upper Jordan Valley) in a relatively narrow geographical range showed the greatest diversity in CO_2 assimilation rate per unit leaf area (A) or per unit chlorophyll (A/Chl). Genetic variation was absent for internal CO_2 concentration (C) and water-use efficiency (WUE), and generally lacking for stomatal conductance (g_s). Leaf area, although quite variable, was not a significant cofactor in assessing genetic potential for photosynthesis. Accessions within a given population showed ten times more variation in A and A/Chl than populations sampled from different locations in a region. Accessions with the highest photosynthetic effeciency were derived from xeric marginal habitats in the Judean and Samarian Mountains in Israel. Some accessions having high photosynthetic capacity ($A = 32\ \mu mol\ m^{-2}\ s^{-1}$) with no significant reduction in leaf size constitute a potentially valuable genetic resource, as yet untapped for genetic improvement of hexaploid wheat (*T. aestivum* L.). Our objectives in the present study were to determine if the genetic diversity underlying photosynthetic capacity in wild emmer is predictable by ecological factors and allozyme markers, as previously found for other characters (Nevo 1987).

Materials and methods

Genetic materials

Seeds of wild emmer wheat were collected from 27 populations at 23 locations distributed across the major ecogeographical range in Israel (Fig. 1, Table 1). Each population comprised four random, single-plant-derived accessions. The same population numbering system appearing in Table 1 was used previously in a larger sample of populations (Nevo and Beiles 1989). In addition to the macrogeographical study, we also sampled two microgeographical subpopulations at Yehudiyya (sun versus shade) (Nevo et al. 1988 a). Furthermore, two subpopulations were sampled at Tabigha along two north-south transects (100 m long) traversing two soil types (Nevo et al. 1988 b). Two random accessions from each transect were chosen for this study to represent each soil type. Subpopulations at Yehudiyya were sampled by collecting seed from pairs of plants under (shade) and outside (sun) individual tree canopies in an open Tabor oak forest. Subpopulations were separated by only a few meters. Macrogeographical and climatological data appear in Table 1.

The 27 populations (108 accessions) were assigned to three sets of nine populations (36 accessions per set), each set repre-

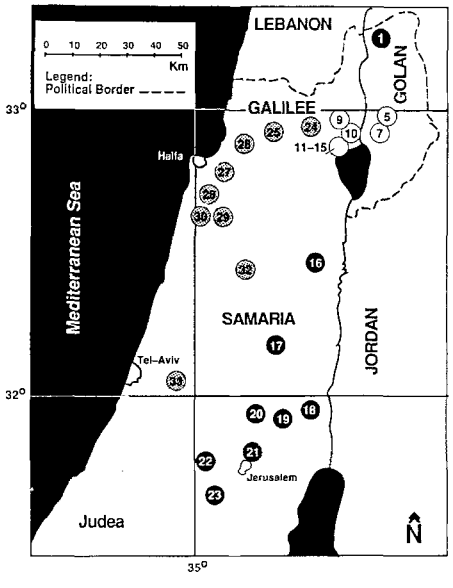

Fig. 1. Geographic distribution of 27 populations, tested for photosynthetic capacity, from three ecogeographical regions of wild emmer wheat, *Triticum dicoccoides*, in Israel. For names of numbered populations see Table 1. Central populations are indicated by *white circles*, mesic (western) populations by *grey circles*, and xeric (northern and eastern) populations by *black circles*

Table 1. Geographical and climatological data for 27 populations of *Triticum dicoccoides* in Israel, included in the photosynthetic yield study

No.[a]	Population	N	Ln	Lt	Al	Tm	Ta	Tj	Td	Tdd	Rn	Rd	Hu 14	Hu an	Dw	Sh	Th	Trd	Ev	Sz	Ma	So	Rv	Rr	Rad
1 (1)	Mt. Hermon	4	35.73	33.30	1,300	11	21	3	18	6	1,400	66	48	60	60	80	–	0	150	2	1	1	30	20	185[b]
5 (2)	Qazrin	4	35.67	32.99	350	18	26	10	16	12	530	50	43	58	58	50	–	60	155	3	5	5	39	26	189[b]
7 (3)	Yehudiyya	4	35.70	32.93	200	19	27	11	16	12	550	47	42	58	58	50	–	100	160	3	5	5	38	25	189[b]
7a (3)	Yehudiyya-shade	4	35.70	32.93	200	19	27	11	16	12	550	47	42	58	58	50	–	100	160	3	5	5	38	25	–
7b (3)	Yehudiyya-sun	4	35.70	32.93	200	19	27	11	16	12	550	47	42	58	58	50	–	100	160	3	5	5	38	25	189[b]
9 (4)	Rosh-Pinna	4	35.52	32.95	700	18	25	9	16	10	697	50	48	58	50	75	–10	35	150	3	5	1	35	22	184
10	Ammiad	4	35.52	32.92	270	19	26	10	16	10	700	48	48	58	50	70	–10	50	150	3	5	1	38	25	186
11 (5)	Tabigha	4	35.53	32.90	0	24	32	15	17	10	436	45	45	57	58	60	–30	120	160	3	5	5	39	25	188
13	Tabigha, basalt, 1985	4	35.53	32.90	0	24	32	15	17	10	436	45	45	57	58	60	–30	120	160	3	5	5	39	25	188
15	Tabigha, t.r., 1985	4	35.53	32.90	0	24	32	15	17	10	436	45	45	57	58	60	–30	120	160	3	5	1	39	25	188
16 (7)	Mt. Gilboa	4	35.42	32.50	150	21	28	12	16	12	400	44	43	58	40	60	–30	160	165	2	3	1	34	24	189
17 (8)	Mt. Gerizim	4	35.28	32.20	800	17	23	8	15	9	700	47	45	60	42	–	10	0	155	2	3	1	38	25	186
18	Gitit	4	35.40	32.10	300	21	29	13	16	12	360	39	39	55	25	–	–25	100	170	2	3	1	38	24	195
19 (9)	Kokhav Hashahar	4	35.34	31.95	600	20	28	12	16	12	400	40	45	59	30	80	–20	25	165	2	3	1	38	22	195
20 (10)	Taiyiba	4	35.30	31.95	450	19	26	10	16	12	400	40	44	58	30	80	–10	25	165	2	3	1	38	22	190
21 (11)	Sanhedriyya	4	35.22	31.80	800	17	24	9	15	9	548	44	51	62	44	102	–10	0	155	2	3	1	30	21	189
22 (12)	Bet-Meir	4	35.03	31.80	500	19	26	11	15	9	582	44	47	60	61	70	–10	100	160	2	3	1	33	25	183
23	Jaba	3	35.08	31.67	660	17	25	9	15	9	500	41	49	62	57	90	–20	30	155	2	3	1	35	21	186
24	Amirim	4	35.45	32.93	600	15	24	8	16	8	850	61	48	60	53	85	0	13	153	2	2	1	35	23	182
25	Nahef	4	35.32	32.93	275	15	24	8	15	9	670	54	49	62	57	62	10	3	155	1	2	1	33	22	181
26	Achihood	4	35.17	32.91	25	19	26	11	15	10	590	49	53	65	62	40	–5	20	148	1	2	1	30	21	180
27	Nesher	4	35.05	32.75	200	19	26	12	14	8	680	55	57	68	82	40	0	5	140	1	2	1	27	19	182
28	Beit-Oren	4	35.03	32.73	400	17	24	11	13	8	700	55	59	69	80	41	5	0	142	1	2	1	25	19	183
29	Daliyya	4	35.06	32.59	200	19	26	12	14	11	670	55	57	67	78	50	–10	100	160	1	2	2	25	20	181
30 (6)	Bat-Shelomo	4	35.02	32.60	75	20	26	13	13	10	650	55	58	68	77	40	–10	30	150	2	2	2	24	20	182
32	Yabad	4	35.15	32.44	375	19	25	11	14	11	550	50	48	63	65	52	–15	160	165	2	2	2	33	22	180
33	Givat-Koach	4	34.92	32.03	75	20	26	12	14	12	540	46	50	64	65	42	–20	105	160	1	2	1	32	26	180

[a] Population numbers according to Nevo and Beiles 1989 and, in parenthesis, the numbers according to Nevo et al. 1982
[b] Estimated values of solar radiation by extrapolation

Symbols of variables

(i) Geographical: Ln = longitude, in decimals; Lt = latitude, in decimals; Al = altitude, in meters

(ii) 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

(iii) Water availability: Rn = mean annual rainfall, in mm; Rd = mean number of rainy days; Huan = mean annual humidity; Hu14 = mean humidity at 14:00 h; 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

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

(v) Biotic: Ma = marginality: 1 = North margin, 2 = West margin, 3 = South-east margin, 5 = central population; Sz = estimate of population size: 1 = small, (from a dozen to few hundred plants), 2 = intermediate, 3 = large

(vi) Solar radiation: Rad = total solar radiation per year

senting a major ecogeographical region of wild emmer distribution in Israel (Table 1, Fig. 1). *Central populations*, assigned to set 1 (5–15), were located in the catchment area of the upper Jordan River on the eastern slopes of the upper Galilee Mountains and the Golan Heights. These plants were robust and were continuously distributed on both terra-rossa and basalt soils. *Xeric margins:* the steppic, marginal populations assigned to set 2 (1, 16–23) were located primarily in eastern Samarian and the Judean Mountains (hot steppe) and one population (no. 1) was located at Mt. Hermon (cold steppe). These plants were generally slender and populations were semi-isolated or isolated on terra-rossa soils. *Mesic margins:* marginal populations from the mesic environment of the western and upper Galilee Mountains, Mt. Carmel, and the Coastal Plain were assigned to set 3 (24–33). These plants were also generally slender and populations were semi-isolated or isolated on terra-rossa as well as rendzina soils.

In addition to these 108 accessions, two plant introductions of *T. dicoccoides* (PI 428042 and PI 428109), representing low and high photosynthetic efficiency in the species (Johnson et al. 1987), were evaluated as checks (control genotypes). Their photosynthetic characteristics were described in detail by Johnson et al. (1988) and Carver et al. (1989), and were used here as a standard of comparison between experiments differing in genotypic composition. Since all replicates of one accession died, all analyses were conducted on at most 107 accessions.

Experimental procedures

To insure uniformity in emergence, all seeds were germinated at 4 °C in petri dishes lined with moistened filter paper before transplanting into pots. The unvernalized plants were then grown in controlled-environment chambers at 20 °C and 14 h light (600 μmol m^{-2} s^{-1} PPFD) for 6 weeks. Light intensity was gradually increased and decreased at the beginning and end, respectively, of the photoperiod each day. Other conditions of plant culture were described by Johnson et al. (1987). All accessions of a set were planted at the same time, but different sets were planted 2 weeks apart to facilitate sequential evaluation of sets at the same growth stage. Each accession was replicated twice (two plants per accession) and arranged in a randomized complete block design for each set in the growth chamber. Also randomized within each replicate were eight plants of each check.

Plants were transferred from the growth chamber to the laboratory to measure steady-state gas exchange characteristics on intact leaves in a temperature- and humidity-controlled reaction chamber, also described by Johnson et al. (1987). A single measurement was taken on the last fully emerged leaf of the main tiller from each plant. The following nine photosynthetic variables were used in this study (the abbreviation appears in parenthesis): (1) CO_2 assimilation rate per unit leaf area (A); (2) CO_2 assimilation rate per mole chlorophyll (A/Chl); (3) single leaf area (LA); (4) internal CO_2 concentration (Ci); (5) water-use efficiency (WUE); (6) stomatal conductance to water vapor (g_s); (7) chlorophyll a concentration (Chl a); (8) chlorophyll b concentration (Chl b); (9) total chlorophyll concentration (Chl total). Calculations of transpiration, A, g_s, and Ci were made according to Von Caemmerer and Farquhar (1981), and WUE was calculated as the ratio of A to transpiration. Chlorophyll concentration was determined using the method of Inskeep and Bloom (1985). The same leaf used to measure assimilation was also used to measure chlorophyll concentration and leaf area (LA).

Due to the time required to collect data for each plant (0.3–0.5 h), each replication was analyzed over 4 consecutive days (1 week). Thus, an entire set was analyzed over 2 consecutive weeks. Nine plants of the wild emmer collection were randomly selected from the appropriate replicate in the chamber and analyzed daily. One plant of each check (PI 428042 and PI 428109) was also measured. Both checks were measured every day for each replicate in all sets to monitor environmental fluctuations throughout the experiment and, thereby, allowed comparison among accessions of different sets. Because seeds of each check were provided by self-pollination of a single plant, any differences among plants were considered nongenetic.

Statistical analysis

We used the SPSS-x (1986) statistical package for conducting uni- and multivariate analyses, as well as the Spatial Autocorrelation Analysis Program, SAAP (Sokal and Oden 1978a, b; Sokal and Wartenberg 1983). Levels of significance for all statistical analyses are as follows: @ $=p<0.10$; * $=p<0.05$; ** $=p<0.01$; *** $=p<0.001$; NS $=p>0.10$. The partitioning of total variation into components representing sets, populations, and accessions within populations appears in Carver and Nevo (1990). In that study, we found the lack of a genetic component within sets in Ci and WUE; hence, we eliminated them from some of the multivariate analyses. Also, all chlorophyll estimates of the controls differed significantly between sets. We adjusted chlorophyll estimates of all our plants in accordance with these controls. The resulting adjusted estimates of chlorophyll variables (including A/Chl) are in line with the average of all controls.

Results

Photosynthetic performances of populations and ecogeographical sets

The three ecogeographical sets differed significantly in their photosynthetic yield as reflected by the nine photosynthetic variables (Table 2). Generally, in most photosynthetic variables, the differences among populations within sets were not significant. However, the three chlorophyll variables differed significantly between populations in the central and mesic marginal sets. Populations within the mesic marginal set also varied in leaf area (LA). In general, the xeric marginal set was superior in photosynthetic performance, based on A and A/Chl. Within this set the population of Sanhedriyya, near Jerusalem, ranked highest in photosynthetic performance (A and A/Chl), whereas Taiyiba was highest in chlorophyll content (Chl total). The best photosynthetic performers in the entire sample of 107 accessions analyzed were, first, from the central population of Ammiad (accession no. 10–165) combining the highest A with a large LA (A = 32.8; A/Chl = 44.6; LA = 5.635), and second, from the xeric population of Kokhav Hashahar (accession no. 19–46; A = 32.4; A/Chl = 46.1; LA = 3.325). For details of differential photosynthetic performance between sets and populations, see Table 2.

Discriminant analysis

We conducted stepwise discriminant analysis (SPSSx 1986) in an attempt to discriminate the three ecogeo-

Table 2. Photosynthetic performance of 27 populations of *Triticum dicoccoides* in Israel, partitioned into three ecogeographical sets: A. central, B1. xeric-cold margin (north), B2. xeric-warm margin (east and south), and C. mesic marginal (western) populations. The means and standard deviations are based on two replicates of four genotypes in each population

	Photosynthetic efficiency		Leaf area	Internal CO_2 concentration	Water use efficiency	Stomatal conductance	Chlorophyll concentration[a]		
	Leaf area (A) Mean+SD	Chlorophyll[a] (A/Chl) Mean+SD	(LA) Mean+SD	(Ci) Mean+SD	(WUE) Mean+SD	(g_s) Mean+SD	a (Chl a) Mean+SD	b (Chl b) Mean+SD	Total (Chl total) Mean+SD
A. *Central populations*									
5. Qazrin	25.5+3.72	29.2+ 3.83	6.6+0.88	209+11.4	4.90+0.494	0.367+0.0379	0.67+0.024	0.18+0.013	0.85+0.036
7. Yehudiyya	21.0+3.44	29.8+ 9.65	7.7+2.36	204+16.6	4.86+0.466	0.297+0.0684	0.54+0.134	0.18+0.050	0.73+0.089
71. Yehudiyya, shade	18.4+3.06	23.2+ 4.39	7.6+1.34	202+12.9	5.15+0.679	0.258+0.0579	0.61+0.071	0.15+0.021	0.77+0.088
72. Yehudiyya, sun	20.3+3.46	32.0+ 7.29	7.2+1.75	204+15.6	4.97+0.569	0.269+0.0246	0.52+0.052	0.12+0.020	0.65+0.071
9. Rosh-Pinna	23.7+5.36	27.5+ 7.56	6.7+0.94	221+25.6	4.64+0.764	0.375+0.1244	0.68+0.041	0.17+0.009	0.85+0.047
10. Ammiad	24.3+5.89	29.0+10.83	6.6+2.90	207+10.9	4.76+0.414	0.353+0.0943	0.67+0.051	0.17+0.013	0.85+0.062
11. Tabigha	22.1+4.26	26.6+ 4.45	7.6+1.62	201+12.7	5.13+0.494	0.299+0.0457	0.68+0.071	0.16+0.017	0.84+0.087
13. Tabigha, basalt	21.5+1.82	26.9+ 1.36	6.7+1.25	214+18.2	4.64+0.655	0.312+0.0091	0.63+0.060	0.15+0.026	0.79+0.090
15. Tabigha, terra-rossa	22.3+5.83	23.6+ 6.33	6.1+0.45	206+26.5	4.89+0.615	0.312+0.0533	0.72+0.023	0.19+0.020	0.90+0.043
Significance (ANOVA) p=	0.456	0.688	0.860	0.825	0.912	0.179	0.003	0.011	0.001
B1. *Xeric-cold marginal (northern) population*									
1. Mt. Hermon	23.5+3.68	31.9+4.15	4.1+0.67	234+ 8.0	4.36+0.268	0.387+0.0612	0.66+0.035	0.17+0.013	0.82+0.046
B. *Xeric-warm marginal (eastern and southern) populations*									
16. Mt. Gilboa	23.5+3.72	31.6+4.22	6.0+1.52	237+10.1	4.44+0.225	0.409+0.0982	0.67+0.055	0.17+0.014	0.84+0.070
17. Mt Gerizim	21.6+2.55	30.7+0.30	5.6+2.08	230+ 6.8	4.69+0.333	0.348+0.0493	0.64+0.094	0.16+0.023	0.79+0.116
18. Gitit	24.4+3.92	34.5+4.43	5.3+0.82	246+14.9	4.07+0.497	0.461+0.0570	0.60+0.030	0.16+0.011	0.76+0.033
19. Kokhav Hashahar	25.5+6.35	34.6+7.85	3.7+0.47	234+ 5.8	4.29+0.363	0.431+0.1248	0.65+0.103	0.17+0.029	0.81+0.129
20. Taiyiba	26.7+1.55	32.9+1.53	4.4+1.23	238+ 5.5	4.24+0.389	0.472+0.0363	0.73+0.051	0.18+0.014	0.91+0.066
21. Sanhedriyya	28.5+1.33	36.4+2.38	4.9+0.84	239+ 5.2	4.49+0.155	0.508+0.0523	0.69+0.055	0.16+0.017	0.85+0.068
22. Bet-Meir	26.3+2.30	36.1+2.85	3.8+0.53	237+ 6.9	4.25+0.094	0.460+0.0512	0.63+0.051	0.15+0.016	0.78+0.063
23. Jaba	26.4+0.11	33.7+0.70	4.6+0.21	228+12.1	4.43+0.655	0.424+0.0473	0.71+0.008	0.18+0.012	0.88+0.008
Signif. (ANOVA, B1+B2) p=0.209		0.433	0.078	0.246	0.468	0.103	0.153	0.237	0.213
C. *Mesic marginal (western) populations*									
24. Amirim	24.4+2.51	27.5+2.83	5.3+0.86	222+ 8.8	5.06+0.513	0.361+0.0828	0.68+0.062	0.16+0.014	0.84+0.076
25. Nahef	22.5+3.70	23.9+3.97	6.0+0.74	219+ 9.2	5.18+0.687	0.340+0.0446	0.70+0.023	0.16+0.003	0.86+0.024
26. Achihood	23.5+4.72	26.6+5.56	6.9+0.98	219+13.6	5.11+0.218	0.349+0.1085	0.68+0.020	0.16+0.006	0.83+0.025
27. Nesher	21.4+1.88	25.7+4.11	5.3+0.73	226+ 4.5	4.67+0.403	0.323+0.0404	0.65+0.047	0.15+0.009	0.80+0.040
28. Beit-Oren	22.4+4.17	23.9+5.38	7.2+2.23	219+ 7.9	5.09+0.220	0.341+0.0720	0.71+0.025	0.16+0.009	0.87+0.035
29. Daliyya	23.2+2.37	29.9+3.74	5.4+0.71	217+ 4.0	5.06+0.440	0.340+0.0388	0.62+0.011	0.14+0.007	0.75+0.015
30. Bat-Shelomo	20.8+4.29	24.4+4.70	6.3+0.87	217+ 8.1	5.30+0.201	0.310+0.0918	0.65+0.047	0.15+0.063	0.80+0.055
32. Yabad	22.9+3.40	31.3+5.47	6.7+0.57	224+ 6.4	5.20+0.144	0.377+0.0641	0.60+0.050	0.14+0.014	0.74+0.064
33. Givat-Koach	26.0+1.14	33.2+3.10	4.0+0.71	216+11.4	5.23+0.436	0.349+0.0679	0.64+0.056	0.14+0.017	0.78+0.067
Significance (ANOVA) p=	0.562	0.047	0.005	0.708	0.601	0.959	0.015	0.004	0.007
Grand mean	23.4+3.91	29.5+6.00	5.9+1.65	221+16.7	4.79+0.533	0.364+0.0867	0.65+0.070	0.16+0.022	0.81+0.082
Ecogeographical sets									
A. Central populations	22.1+4.29	27.5+6.57	7.0+1.56	207+16.6	4.88+0.514	0.316+0.0704	0.64+0.086	0.16+0.029	0.80+0.098
B1. Xeric-cold margin	23.5+3.68	31.9+4.15	4.1+0.67	234+ 8.0	4.36+0.268	0.387+0.0621	0.66+0.035	0.17+0.013	0.82+0.046
B2. Xeric-warm margins	25.3+3.57	33.8+3.93	4.8+1.27	236+ 9.4	4.36+0.366	0.440+0.0779	0.66+0.070	0.17+0.019	0.83+0.085
B. Xeric margins	25.1+3.57	33.6+3.93	4.7+1.23	236+ 9.2	4.36+0.353	0.434+0.0774	0.66+0.066	0.17+0.018	0.83+0.081
C. Mesic (west) margins	23.0+3.28	27.4+5.06	5.9+1.33	220+ 8.4	5.10+0.391	0.343+0.0656	0.66+0.050	0.15+0.013	0.81+0.062
Significance (ANOVA) p=	0.004	<0.00005	<0.00005	<0.00005	<0.00005	<0.00005	0.224	0.013	0.453

[a] Adjusted according to the average of the controls

Table 3. Discriminant analysis of three ecological sets of populations of *Triticum dicoccoides* in Israel, by all nine photosynthetic variables in 107 genotypes (see Fig. 2a)

(a) *Variables chosen*

Step	Variable entered	Variables in	Wilks' lambda	Significance
1.	Intercellular CO_2 concentration (Ci)	1	0.50715	<0.00005
2.	Photosynthetic water-use efficiency (WUE)	2	0.30399	<0.00005
3.	Photosynthetic efficiency per chlorophyll (A/Chl)	3	0.24638	<0.00005
4.	Leaf area (LA)	4	0.21320	<0.00005
5.	Total chlorophyll concentration (Chl total)	5	0.19544	<0.00005
6.	Photosynthetic efficiency per leaf area (A)	6	0.08866	<0.00005
7.	Stomatal conductance to water (g_s)	7	0.08866	<0.00005
8.	Chlorophyll a concentration (Chl a)	8	0.07261	<0.00005
9.	Chlorophyll b concentration (Chl b)	9	0.06893	<0.00005

(b) *Pairwise comparisons: F statistics and their significances*
(each F statistic has 9 and 96 degrees of freedom)

Ecological set	1 Central populations	2 Xeric margin
2 Xeric margin	F=43.802 p<0.00005	
3 Mesic margins	F=16.253 p<0.00005	40.720 0.00005

(c) *Canonical discriminant functions*

Function	Eigenvalue	Percent of variance	Canonical correlation	After function	Wilks' lambda	χ^2	df	Significance
				0	0.06893	267.47	18	<0.00005
1	4.7682	75.89	0.90919	1	0.39760	92.231	8	<0.00005
2	1.5151	24.11	0.77614					

(d) *Classification results*

Actual set	No. of genotype	Predicted set membership		
		1	2	3
1. Central populations	36	31 86.1%	1 2.8%	4 11.1%
2. Xeric margin	35	0 0.0%	35 100.0%	0 0.0%
3. Mesic margin	36	5 13.9%	0 0.0%	31 86.1%

90.65% percent of genotypes were correctly classified

graphical sets of wild emmer involving central, mesic, and xeric marginal populations. The nine photosynthetic variables discriminated significantly between the three sets (Fig. 2). They entered the analysis as follows: Ci, WUE, A/Chl, LA, Chl total, A, g_s, Chl a, Chl b. Pairwise comparison indicates that each set is significantly ($p<0.00005$) separated from the other two sets (Table 3b). The first two canonical discriminant functions were highly significant ($p<0.00005$). Out of 107 genotypes tested, 97 (91%) were correctly classified into their respective sets (Table 3c and d).

Correlations between photosynthetic characters and ecogeographical parameters

The Spearman rank correlation matrix among nine photosynthetic characters (4A) and with ecogeographical variables (4B) in 23 populations of *T. dicoccoides* in Is-

Table 4. Spearman rank correlations among nine photosynthetic variables, (**A**), and with ecogeographical variables (**B**) in 26 populations of *Triticum dicoccoides* in Israel. Shade population excluded. Tabigha and Yehudiyya subpopulations combined, thus N = 23

A. *Among photosynthetic variables*

A/Chl	0.698***							
LA	−0.639***	−0.699***						
Ci	0.459*	0.606**	−0.627***					
WUE	−0.495*	−0.631***	0.562**	−0.720***				
g_s	0.831***	0.776***	−0.593**	0.797***	−0.705***			
Chl a	0.321	−0.256	0.047	0.097	−0.041	0.177		
Chl b	0.440*	0.072	−0.053	0.129	−0.459*	0.400@	0.649***	
Chl total	0.361@	−0.223	0.049	0.076	−0.142	0.218	0.959***	0.774*
	A	A/Chl	LA	Ci	WUE	g_s	Chl a	Chl b

Abbreviations: A = CO_2 assimilation rate (leaf area basis); A/Chl = CO_2 assimilation rate (chlorophyll basis); LA = single leaf-area; Ci = internal CO_2 concentration; WUE = water use efficiency; g_s = stomatal conductance; Chl a = chlorophyll a concentration, adjusted in accordance with the average of the controls; Chl b = chlorophyll b concentration, adjusted in accordance with the average of the controls; Chl total = total chlorophyll concentration, adjusted in accordance with the average of the controls; Rad-Extra. = correlation with solar radiation, including four extrapolated values

B. *Between photosynthetic and ecogeographical variables*

	Ln	Lt	Al	Tm	Ta	Tj	Td	Tdd	Rn	Rd	
A	−0.012	−0.453*	0.436*	−0.123	−0.008	−0.244	0.209	0.180	−0.374@	−0.505*	
A/Chl	−0.001	−0.661***	0.418*	0.075	0.159	−0.009	0.210	0.357@	−0.521*	−0.692***	
LA	0.236	0.567**	−0.412@	0.101	0.022	0.051	−0.054	0.004	0.217	0.356@	
Ci	−0.108	−0.547**	0.582**	−0.146	−0.204	−0.180	0.112	−0.106	−0.242	−0.413*	
WUE	−0.296	0.360@	−0.501*	−0.002	−0.163	0.097	−0.536**	−0.026	0.354@	0.593**	
g_s	0.058	−0.511*	0.586**	−0.059	−0.055	−0.232	0.279	0.153	−0.403@	−0.562**	
Chl a	0.047	0.055	0.210	−0.357@	−0.331	−0.428*	0.106	−0.409*	0.065	0.022	
Chl b	0.603**	0.191	0.374@	−0.194	−0.009	−0.422*	0.674***	−0.086	−0.154	−0.232	
Chl total	0.156	0.089	0.271	−0.353@	−0.270	−0.430*	0.207	−0.342	0.015	−0.045	

	Hu14	Huan	Dw	Sh (N = 21)	Th (N = 20)	Trd	Ev	Rv	Rr	Rad (N = 20)	Rad-Extr.
A	−0.176	−0.243	−0.441*	0.674***	−0.337	0.015	0.288	0.212	0.204	0.368	0.302
A/Chl	−0.423*	−0.306	−0.467*	0.581**	−0.518*	0.208	0.634***	0.227	0.266	0.468*	0.460*
LA	0.057	−0.004	0.275	−0.494*	0.240	0.143	−0.302	0.055	0.022	−0.338	−0.187
Ci	−0.200	−0.102	−0.489*	0.558**	−0.118	−0.261	0.307	−0.064	−0.240	0.591**	0.365@
WUE	0.526**	0.557**	0.622**	−0.645**	0.325	0.065	−0.332	−0.384@	−0.049	−0.814***	−0.731***
g_s	−0.328	−0.315	−0.586**	0.710***	−0.337	−0.020	0.400@	0.180	0.037	0.537*	0.449*
Chl a	0.267	0.053	−0.194	0.418@	0.253	−0.464*	−0.369@	−0.030	−0.295	0.157	0.054
Chl b	−0.368@	−0.560**	−0.586**	0.585**	−0.198	−0.188	−0.067	0.540**	0.114	0.639**	0.567**
Chl total	0.138	−0.095	−0.283	0.434*	0.180	−0.429*	−0.333	−0.128	−0.186	0.320	0.210

Abbreviations: For ecogeographical variables see Table 1; for photosynthetic variables, see Table 4A. Significance: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; @ = $p < 0.10$

Table 5. Autocorrelation of the means of nine photosynthetic variables in 27 populations of *T. dicoccoides* in Israel (ten distance classes, Moran's I, expected value = −0.04, N = 27)

Distance:	1	2	3	4	5	6	7	8	9	10	Summary of Moran's I		
Low dist.:	0–17	17–26	26–40	40–50	50–59	59–74	74–81	81–97	97–115	115–164	Signif.	Mono-tonic	Inter-cept
Upper dist.:													
N:	36	36	37	35	37	36	35	36	36	26			
A	0.30*	0.41**	0.22	0.09	0.03	−0.19	0.27*	−0.49**	−0.63***	−0.54**	6	1	6
A/Chl	0.50***	0.57***	0.45**	0.11	0.28*	−0.30	−0.22	−0.83***	−0.78***	−0.25	6	1	6
LA	0.46***	0.69***	0.15	0.02	0.20	−0.15	0.08	−0.76***	−0.68***	−0.59***	5	1	6
Ci	0.67***	0.88***	0.02	−0.22	0.08	−0.28	−0.06	−0.70***	−0.63***	−0.24	4	1	4
WUE	0.40**	0.23	0.29*	−0.15	0.22	−0.59**	0.09	−0.50**	−0.38*	−0.07	5	2	4
g_s	0.53***	0.63***	0.22	−0.04	0.21	−0.21	0.13	−0.73***	−0.86***	−0.39*	5	1	4
Chl a	0.37**	−0.32	−0.07	−0.25	−0.12	−0.21	0.10	0.39**	−0.33*	0.08	3	2	2
Chl b	0.04	0.01	0.01	−0.08	−0.11	−0.23	0.04	0.04	−0.23	0.15	0	6	4
Chl total	0.30*	−0.31	−0.08	−0.23	−0.12	−0.26	0.23	0.32*	−0.36*	0.19	3	2	2
Average	0.40	0.31	0.13	−0.08	0.07	−0.27	0.07	−0.36	−0.54	−0.18			

Summary: 37 out of 90 I values are significant

Level of significance: * $p<0.05$; ** $p<0.01$; *** $p<0.001$

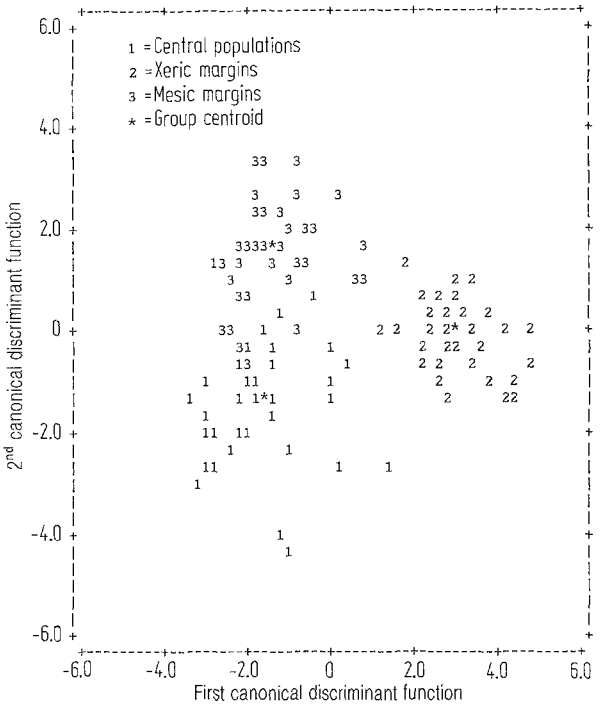

Fig. 2. Discriminant analysis between three ecogeographical regions of *Triticum dicoccoides*, based on nine photosynthetic characteristics

rael is given in Table 4. Notably, about half of the correlations among photosynthetic variables (Table 4 A) were highly correlated (e.g., g_s and A, $r_s = 0.831$***). The other half of the correlation matrix displayed low or even very low correlation, i.e., almost independent (e.g., LA and Chl b, $r_s = -0.053$ NS). The ecogeographical variables also displayed the entire range from high (e.g., Ta and Tm, $r_s = 0.884$***) to low (Rn and Ln, $r_s = -0.006$).

The correlations between photosynthetic and ecogeographical variables (Table 4 B) displayed by far a higher number of significant entries than that expected by chance. The six ecogeographical variables most distinctly correlated with photosynthetic variables (number of significant correlations in parenthesis) were: Sharav, Sh (8), Dew nights, Dw (6), Radiation, Rad (5), Rainy days, Rd (5), Altitude, Al (5), and atitude, Lt (5). On the other hand, the ranking of the photosynthetic variables (number of correlations with ecogeographical variables in parenthesis) were: A/Chl (10), Chl b (8), WUE (8), g_s (6), Ci (6), A (5), Chl total (3), Chl a (3), LA (2). The highest correlation with environment was between WUE and Radiation ($r_s = -0.814$***).

Autocorrelation

Spatial autocorrelation analysis quantifies spatial relations among a set of univariate observations. It gives a measure of the level of correlation of the observed values (in our case photosynthetic characteristics) at each local-

Table 6. Coefficients of multiple regressions (R^2) of photosynthetic variables as the dependent variables and principal components of the geographic and climatic variables as the independent variables, in 23 populations of *T. dicoccoides* in Israel. The subpopulations of Tabigha and Yehudiyya were regarded as two populations, and the shade subpopulation is excluded. See structure of principal components at bottom of table

	Stepwise model					
	With 4 components from 18 ecogeographic variables (GC1–GC4)			3 components from water var. (W1–W3) & 2 components from temp. var. (T1, T2)		
Photosynthetic effic. per leaf area (A)	GC3 0.379**	GC3 GC2 0.427**		W2 0.133 @	W2 T1 0.319*	W2 T1 W3 0.392*
Photosynthetic effic. per chlorophyll (A/Chl)	GC3 0.501***	GC3 GC1 0.601***	GC3 GC1 GC4 0.698***	T2 0.256*	T2 W2 0.367*	T2 W2 T1 0.425*
Leaf area (LA)	GC3 0.321**	GC3 GC2 0.467**		–		
Intercellular CO_2 concentration (Ci)	GC3 0.436***	GC3 GC2 0.535***		W2 0.112	W2 T1 0.409**	W2 T1 T2 0.470**
Photosynthetic water use efficiency (WUE)	GC1 0.342**	GC1 GC3 0.589***	GC1 GC3 GC4 0.629***	T2 0.527***	T2 W2 0.584***	T2 W2 T1 0.672***
Stomatal conductance to H_2O (g_s)	GC3 0.552***	GC3 GC1 0.635***	GC3 GC1 GC2 0.691***	W2 0.223*	W2 T1 0.504***	W2 T1 T2 0.633***
Chlorophyll a concentration (Chl a)	GC4 0.230*			W3 0.313**		
Chlorphyll b concentration (Chl b)	GC1 0.441***	GC1 GC4 0.555***		T2 0.369**	T2 W3 0.552**	
Chlorophyll (a+b) concentration (Chl total)	GC4 0.238*			W3 0.323**		

Level of significance: *=p<0.05; **=p<0.01; ***=p<0.001; @=p<0.10

Structure of Principal Components (GC=Geography-Climate; W=Water; T=Temperature)

Components	GC1	GC2	GC3	GC4	W1	W2	W3	T1	T2
Ln	0.202	0.061	0.242	−0.092	–	–	–	–	–
Lt	0.090	0.131	0.416	−0.052	–	–	–	–	–
Al	0.047	−0.221	−0.165	−0.026	–	–	–	−0.181	0.227
Ta	0.084	0.264	0.107	−0.169	–	–	–	0.203	0.130
Td	0.189	0.001	0.127	−0.066	–	–	–	−0.034	0.476
Tdd	−0.012	0.057	−0.028	0.174	–	–	–	0.172	0.130
Tj	−0.016	0.242	0.038	−0.117	–	–	–	0.207	−0.106
Tm	0.018	0.237	0.050	−0.104	–	–	–	0.212	−0.009
Rad	0.198	0.121	−0.089	−0.371	–	–	–	0.059	0.462
Trd	−0.105	−0.039	0.070	0.507	0.144	0.077	0.698	0.158	0.045
Dw	−0.137	0.031	0.169	0.122	0.228	0.181	0.353	–	–
Ev	−0.033	−0.111	−0.151	0.339	−0.001	−0.133	0.235	–	–
Hu14	−0.107	0.061	0.017	−0.159	0.255	−0.107	−0.048	–	–
Huan	−0.151	0.018	−0.027	−0.046	0.296	−0.145	0.020	–	–
Rd	−0.037	−0.052	0.234	0.097	−0.062	0.501	0.161	–	–
Rn	−0.007	−0.141	0.135	0.098	−0.184	0.535	0.009	–	–
Rr	0.005	−0.067	0.052	0.377	−0.150	0.197	0.331	–	–
Rv	0.137	0.003	0.007	0.029	−0.264	0.056	−0.066	–	–

(for abbreviations see Table 1)

ity with values of the same variables at other geographic sections. The method was extended to biology to include the computation of correlograms for spatial autocorrelation. These show the autocorrelation 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 photosynthetic variables across the entire geographic range given in our study, including all 27 populations. We partitioned the space into ten distance classes, so that each class contained equal numbers of locality pairs. The

Table 7. Allozymic potential markers for photosynthetic variables, found among 107 genotypes from 27 populations of *T. dicoccoides* in Israel. Values in Table are average photosynthetic values of each genotype across all populations, and in parenthesis each average deviation from population means. For variable abbreviations see Table 4

Locus	Geno-type	N	A	A/Chl	LA	Ci	WUE	g_s	Chl a	Chl b	Chl total
A. For photosynthetic efficiency											
Aat-3A	aa	97	23.57(+0.06)	29.80(+0.10)	5.77(−0.02)	221(−0.25)	4.78(+0.02)	0.37(+0.00)	0.651(0.000)	0.162(+0.000)	0.812(+0.000)
	bb	6	21.31(−1.03) !!!	24.68(−1.41) !!!	6.92(−0.17)	217(+2.63)	4.85(−0.16)	0.32(−0.01)	0.668(−0.002)	0.155(−0.002)	0.825(−0.003)
Adh-1B	aa	5	26.36(+1.57) !!!	33.88(+1.81) !!!	4.31(−0.63) !!!	229(+0.55) !!!	4.42(−0.08)	0.44(+0.03)	0.650(0.000)	0.166(−0.000)	0.814(−0.001)
	bb	79	23.32(+0.02)	29.25(+0.04)	6.01(+0.02)	218(−1.49)	4.89(+0.05)	0.35(−0.00)	0.651(−0.002)	0.160(+0.001)	0.811(−0.001)
Est-4B	aa	31	24.56(−0.13)	30.30(−0.37)	5.27(+0.01)	223(−1.63)	4.80(+0.03)	0.38(−0.01)	0.669(+0.003)	0.161(+0.001)	0.829(+0.003)
	cc	33	22.02(−0.37)	27.85(−0.15)	6.54(+0.00)	219(+2.62)	4.80(−0.03)	0.34(+0.00)	0.641(−0.006)	0.163(−0.001)	0.804(−0.007)
	dd	4	24.74(+2.15) !!!	34.58(+2.89) !!!	4.35(−0.79) !!!	231(+0.28)	4.57(−0.02)	0.41(+0.04) !!!	0.632(−0.007)	0.156(−0.004)	0.786(−0.010)
	null	26	24.47(+0.55)	30.42(+0.46)	5.51(−0.11)	223(−0.52)	4.84(+0.03)	0.38(+0.01)	0.660(+0.005)	0.160(0.000)	0.817(+0.005)
Est-5B	aa	68	23.61(+0.07)	29.86(−0.00)	5.78(−0.06)	222(−0.31)	4.79(+0.02)	0.37(−0.00)	0.653(+0.004)	0.162(+0.001)	0.815(+0.005)
	bb	1	18.01(−5.51)	26.29(−5.31)	8.17(+2.21)	227(−9.88)	4.55(+0.11)	0.28(−0.13)	0.644(−0.030)	0.166(−0.001)	0.811(−0.030)
	cc	22	23.73(−0.05)	28.91(+0.09)	5.58(−0.09)	226(+1.84)	4.78(−0.02)	0.38(+0.01)	0.665(−0.006)	0.160(−0.002)	0.823(−0.008)
	ee	6	19.98(−1.09) !!!	27.67(−0.63)	7.28(+0.29) !!!	208(+0.35)	4.68(−0.17)	0.29(−0.01) !!!	0.584(−0.014) !!!	0.138(−0.007) !!!	0.725(−0.021) !!!
Gdh-B	bb	101	23.30(−0.05)	29.28(−0.08)	5.91(−0.01)	220(−0.36)	4.81(+0.02)	0.36(−0.00)	0.652(0.000)	0.161(+0.000)	0.812(0.000)
	cc	4	25.41(+1.17) !!!	34.00(+2.12) !!!	4.28(−0.33) !!!	234(+4.25) !!!	4.40(−0.19) !!!	0.43(+0.04) !!!	0.639(−0.014)	0.159(−0.005)	0.799(−0.016)
Hk	aa	7	19.53(+0.03)	28.73(+0.52) !!!	7.23(−0.14)	201(−1.84) !!!	5.17(+0.12) !!!	0.26(+0.00)	0.548(−0.012) !!!	0.131(−0.003) !!!	0.681(−0.016) !!!
	bb	51	23.96(+0.04)	29.64(+0.11)	5.63(+0.02)	223(−0.22)	4.78(+0.04)	0.38(−0.00)	0.665(−0.001)	0.164(−0.000)	0.829(−0.002)
	cc	8	21.56(0.00)	28.18(0.00)	7.64(0.00)	202(0.00)	4.99(0.00)	0.30(0.00)	0.611(0.000)	0.174(0.000)	0.786(0.000)
Pept-1B	aa	19	19.79(−1.21) !!!	26.53(−1.07) !!!	6.97(−0.02)	211(+3.18)	4.89(−0.07)	0.28(−0.01)	0.599(−0.015) !!!	0.156(−0.004)	0.757(−0.019) !!!
	bb	83	24.12(+0.15)	30.02(−0.00)	5.59(+0.02)	224(−1.06)	4.78(+0.03)	0.38(+0.00)	0.664(+0.004)	0.162(+0.001)	0.825(+0.005)
Pgi-A	bb	21	23.49(+0.97)	29.24(+1.69) !!!	6.42(+0.07)	216(−2.70) !!!	4.92(+0.10) !!!	0.35(+0.01)	0.651(−0.009)	0.159(−0.001)	0.810(−0.010)
	dd	75	23.13(−0.23)	29.33(−0.30)	5.80(−0.10)	222(+0.71)	4.75(−0.02)	0.36(−0.00)	0.646(−0.001)	0.161(−0.000)	0.807(−0.002)
	ee	8	26.32(+0.23)	32.94(−0.54)	4.29(+0.12)	223(−1.21)	4.81(+0.02)	0.39(−0.00)	0.693(+0.025) !!!	0.167(+0.006)	0.856(+0.030) !!!
6Pgd-1A	aa	101	23.43(+0.04)	29.55(+0.11)	5.87(−0.03)	220(−0.23)	4.81(+0.01)	0.36(+0.00)	0.650(−0.001)	0.161(0.000)	0.811(−0.002)
	bb	2	20.01(−1.37) !!!	22.20(−3.48) !!!	5.37(+0.05)	227(+0.38)	4.68(+0.00)	0.29(−0.03)	0.684(+0.035)	0.144(−0.001)	0.828(+0.033)
6Pgd-1B	aa	2	20.01(−1.37) !!!	22.20(−3.48) !!!	5.37(+0.05)	227(+0.38)	4.68(+0.00)	0.29(−0.03)	0.684(+0.035)	0.144(−0.001)	0.828(+0.033)
	bb	101	23.43(+0.04)	29.55(+0.11)	5.87(−0.03)	220(−0.23)	4.81(+0.01)	0.36(+0.00)	0.650(−0.001)	0.161(0.000)	0.811(−0.002)

Locus	Genotype	N	A	A/Chl	LA	Ci	WUE	g_s	Chl a	Chl b	Chl total
B. For other photosynthetic parameters only											
Adh-1A	aa	71	23.66(+0.03)	29.69(+0.15)	5.90(+0.03)	221(−0.52)	4.84(+0.01)	0.37(+0.00)	0.653(−0.002)	0.161(+0.000)	0.813(−0.002)
	bb	13	22.60(+0.58)	28.59(+0.13)	5.97(−0.32)	208(−5.99) !!!	5.01(+0.21) !!!	0.32(−0.00)	0.638(+0.002)	0.158(+0.002) !!!	0.799(+0.005)
Ipor-B	aa	97	23.21(+0.04)	29.08(+0.05)	5.92(−0.01)	219(−0.19)	4.84(+0.02)	0.35(+0.00)	0.651(−0.000)	0.161(0.000)	0.811(−0.000)
	bb	9	25.92(−0.43)	34.66(−0.19)	5.13(+0.03)	242(+0.65) !!!	4.24(−0.08) !!!	0.48(−0.00)	0.652(−0.008)	0.163(−0.002)	0.816(−0.010)
Mdh-2	aa	10	21.11(+0.62)	28.76(+1.04)	6.67(−0.22)	208(−1.56) !!!	5.11(+0.12) !!!	0.30(−0.01)	0.591(−0.007) !!!	0.140(−0.003) !!!	0.733(−0.011) !!!
	bb	91	23.73(−0.04)	29.69(−0.02)	5.78(+0.03)	223(+0.02)	4.75(+0.00)	0.37(−0.00)	0.659(−0.000)	0.164(−0.000)	0.822(−0.001)
	cc	5	22.92(−0.51)	28.67(−1.02)	5.41(−0.24)	215(+0.25)	4.93(−0.07)	0.34(−0.00)	0.633(+0.006)	0.147(+0.003)	0.780(+0.008)
Pept-2	aa	1	23.61(+0.06)	32.44(+0.58)	3.67(−0.41)	226(−8.25)	4.44(+0.08)	0.36(−0.02)	0.629(−0.028)	0.171(+0.003)	0.801(−0.024)
	bb	67	23.47(−0.27)	29.59(−0.31)	5.73(+0.01)	223(+0.02)	4.76(+0.02)	0.37(−0.01)	0.656(−0.001)	0.163(−0.001)	0.818(−0.002)
	cc	5	22.77(−0.56)	29.25(−0.57)	5.57(+0.10)	238(+7.53) !!!	4.51(−0.15) !!!	0.41(+0.02)	0.650(−0.005)	0.160(−0.002)	0.810(−0.007)
6Pgd-2	aa	66	23.96(−0.16)	29.90(−0.30)	5.62(+0.06)	224(−0.85)	4.78(+0.02)	0.38(−0.00)	0.662(+0.001)	0.163(+0.001)	0.824(+0.002)
	bb	2	24.91(+0.74)	32.15(+0.35)	4.91(−0.11)	235(+1.00) !!!	4.54(+0.07)	0.43(+0.02)	0.699(+0.018) !!!	0.171(+0.003) !!!	0.868(+0.019) !!!
	cc	22	21.29(+0.20)	28.23(+0.79)	7.09(−0.03)	206(+0.63)	4.92(+0.01)	0.30(+0.00)	0.603(−0.009)	0.156(−0.003)	0.762(−0.012)
C. Single genotypes for further analysis											
Aat-1B	null	1	26.27(−0.08)	33.55(−0.49)	4.69(+0.11)	230(+1.33) !!!	4.28(−0.15) !!!	0.43(+0.00)	0.719(+0.008) !!!	0.196(+0.013) !!!	0.881(+0.002) !!!
Adh-2B	null	1	28.63(+2.38) !!!	39.09(+3.00) !!!	4.53(+0.74) !!!	242(+5.00) !!!	4.20(−0.05)	0.52(+0.06) !!!	0.634(+0.001)	0.141(−0.006) !!!	0.776(−0.005)
Est-4A	null	1	26.31(−0.04)	33.43(−0.31)	4.34(−0.25)	240(+11.3) !!!	3.86(−0.57) !!!	0.47(+0.05) !!!	0.704(−0.007)	0.176(−0.007)	0.871(−0.008)
Est-5A	ee	1	19.34(−4.94) !!!	20.18(−8.79) !!!	10.85(+4.28) !!!	194(−13.8) !!!	5.35(+0.59) !!!	0.26(−0.10) !!!	0.725(+0.053) !!!	0.175(+0.001) !!!	0.901(+0.056) !!!
Gdh-A	null	1	27.47(+3.09) !!!	31.33(+3.79) !!!	5.32(−0.01)	235(+12.6) !!!	4.45(−0.61) !!!	0.47(+0.10) !!!	0.684(+0.006)	0.164(0.000)	0.848(+0.006)
Ipor-A	null	1	27.54(+5.30) !!!	30.26(+6.63) !!!	5.47(−0.61) !!!	186(−20.0) !!!	5.37(+0.48) !!!	0.36(+0.05) !!!	0.715(−0.001)	0.195(+0.009)	0.906(+0.003)
Nadh-1B	cc	1	27.97(+4.30) !!!	35.16(+7.66) !!!	5.45(−1.23) !!!	249(+27.8) !!!	3.90(−0.75) !!!	0.56(+0.18) !!!	0.625(−0.053) !!!	0.160(−0.013) !!!	0.791(−0.060) !!!
Nadh-2A	aa	1	19.65(−4.70) !!!	30.20(−4.33) !!!	5.48(+0.19) !!!	268(+21.4) !!!	3.34(−0.74) !!!	0.49(+0.03) !!!	0.559(−0.039) !!!	0.161(0.000) !!!	0.726(−0.035) !!!
	cc	1	18.75(−4.92) !!!	20.90(−6.60) !!!	6.46(−0.22) !!!	222(+1.25) !!!	4.56(−0.08) !!!	0.29(−0.09) !!!	0.680(+0.003) !!!	0.180(+0.008) !!!	0.851(0.000) !!!
Est-5B	bb see part A										
Pept-2	aa see part B										

!!! = The photosynthetic variable associated with this allele (above the exclamation mark signs).

results appear in Table 5. The following are the main points. (1) *Average coefficients:* about half of the average autocorrelation coefficients over all tested variables in all ten distance groups were $I=0.27-0.88$, $p<0.05-0.001$. Note that while values of I in columns 1, 2, 3, 5, and 7 were largely positive, I's in columns 4, 6, 8, 9, and 10 were mainly negative. This indicates that the patterns of photosynthetic variation vary geographically. While most close sites displayed positive autocorrelations, far sites were negative. Note that groups 5, 7, and 10 deviated from monotonic expectations. (2) *Low order:* short distance (0–26 km) autocorrelations. Most Moran's I estimates across short distances were high ($I=0.30-0.88$) and significant (mostly $p<0.001$). Two correlations were negative and two were very low in this low distance. (3) *Medium order:* medium distance (27–81 km) autocorrelations. Most I's across medium distances were low (0.05–0.25) and largely nonsignificant, except for some medium and significant I's (0.45–0.59). All variables displayed large deviations from the expected monotonicity. (4) *High order:* long distance (81–164 km). More than half of the I's across long distances were medium to high and highly significant (mostly $p<0.001$), including two positive ones.

The summary of Moran's I is given at the bottom and at the right hand side of Table 5. Out of 90 I values, 37 were significant. The number and level of significance across the 164-km distance vary among the nine photosynthetic variables and in each variable across the geography sampled. Monotonic series extend only across short geographic distances. This lack of monotonicity and differential patterns across variables and distance groups clearly indicates nonrandomness and highly structured variation in photosynthetic characteristics, and excludes migration as a dominant factor of differentiation. We therefore interpret this as the clear result of natural selection on photosynthetic capacity.

Multiple regression analysis with ecology

We conducted stepwise multiple regression (SPSSx 1986) analysis, employing photosynthetic characters as dependent variables and principal components of the ecogeographical variables as independent variables, in an attempt to explain the variances in photosynthetic characters. We used principal component analysis for transforming our set of ecogeographical variables to a new set of uncorrelated components (PC). We ran stepwise multiple regression (MR) on these PCs. The first MR was conducted on four PCs extracted from 18 geographical and climatic variables (GC1–GC4). The second MR was conducted on five PCs extracted from two sets of climatic variables: (i) three PCs from nine water-availability variables (W1–W3) and two PCs from eight temperature variables (T1, T2). See structure of PC at the bottom of Table 6.

Table 8. Coefficients of multiple regressions (R^2) of photosynthetic variables as the dependent variables and allozyme frequencies as the independent variables, in 23 populations of *T. dicoccoides* in Israel. The subpopulations of Tabigha and Yehudiyya were regarded as two populations, and the shade subpopulation is excluded

	Stepwise model		
Photosynthetic effic. per leaf area (A)	Pept-1B a 0.387**	+Est-5A b 0.555**	+Pgi-A e 0.694***
Photosynthetic effic. per chlorophyll (A/Chl)	Est-5A c 0.210*	+6-Pgd-2 b 0.349*	+Hk a 0.461*
Photosynthetic effic. per adj. chlorophyll (A/Chl (adj))	Est-5A null 0.317*	+Ipor-B b 0.497**	+Adh-2B b 0.624**
Leaf area (LA)	Pept-1B a 0.250*	+Aat-3A b 0.403*	+Adh-2B b 0.499*
Intercellular CO_2 concentration (Ci)	Pept-1B a 0.371**	+Ipor-B b 0.598***	+Est-5A d 0.695***
Photosynthetic water use efficiency (WUE)	Ipor-B b 0.205@	+Est-5A b 0.372*	+Pgi-A e 0.511*
Stomatal conductance to H_2O (g_s)	Ipor-B b 0.449**	+Pept-1B a 0.708***	+Adh-2B b 0.799***
Chlorophyll a concentration (Chl-a)	Hk b 0.262*	+Pgi-A e 0.455**	+Ipor-B b 0.597**
Chlorophyll a concentration (adj) (Chl-a (adj))	Hk a 0.417**	+Nadh-2A a 0.531**	+Pgi-A e 0.611**
Chlorophyll b concentration (Chl-b)	Est-4B null 0.290*	+Pgi-A e 0.448**	+Est-4B c 0.565**
Chlorophyll b concentration (adj) (Chl-b (adj))	Pgi-A e 0.264*	+Mdh-2 c 0.475**	+Adh-2B b 0.554**
Chlorophyll (a+b) concentration (Chl-total)	Pgi-A e 0.250*	+Ipor-B b 0.444**	+Hk a 0.554**
Chlorophyll (a+b) concentration (adj) (Chl-total (adj))	Hk a 0.335**	+Est-4B null 0.464**	+Pgi-A e 0.578**

Level of significance: *=p<0.050; **=p<0.01; ***=p<0.001; @=p<0.10

A substantial amount of the variance in all nine photosynthetic variables is largely ($R^2=0.230-0.698$) and significantly ($p<0.05-0.001$) explained by one to three PCs of the 18 ecogeographical variables (Table 6). For example, the variance in A/Chl is largely and significantly explained ($R^2=0.698$***) by three PCs comprising climatic and geographic variables. Climatic variables alone significantly explain a substantial amount of the variance of all photosynthetic variables (R^2 up to 0.672*** in WUE). The main climatic variables explaining the variance and represented by the PCs were water-availability factors (Huan, Rn, Rv, Dw), radiation (Rad), and temperature variables (Td, Tm).

Association of photosynthetic characters with allozymes

Univariate analysis of single allozymes. We used a breakdown program (SPSSx 1986) to assess the associations of photosynthetic variables with allozymes (for all allozymic data and specifications, see Nevo and Beiles 1989). Potential allozyme markers for the nine photosynthetic variables found among 107 genotypes from 27 populations of *T. dicoccoides* in Israel are given in Table 7. Entries in Table 7 are the average photosynthetic values of each genotype across all populations. For the purpose of standardization, we have presented in addition to each allozyme mean the average deviation of this allozyme from the corresponding mean of its own population, designated as "mean deviation" and appearing in parentheses. In cases where high values are associated with positive "mean deviation", the association of the allozyme genotype with high level of the parameter is substantiated. The exclamation marks indicate isozyme loci and allozyme genotypes distinctly associated with a particular photosynthetic variable. For example, the following allozyme genotypes are distinctly associated with A: *Adh-1Baa*, *Est-4Bdd*, *Gdh-Bcc*, *Pept-1Bbb*, etc. Similar distinct associations are given in Table 7 for all other photosynthetic variables. Allozyme genotypes represented by single accessions (i.e., having no repetitions in our sample) with distinct association of photosynthetic characters provide potential candidates for further analysis, as listed in Table 7c.

Multilocus allozymic correlation with photosynthetic characters. We ran a stepwise multiple regression analysis using the photosynthetic variables as dependent variables, and allozyme frequencies as the independent variables. For all photosynthetic variables, a combination of three allelic frequencies explains substantially the photosynthetic variance ($R^2 = 0.46^{*} - 0.80^{***}$). Thus, allozyme combinations may provide good indicators for high photosynthetic capacity (Table 8).

Discussion

We will discuss the photosynthetic characteristics in a genetic background perspective, as follows: (i) genetic organization in nature; (ii) genetic diversity and resources of wild cereals in the Near East Fertile Crescent; (iii) predictive method by allozyme markers and ecology; (iv) photosynthetic variation in wild emmer and its predictability; and (v) genetic resources of *T. dicoccoides* and breeding.

Organization of genetic diversity in nature

Recent reviews of genetic diversity in natural populations of plants (Hamrick et al. 1979), and animals and plants (Nevo 1983, 1988b; Nevo et al. 1984a) indicate that genetic polymorphism and heterozygosity, based on allozymes, are structured on a massive scale. Recently, Nevo (1988b) reviewed the evolutionary significance of genetic diversity in natural populations of plants and animals, using the environmental-genetic correlation methodology, at three geographic levels: (i) local: several species of wild cereals, land snails, and barnacles in Israel; (ii) regional: 38 species in Israel; of these, 21 ranged from the Mediterranean region to the Negev desert; also included were two species of wild cereals in the Near East Fertile Crescent; and (iii) global: 1,111 species of animals and plants ranging worldwide. The species involved in these local, regional, and global analyses were largely taxonomically unrelated. They varied in their ecologies, demographies, life histories, and other biological variables. They were mostly tested for allozymic diversity by routine horizontal starch gel electrophoresis at 25 gene loci on average (range 14–50 loci). In addition, two published studies were reviewed on DNA polymorphisms (restriction fragment length polymorphisms, RFLPs), and several additional unpublished RFLP studies in animals and plants in Israel and the correlation between RFLPs and allozymes were reviewed in Nevo (1990).

The results at all three geographic levels indicated that: (i) the levels of genetic diversity vary nonrandomly among populations, species, and higher taxa; and (ii) genetic diversity is partly correlated with, and predictable primarily by, ecological factors. These results corroborate the adaptive, environmental theory of genetic diversity, and they were confirmed for several allozyme loci in controlled laboratory experiments on pollution biology (Nevo 1990). The genetic patterns obtained are inconsistent with the neutral theory of molecular evolution. In contrast, natural selection in its various forms appears to be a major differentiating and orienting force of evolutionary change in protein and also, most likely, in DNA polymorphisms.

Genetic diversity and resources of wild cereals in the Near East

Our population genetic studies in wild emmer wheat (Nevo et al. 1982; Nevo and Beiles 1989) and in wild barley (Nevo et al. 1986a) revealed large amounts of genic diversity across the species ranges of the progenitors in Israel in particular, and in the Near East Fertile Crescent in general. This rich genetic diversity is geographically structured and differentiated in accordance with varying ecologies on the regional and local scales. Furthermore, the rich allozymic variation found is associated, as described below, with large variation of phenotypic quantitative traits of agronomic importance, disease resistances against powdery mildew and the various rusts, and high content of seed storage proteins (reviewed

in Nevo 1983, 1988 a; see also Avivi 1978; Feldman 1979; Grama et al. 1983; Levy and Feldman 1988, 1989; Nevo and Payne 1987; Nevo et al. 1984 b, 1985, 1986 b, c). If these agronomically important characters display wide geographic variation across the species ranges, can they be efficiently identified and screened without the need of massive nondiscriminatory expensive collections? Can sampling and screening strategies be optimized?

Predictive method by allozyme markers and ecology

Evaluation and use of genetic resources were discussed by Brown and Clegg (1983), and the use of isozymes in plant genetics and breeding was discussed by Tanksley and Orton (1983). We have developed preliminary guidelines in wild barley and wild wheat for predictive sampling strategies in an attempt to optimize the identification of elite genotypes resistant to various diseases, including powdery mildew in wild barley, as well as powdery mildew, leaf rust and stripe rust in wild emmer. Likewise, we developed predictive guidelines for agronomic characters, as well as for protein content (reviewed in Nevo 1987; see also Nevo et al. 1984 b, 1985, 1986 b, c).

Photosynthetic variation in wild emmer and its predictability

Our present analysis of photosynthetic characteristics in wild emmer wheat reveals geographical organization of these traits, regionally and locally, as revealed in our discriminant, correlation, and Anova analyses. First, we have shown that populations from the xeric margins display high photosynthetic capacity. Second, we have shown that populations within a set and, most importantly, individuals within populations vary drastically in their photosynthetic genotypes (Carver and Nevo 1990). This makes wild emmer wheat a very good genetic resource for wheat improvement, not only for disease resistances, protein and glutenin content, drought and salt ecological tolerances, and herbicide resistance (Snape et al. 1991 a, b), but also for photosynthetic performance. Can this variation also be predicted by ecological and genetic markers, as was the case for other agronomically important traits?

Here we succeeded, using our predictive methodology by ecology and allozymes, in identifying elite photosynthetic populations and genotypes. As in our previous analyses, we used a breakdown program calculating allozyme genotype means for each photosynthetic characteristic, and used a multiple regression analysis to obtain the best ecological correlates and multilocus allozyme markers for future educated screening of elite genotypes. These results add photosynthetic capacity of wild emmer to the other rich genetic resources in this wild progenitor of all wheats, as a valuable source for wheat improvement. Multilocus allozyme markers identifying a series of agronomically important traits, including photosynthesis, could provide optimal donors for breeding.

Genetic resources of T. dicoccoides and application in breeding

Research on wheat improvement by the transfer of desirable genetic material from wild emmer to cultivated wheat started at the Volcani Center of Agricultural Organization (ARO) in Israel in 1965, when genes for stripe rust resistance and high protein content were successfully incorporated into cultivated wheat (Gerechter-Amitai and Grama 1974; Grama and Gerechter-Amitai 1974). Utilization of wild emmer in breeding was initiated by the findings in 1964 that wild emmer indigenous to Israel is 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 was considerably higher than that in cultivated wheat, ranging from 20%–24% (Gerechter-Amitai and Grama 1977). Later, extended research revealed protein values in wild emmer ranging from 13.9% to 28.0% (Grama et al. 1983); similar results were reported by Avivi (1978) and later by Nevo et al. (1986 c) and by Levy and Feldman (1989). The current breeding program in ARO utilizes a selection of wild emmer G-25 that is both resistant to stripe rust, has a protein content of 20.5% and a kernel weight of 31.5 mg, thus combining several desirable traits in a donor. 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). The resistant accessions of wild emmer found in our studies (reviewed in Nevo 1987) are currently being used to develop enhanced hexaploid and tetraploid wheat germ plasm resistant to the rusts *P. recondita tritici* and *P. striiformis* and to the powdery mildew, *Erysiphe graminis tritici*.

Recently, it has been shown that hexaploid emmer wheat derivatives grown under New Zealand conditions affect: (i) the relationship between protein composition and quality parameters; (ii) foliar urea sprays on plant and grain nitrogen and baking quality; and (iii) nitrogen fertilization and stage of grain development on protein composition (Grama et al. 1987 a, b; Cressey et al. 1987). A new gene for resistance to *Puccinia striiformis*, Yr 15, was found in *T. dicoccoides* sel. G-25 (Gerechter-Amitai et al. 1989 a); race-specificity of temperature-sensitive genes for resistance to *Puccinia striiformis* were also found in *T. dicoccoides* (Gerechter-Amitai and van Silfhout 1989), and additional resistance to yellow rust in *T. dicoccoides* was found in 19 out of 29 selections studied, possessing genes that were different from the gene in *T. dicoccoides* sel. G-25 (Gerechter-Amitai et al. 1989 b). Finally, resistance to the herbicides difenzoquat, chlortoluron, and metoxuron, commonly used on cultivat-

ed wheats, were found in natural populations of *T. dicoccoides*, and the implications in breeding these resistances in cultivated wheats were discussed (Snape et al. 1991 a, b).

Conclusions

Multidisciplinary studies of wild emmer, *T. dicoccoides*, in Israel, indicate its importance in wheat improvement. The Near East in general, and Israel in particular (Nevo 1986), are the centers of origin and diversity of wild emmer, where it developed wide genetic adaptations against multiple pathogens and diverse ecological stresses. We have now added to the list of potential, largely untapped, genetic resources of wild emmer its photosynthetic capacity (Carver and Nevo 1990, and the present study), as well as its herbicide resistance (Snape et al. 1991 a, b). Genetic variation is transferrable from the wild to the cultivated gene pool: thus, genes of wild emmer are optimal for future wheat improvement.

The rich genetic diversity of wild emmer described previously (Nevo 1983, 1988 a) and elsewhere (Grama et al. 1983; Feldman 1979; Levy and Feldman 1989) for multiple disease resistances, agronomic traits of economic significance, and environmental adaptations, as well as for photosynthetic capacity (Carver and Nevo 1990 and this study) is ecogeographically structured and is predictable by ecology and allozyme markers. Consequently, conservation and utilization programs should maximize sampling strategies (e.g., Marshall and Brown 1975) by following the ecological genetic factors and allozyme/DNA markers as effectively predictive guidelines. Our predictive methodology, by ecology and allozymes, is correlative and should be improved by using isozyme and DNA genetic markers linked to traits of agronomic importance. We recently started using DNA restriction polymorphisms, RFLPs, of chromosomally located clones. Our predictive methodology, if further developed by additional isozyme and DNA markers and verified by testcrosses and gene mapping, could substantially contribute to optimize sampling, conservation, and utilization of the as yet largely untapped genetic resources of wild gene pools for crop improvement.

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