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Genetic diversity in wild diploid wheats *Triticum monococcum* var. *boeoticum* and *T. urartu* (Poaceae)*

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Summary. The genetic diversity of two wild diploid wheat species, *Triticum monococcum* var. *boeoticum* and *T. urartu*, was assessed using starch gel electrophoresis. Genetic diversity is uniformly low in both species. Number of alleles per locus was very low with a mean of 1.22 for *T. monococcum* var. *boeoticum* and 1.19 in *T. urartu*. Percentage of polymorphic loci was also low, with a mean of 19.71 for *T. monococcum* var. *boeoticum* and a mean of 18.35 for *T. urartu*. Mean gene diversity was low with a mean of 0.052 in populations of *T. monococcum* var. *boeoticum* and a mean of 0.040 in populations of *T. urartu*. Genetic affinities of the species and of populations were computed using Nei's identity index (NI). Overall genetic affinities of the two species are NI = 0.697. The genetic affinities of different populations of a species are uniformly high with NIs ranging from 0.894 to 1.000 in *T. monococcum* var. *boeoticum* and from 0.898 to 1.000 in *T. urartu*.

Key words: Leaf isozymes – *Triticum* – Monococcum wheat – *urartu* – Starch gel electrophoresis

Introduction

Modern methods of crop breeding and production have severely reduced genetic diversity in many crop plants (Frankel and Hawkes 1975). This reduction in genetic diversity may severely limit breeding programs for new adaptive traits such as disease resistance, drought and heat tolerance, etc. Recently, plant breeders have turned to the wild relatives of crop plants to enrich the germplasm of modern cultivars (Harlan 1981). Cultivated wheat is one group which has already benefited from such a program (Sharma and Gill 1983).

The wheat genus *Triticum* L. is a polyploid complex comprising both domesticated and wild species. Domesticated diploid wheat *T. monococcum* L. var. *monococcum* (2n = 14) is still cultivated in mountainous areas of southeastern Europe and Turkey (Harlan 1981). Tetraploid macaroni wheat, *T. turgidum* L. var. *durum* (2n = 4x = 28), and hexaploid bread wheat, *T. aestivum* L. var. *aestivum* (2n = 6x = 42), are widely cultivated in temperate and subtropical regions of the world and are two of the most important cereals in world agriculture. Several diploid and tetraploid *Triticum* species are wild or weedy. Hexaploid wheat is found only in cultivation (Waines 1983).

Knowledge of the amount and distribution of genetic variability within the wild species is important to the optimal use of their genetic resources in plant breeding programs. Starch gel electrophoresis is a quick, inexpensive, and reliable method to estimate genetic variability (Rick et al. 1977; Brown 1978). Wild tetraploid wheat *T. turgidum* var. *dicoccoides* Körn has already been examined electrophoretically (Nevo et al. 1982) and the application of this variation to the breeding of durum wheat has been discussed (Nevo 1983). Cultivated hexaploid and, in some cases, tetraploid wheats have been subjected to rather extensive genetic analysis of eight enzyme systems (reviewed in Hart and Gale 1987).

Little is known about the nature of genetic variability in diploid wheats, a source of genetic variation for culti-

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vated tetraploid and hexaploid wheats. For this reason, an electrophoretic study of two diploid species, the widespread *T. monococcum* var. *boeoticum* Boiss. and the more restricted *T. urartu* Tum., was undertaken to assess the genetic diversity within each species.

Triticum monococcum var. *boeoticum* is widely distributed throughout the eastern Mediterranean countries of Armenia, Azerbaijan, Bulgaria, Crimea, Greece, Hungary, Iran, Iraq, Lebanon, Syria, and Turkey. *Triticum urartu* is restricted mainly to the fertile crescent and is distributed in Armenia, Azerbaijan, Iran, Iraq, Lebanon, Syria, and Turkey (Johnson 1975). The two species are variable with respect to spike and spikelet characteristics, and occupy a wide range of habitats (Johnson 1975). The two species are reproductively isolated by some cross-compatibility barriers and by F_1 hybrid sterility (Sharma and Waines 1981). They both share a variant of the wheat A genome, present in domesticated tetraploid (BBAA) and hexaploid (BBAADD) wheats, where the female parent genome is listed first.

Materials and methods

Seeds of *T. monococcum* var. *boeoticum* and *T. urartu* were collected in 1972 from 17 different populations in Turkey, Iraq, and Lebanon. Population 1: 44.5–45.9 km west of Kiziltepe, Mardin, Turkey; altitude 600 m. Population 2: 83.8 km west of Kiziltepe, Mardin, Turkey; altitude 670 m. Population 3: 2.9 km south of Viransehir, Urfa, Turkey; altitude 600 m. Population 4: 52.5 km northeast of Urfa, near Hilvan; altitude 650 m. Population 5: 62.0 km northeast of Urfa and east of Hilvan; altitude 700 m. Population 6: 1 km northeast of Salahadin, Iraq; altitude 1,100 m. Population 7: 21 km south of Harir, between Rowandus and Shaqlawa, Iraq; altitude 1,000 m. Population 8: 13 km west of Shaqlawa, Iraq; altitude 1,000 m. Population 9: 5.5 km north of Dohuk, Iraq; altitude 750 m. Population 10: 24 km northeast of Dohuk toward Amadiya, Iraq; altitude 950 m. Population 11: 6 km east of Suara Tuka, Iraq; altitude 1,050 m. Population 12: between Kfar Kouk and Aiha, Lebanon; altitude 1,000 m. Population 13: between Kfarkouk and Aiha, Lebanon; altitude 600 m. Population 14: 44.5 km west of Kiziltepe, Mardin, Turkey; altitude 600 m. Population 15: 53.8 km west of Kiziltepe, Mardin, Turkey, altitude 625 m. Population 16: 5.4 km south of Viransehir, Urfa, Turkey; altitude 600 m. Population 17: 10 km west of Baal Bek on the road to Bashari, Lebanon; altitude 1,000 m.

A separate accession number was assigned to the seeds of each wild mother plant. Seeds from numerous mother plants were collected from each population. These seeds were germinated and grown in fields at the University of California Riverside Experiment Station, in either 1975 or 1976. Seeds produced by these plants were used for electrophoretic analysis. A single seed from each accession line was germinated and grown for 1–2 weeks on paper towels.

Three different gel and electrode buffer systems were used: LiOH-borate (LB) pH 8.3, morpholine citrate (MC) pH 7.0, and TRIS-EDTA-maleic acid (TEM) pH 7.4 (Ellstrand 1984). A 12% starch concentration was used.

Crude extracts were prepared by crushing the emerging leaves in 0.1 *M* TRIS-HCl buffer pH 8.0, and 0.1 *M* 2-mercaptoethanol. Extracts were absorbed on paper wicks (Whatman No. 3) and inserted into a slit in each gel. LB gels were run at 754 mA until the borate front had migrated approximately 7 cm. To prevent separation of LB gels, wicks were removed after 1 h. MC gels were run at 30 mA for 4.5 h. TEM gels were run at 50 mA for 4 h.

A total of 326 individuals were analyzed for 12 different enzyme systems using horizontal starch gel electrophoresis. The enzymes assayed include: acid phosphatase (ACP), alcohol dehydrogenase (ADH), glutamate dehydrogenase (GDH), glutamate oxaloacetate transaminase (GOT), isocitric dehydrogenase (IDH), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGD), shikimate dehydrogenase (SKDH), and triosephosphate isomerase (TPI).

GDH, GOT, PGI, and TPI were stained on an LB gel. IDH, MDH, ME, and SKDH were stained on an MC gel. ACP, ADH, PGM, and 6PGD were stained on a TEM gel.

ACPH was stained with 50 mg fast garnet GBC salt, 5 ml alpha naphthyl acid phosphate (5 mg/ml 50% acetone), and 50 ml water. ADH, GOT, and MDH were stained as in Brown et al. (1978). GDH was stained as in Smith-Huerta (1986). IDH, ME, PGI, PGM, 6PGD, SKDH, and TPI were stained as in Ellstrand (1984).

The number of loci per enzyme and their alleles were inferred by half-sib comparisons, pollen leachate studies (Weeden and Gottlieb 1979), and from past electrophoretic studies of *Triticum* (Yaghoobi-Saray 1979; Nevo et al. 1982; McIntosh 1983; Hart and Gale 1987). Homologies of loci and alleles between the two diploid species were based on similarities in electrophoretic mobilities. Alleles are named by migration distance in millimeters under standard running conditions.

The genetic similarity between and among populations of *T. monococcum* var. *boeoticum* and *T. urartu* was calculated using Nei's Identity corrected for finite samples (Nei 1978). Genic diversity was calculated for each population (Nei 1975).

Results

Sixteen loci were resolved and scoreable in *T. monococcum* var. *boeoticum*, and 15 in *T. urartu* (Table 1). Locus *Mdh-1* was resolved in *T. monococcum* var. *boeoticum* but not in *T. urartu*. The remaining 15 loci were resolved in both species (Table 1).

Of the 16 loci examined, 3 were monomorphic in this sample, and the same were shared by both species. These loci include *Got-1*, *Got-2*, and *Pgm-1* (Table 1). One locus, *Tpi-2*, was monomorphic in both species, but was fixed for a different species-specific allele (Table 1). Another locus, *Skdh*, was monomorphic in *T. urartu*, and fixed for another allele in all but a single population of *T. monococcum* var. *boeoticum* (Table 1). One locus, *6Pgd-2*, was polymorphic for the same alleles in most populations of both species. Locus *Mdh-1* was also polymorphic in most populations of *T. monococcum* var. *boeoticum*, but was not resolved in even a single individual of *T. urartu* (Table 1). The remaining 9 loci had alleles which were common to both species, and were also polymorphic to some extent. However, one allele or another usually predominated. These loci included *Acp*, *Adh*, *Gdh*, *Idh*, *Mdh-2*, *Me-1*, *Pgi*, *6Pdg-1*, and *Tpi-1* (Table 1).

Table 1. Allele frequencies in populations of *Triticum monococcum*, var. *boeoticum* and *T. urartu*. Alleles are designated by distance migrated from origin in millimeters. *N* – number of individuals sampled per population

Locus	Allele	*T. monococcum* var. *boeoticum*													*T. urartu*			
		Locality	Turkey					Iraq							Lebanon	Turkey			Lebanon
		Pop.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
		N	11	12	8	21	19	39	18	17	28	24	15	26	11	12	19	22	24
Acp	7		1.00	1.00	1.00	1.00	0.90	0.92	1.00	0.88	1.00	1.00	1.00	0.96	1.00	1.00	0.95	1.00	1.00
	8		0.00	0.00	0.00	0.00	0.10	0.08	0.00	0.12	0.00	0.00	0.00	0.04	0.00	0.00	0.05	0.00	0.00
Adh	9		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
	10		1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	0.86	1.00	1.00	1.00	0.96
	12		0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00
Gdh	20		1.00	1.00	1.00	1.00	1.00	1.00	0.06	0.94	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	22		0.00	0.00	0.00	0.00	0.00	0.00	0.94	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Got-1	23		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Got-2	37		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Idh-1	20		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.61
	22		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.75	1.00	1.00	0.39
Mdh-1	13		0.00	0.00	0.00	0.00	0.00	0.04	0.05	0.03	0.05	0.04	0.00	0.10	0.05	–	–	–	–
	16		0.27	0.00	0.38	0.86	0.00	0.56	0.10	0.78	0.95	0.96	0.00	0.00	0.95	–	–	–	–
	17		0.73	1.00	0.62	0.14	1.00	0.40	0.85	0.19	0.00	0.00	1.00	0.90	0.00	–	–	–	–
Mdh-2	22		1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.82	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00	1.00
	24		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.00
Me-1	16		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00
	19		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
	21		1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	1.00	1.00	1.00	1.00	1.00	0.96	0.97	1.00	1.00
	22		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pgi	6		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
	9		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.91	1.00	1.00	1.00	1.00
Pgm-1	12, 14[a]		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
6Pgd-1	8		0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.02	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.04
	10		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	11		1.00	1.00	1.00	1.00	1.00	0.96	1.00	1.00	0.90	1.00	1.00	0.92	1.00	1.00	1.00	1.00	0.96
6Pgd-2	16		0.40	0.33	0.00	0.33	0.28	0.23	0.61	0.82	0.64	0.62	0.80	0.62	0.64	0.42	0.21	0.32	0.54
	17		0.60	0.67	1.00	0.67	0.72	0.77	0.39	0.18	0.36	0.38	0.20	0.38	0.36	0.58	0.79	0.68	0.46
Skdh	11		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00
	13		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96	1.00	0.00	0.00	0.00	0.00
	16		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00	1.00
Tpi-1	33		1.00	1.00	1.00	0.76	0.87	1.00	0.97	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	36		0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	38		0.00	0.00	0.00	0.24	0.13	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tpi-2	41		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00	1.00
	44		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00

– Does not stain

[a] Appear as a doublet, one band migrating 12 mm, the other 14 mm

The number of alleles per locus was very low in both species. Values for populations of *T. monococcum* var. *boeoticum* ranged from 1.06 to 1.44, with a mean of 1.22 for the species (Table 2). Values for populations of *T. urartu* ranged from 1.07 to 1.27, with a mean of 1.19 (Table 2). Percentage of polymorphic loci was also low, ranging in populations of *T. monococcum* var. *boeoticum* from 6.25 to 37.50, with a mean of 19.71 (Table 2). Values in *T. urartu* populations ranged from 6.70 to 26.70, with a mean of 18.35 (Table 2). Mean gene diversity was also

low in both species. Values ranged from 0.020 to 0.086, with a mean of 0.052 in populations of *T. monococcum* var. *boeoticum* (Table 2). Values ranged from 0.029 to 0.075 in populations of *T. urartu*, with a mean of 0.040 (Table 2).

Nei's identities and distances were calculated to compare the genetic affinities of the two species and the affinities of the individual populations. Values for the overall affinities of the two species are Nei's identity = 0.697. The values for population comparisons are reported in Table 3. The genetic affinities between different populations of a species are extremely high. Nei's identity values range from 0.894 to 1,000 in *T. monococcum* var. *boeoticum*, and from 0.898 to 1.000 in *T. urartu* (Table 3). Genetic affinities between the two different species are lower, with Nei's identity values ranging from 0.703 to 0.817 (Table 3).

Table 2. The mean number of alleles per locus, percentage of polymorphic loci, and mean gene diversity in populations of *Triticum monococcum* var. *boeoticum* and *T. urartu*

Population no.	Alleles per locus	Polymorphic loci (%)	Mean gene diversity
1	1.13	12.50	0.055
2	1.06	6.25	0.028
3	1.06	6.25	0.029
4	1.19	18.75	0.066
5	1.19	18.75	0.051
6	1.38	31.25	0.075
7	1.31	25.00	0.057
8	1.44	37.50	0.086
9	1.31	25.00	0.052
10	1.13	12.50	0.034
11	1.06	6.25	0.020
12	1.31	31.25	0.060
13	1.25	25.00	0.060
Mean *T. monococcum* var. *boeoticum*	1.22	19.71	0.052
14	1.20	20.00	0.063
15	1.20	20.00	0.032
16	1.07	6.70	0.029
17	1.27	26.70	0.075
Mean *T. urartu*	1.19	18.35	0.040

Discussion

The genetic diversity of both *T. monococcum* var. *boeoticum* and *T. urartu* is uniformly low. Both species have low values for alleles per locus, for percent polymorphic loci, and for mean gene diversity. Low diversity is often observed in highly self-pollinating diploid plants such as these *Triticum* species (Nevo 1978; Hamrick et al. 1979; Smith-Huerta 1986). *Triticum monococcum* var. *boeoticum* and *T. urartu* were previously reported to have higher levels of genetic diversity than in the present study (Yaghoobi-Saray 1979). The difference is probably attributable to the enzyme systems used to measure diversity. Only five enzyme systems were common to both studies. Seven of the enzyme systems used in the present study were not examined by Yaghoobi-Saray. Three of the enzyme systems used by Yaghoobi-Saray were not utilized in the present study. These three enzyme systems – alkaline phosphatase, peroxidase, and esterase – accounted for much of the genetic diversity observed by Yaghoobi-Saray. *Triticum turgidum* var. *dicoccoides* and several species in the closely related *Aegilops* genus showed higher levels of genetic diversity in previous studies (Mendlinger 1980; Nevo et al. 1982). The *Aegilops* species had much more genetic variation than is expected for highly self-pollinated diploids (Mendlinger 1980). *Triticum turgidum* var. *dicoccoides* is also highly self-pollinating like the other species, but differs in ploidy level. It combines the

Table 3. Genetic affinities of populations of *Triticum monococcum* var. *boeoticum* and *T. urartu* as measured by Nei's Identity

Pop. no.	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	0.997	0.991	0.975	0.995	0.993	0.939	0.969	0.964	0.966	0.987	0.994	0.964	0.773	0.777	0.779	0.817
2		0.985	0.949	0.999	0.978	0.938	0.941	0.932	0.933	0.987	0.995	0.932	0.763	0.768	0.769	0.805
3			0.976	0.986	0.995	0.915	0.953	0.951	0.953	0.951	0.968	0.951	0.767	0.782	0.778	0.804
4				0.951	0.991	0.898	0.978	0.991	0.991	0.935	0.947	0.989	0.761	0.767	0.769	0.804
5					0.977	0.933	0.936	0.928	0.929	0.982	0.991	0.927	0.757	0.764	0.764	0.798
6						0.918	0.972	0.978	0.980	0.957	0.971	0.979	0.771	0.780	0.780	0.813
7							0.913	0.894	0.895	0.940	0.942	0.894	0.705	0.703	0.709	0.752
8								0.993	0.994	0.957	0.958	0.993	0.778	0.770	0.778	0.804
9									1.000	0.937	0.944	0.999	0.758	0.756	0.762	0.807
10										0.937	0.944	1.000	0.762	0.759	0.765	0.809
11											0.998	0.936	0.754	0.747	0.755	0.804
12												0.943	0.764	0.762	0.767	0.812
13													0.757	0.754	0.760	0.805
14														0.997	0.999	0.922
15															1.000	0.898
16																0.903

genomes of an unknown *Aegilops* species (BB) as female parent and *T. urartu* (AA) (J. Dvorak, personal communication). Since each locus is duplicated, many more "alleles" are present. A similar relationship of genetic diversity to breeding system and polyploidy was observed in the genus *Clarkia*. Two diploid progenitors, *C. epilobioides* and *C. modesta*, had fewer polymorphic loci than their tetraploid derivative, *C. similis*, and all have a highly selfing breeding system (Smith-Huerta 1986). Like the *Aegilops* species, wild barley is also a self-pollinating diploid grass which exhibits more genetic diversity than expected (Brown et al. 1978).

The populations of both *T. monococcum* var. *boeoticum* and *T. urartu* were genetically very uniform across the populations studied, as evidenced by the uniformly high Nei's identities found in all population comparisons. Even the comparisons between the species *T. monococcum* var. *boeoticum* and *T. urartu* yielded high Nei's identities. Several species of *Aegilops* also showed this pattern of uniformity and similarity (Mendlinger 1980). Populations of *T. turgidum* var. *dicoccoides* showed a much greater range of Nei's identity values, indicating that the populations of *T. turgidum* var. *dicoccoides* showed less genetic similarity than did some populations of *T. monococcum* var. *boeoticum* and *T. urartu*.

The information in this study may be useful to population geneticists and plant breeders who wish to understand the population structure of diploid wheats. Agronomic characteristics and variation in genes controlling disease and insect resistance in wild and domesticated diploid wheat have already been investigated (Sharma et al. 1981; Gill et al. 1983; Waines 1983). The pattern of genetic diversity found in these two species may suggest the optimal sampling strategy for this group. Marshall and Brown (1975) suggest methods to optimally sample species with low and uniform diversity, such as *T. monococcum* var. *boeoticum* and *T. urartu*. They suggest that several large well-chosen populations should be sampled heavily rather than sampling a few individuals from many populations. This appears to be the best method for obtaining the greatest diversity of genotypes for germplasm collections and for breeding purposes.

References

Brown AHD (1978) Isozymes, plant population genetic structure and genetic conservation. Theor Appl Genet 52:145–157

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

Ellstrand NC (1984) Multiple paternity within the fruits of the wild radish *Raphanus sativus*. Am Nat 123:819–828

Frankel OH, Hawks JG (eds) (1975) Crop genetic resources for today and tomorrow. Cambridge University Press, Cambridge

Gill BS, Browder LE, Hatchett JH, Harvey TL, Martin TJ, Raupp WJ, Sharma HC, Waines JG (1983) Disease and insect resistance in wild wheats. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp, Kyoto, pp 785–792

Hamrick JL, Linhart YB, Mitton JB (1979) Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. Annu Rev Ecol Syst 10:173–200

Harlan JR (1981) Early history of wheat: earliest traces to the sack of Rome. In: Evans LT, Peakcock WJ (eds) Wheat science, today and tomorrow. Cambridge University Press, Cambridge, pp 1–19

Hart GE, Gale MD (1987) Biochemical/Molecular loci of hexaploid wheat (*Triticum aestivum*, $2n=42$, Genomes AABBDD). In: O'Brien SJ (ed) Genetic maps 1987. Cold Spring Harbor Laboratory Press, Cold Spring Harbor/NY pp 678–684

Johnson BL (1975) Identification of the apparent B-genome donor of wheat. Can J Genet Cytol 17:21–39

Marshall DR, Brown AHD (1975) Optimum sampling strategies in genetic conservation. In: Frankel OH, Hawks JG (eds) Crop genetic resources for today and tomorrow. Cambridge University Press, Cambridge, pp 53–80

McIntosh RA (1983) The wheat gene catalogue. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp, Kyoto, pp 893–940

Mendlinger S (1980) Genetic variation and population structure in the diploid species of the wheat group (*Triticum Aegilops*) as revealed by electrophoretically discernible leaf proteins. PhD Thesis, Hebrew University, Israel

Nei M (1975) Molecular population genetics and evolution. North Holland, Amsterdam

Nei M (1978) Estimation of the average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590

Nevo E (1978) Genetic variation in natural populations: patterns and theory. Theor Popul Biol 13:121–177

Nevo E (1983) Genetic resources in wild emmer wheat: structure, evolution and application in breeding. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp, Kyoto, pp 421–431

Nevo E, Goldberg E, 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

Rick CM, Fobes JF, Holle M (1977) Genetic variation in *Lycopersicum pimpinellifolium:* evidence of evolutionary change in mating systems. Plant Syst Evol 127:139–170

Sharma HC, Gill BS (1983) Current status of wide hybridization in wheat. Euphytica 32:17–31

Sharma HC, Waines JG (1981) The relationship between male and female fertility and among taxa in diploid wheats. Am J Bot 68:449–451

Sharma HC, Waines JG, Foster KW (1981) Variability in primitive and wild wheats for useful genetic characters. Crop Sci 21:555–559

Smith-Huerta NL (1986) Isozymic diversity in three allotetraploid *Clarkia* species and their putative diploid progenitors. J Hered 77:349–354

Waines JG (1983) Genetic resources in diploid wheats: the case for diploid commercial wheats. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp, Kyoto, pp 115–122

Weeden NG, Gottlieb LD (1979) Distinguishing allozymes and isozymes of phosphoglucoisomerase by electrophoretic comparisons of pollen and somatic tissues. Biochem Genet 17:287–296

Yaghoobi-Saray J (1979) An electrophoretic analysis of genetic variation within and between populations of five species in *Triticum-Aegilops* complex. PhD Thesis, University of California, Davis