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Ecogeographical distribution of HMW glutenin alleles in populations of the wild tetraploid wheat *Triticum turgidum* var. *dicoccoides*

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Summary. Polymorphism of high molecular weight (HMW) glutenin subunits in 466 accessions of the wild tetraploid wheat *Triticum turgidum* var. *dicoccoides* in Israel was characterized with regard to the ecogeographical distribution of the HMW glutenin alleles, both between and within 22 populations, and along transects in a single population. While some populations were monomorphic for all the HMW glutenin loci, namely, *Glu-A1-1, Glu-A1-2, Glu-B1-1* and *Glu-B1-2,* others contained up to four alleles per locus. Intrapopulation variability could be predicted by the geographical distribution: marginal populations tended to be more uniform than those at the center of distribution. The various HMW glutenin alleles tended to be clustered, both at a regional level and within a single population along transects of collection. It is suggested that this clustering is due to selection pressures acting both at a regional and at a microenvironmental level. This was confirmed by the significant correlations found between the MW of subunits encoded by *Glu-A1-1* and the populations' altitude, average temperature and rainfall. The possible selective values of seed storage proteins are discussed.

Key words: Wild tetraploid wheat – Selective value – Seed storage proteins

Introduction

Genetic control and polymorphism of high molecular weight (HMW) glutenins – a fraction of the storage proteins in the wheat kernel – were previously studied in the wild tetraploid wheat, *Triticum turgidum* var. *dicoccoides* ($2n=28$; genome AABB), the progenitor of most cultivated wheats (Levy et al. 1988). Two gene clusters (*Glu-A1* and *Glu-B1*) homologous to those of common wheat were identified on the long arms of chromosomes 1A and 1B, respectively. Each cluster was shown to contain two closely linked genes: *Glu-A1* consisting of *Glu-A1-1* and *Glu-A1-2,* and *Glu-B2,* consisting of *Glu-B1-1* and *Glu-B1-2.* Each gene showed a characteristic and high degree of variation, in contrast to enzymes' genes in the same species (Nevo et al. 1982). Although it is assumed that seed storage proteins might have additional functions other than providing amino acids to the young seedling, the adaptive value of their wide interspecific (Ladizinsky 1983) and intraspecific variation (Levy et al. 1988) has not been accounted for. Moreover, the neutralist-selectionist controversy on the nature of polymorphism in proteins (Lewontin 1974) has not been adequately resolved with regard to seed storage proteins. One of the few works that deals with the issue is that of Nevo et al. (1983), which suggests that variation in Hordeins is associated with microenvironmental differences in soil type.

In the present work we investigated the inter- and intra-population distribution of HMW glutenin alleles in var. *dicoccoides,* and examined whether this distribution is accountable by ecogeographical factors.

Materials and methods

Plant material and ecogeographical characteristics

Four hundred and eighty-four accessions of var. *dicoccoides* were randomly collected from 22 populations in Israel. The location, number of plants and geographical data on these populations are given in Table 1; the sites of collection are indicated in the map of Israel (Fig. 1). This collection is a sample of the

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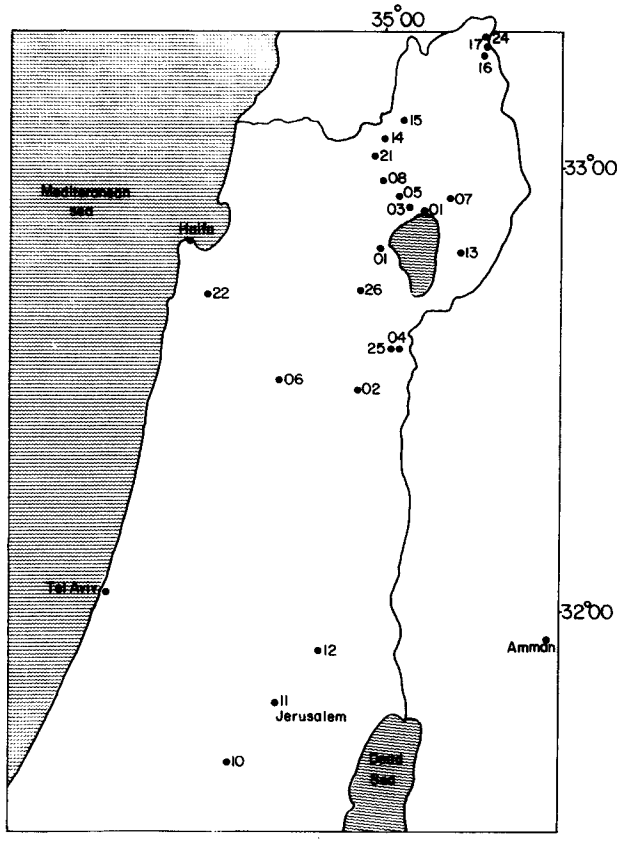

distribution of var. *dicoccoides* in Israel, and represents a wide spectrum of habitats. The size of the sampling area as well as the number of plants collected varied in different populations. Some populations, particularly the marginal ones (04, 10, 11, 12, 13, 14, 15, 16, 17, 21, 22, 24 and 25), were sparsely distributed, restricted to a section of the habitat and isolated from other populations; in these populations fewer plants could be collected, but most of the area was sampled. In other populations, particularly the central ones (01, 02, 03, 05, 06, 07, 08, 09 and 26), plants were abundant at the site of collection and in the surrounding area; in these cases, a representative area was sampled. Sampling area varied from 500 to 2,000 m².

In addition, 183 accessions were collected along four transects from a single population at Ammi'ad (Fig. 2). These accessions were kindly provided and are maintained by Dr. Y. Anikster, Tel Aviv University. Note that population 05 (Table 1) was at a different site, south of Ammi'ad. The method of collection and the transects were previously described (Anikster 1986). In summary, plants were collected along four transects (Fig. 2A–D); accession numbers are shown in Fig. 3. Transect A consisted mainly of a north-facing slope up to accession-33, where it was dissected by a wadi (accessions 33–45) and then continued on a south-facing slope (accessions 46 to 53). Transect B began at the top of a ridge (100–106), continued on an east-facing slope (107–137) and gradually leveled off to a valley (138–150). Transect C had a south-eastern exposure with a steep incline, and is about 500 m west of the

Fig. 1. A map of central and northern Israel. The sites at which accessions of var. *dicoccoides* were collected are indicated by the population number

Table 1. Ecogeographical data and number of plants (*N*) of 22 populations of var. *dicoccoides* in Israel

Population no. and location	*N*	Altitude (m)	Longitude[a]	Latitude[a]	Soil. type[b]	Average temperature[c]	Average annual rainfall (mm)
01 – S. Almagor	31	– 180	2,070	2,560	b	1	430
02 – Gilboa Mt.	19	350	1,900	2,120	tr	3	450
03 – N. W. Almagor	29	25	2,024	2,568	b	2	500
04 – N. Kokhav HaYarden	13	0	2,000	2,230	b	2	400
05 – S. Ammi'ad	28	220	2,010	2,600	tr	2	500
06 – Ta'anakh	21	250	1,700	2,125	tr	4	450
07 – Yahudiya	33	150	2,140	2,590	b	2	480
08 – E. Zefat	46	650	1,980	2,630	tr	3	700
09 – Arbel Mt.	36	110	1,960	2,470	tr	2	477
10 – W. Jaba	15	450	1,580	1,200	tr	4	450
11 – Jerusalem	10	800	1,700	1,340	tr	4	530
12 – Taiyiba	8	750	1,830	1,460	tr	4	450
13 – Elial	18	420	2,174	2,459	b	3	500
14 – S. Rihaniya	11	640	1,970	2,740	tr	4	640
15 – Ramot Naftali	24	500	2,020	2,790	tr	4	640
16 – Mas'ada	31	950	2,210	2,940	tr	5	1,040
17 – Majdal-Shams	17	1,100	2,220	2,960	tr	5	1,370
21 – N. Dalton	11	750	1,960	2,700	b	5	640
22 – Nahal Oren	15	250	1,540	2,360	tr	3	650
24 – Hermon Mt.	29	1,575	2,220	2,980	tr	6	1,400
25 – W. Kokhav HaYarden	10	150	2,000	2,230	b	3	400
26 – Kafr Kama	29	225	1,920	2,360	b	2	530

[a] Longitude and latitude are relative values which correspond to the Israeli net of coordinates
[b] b = basaltic, tr = terra rossa soils
[c] The average annual temperature is given as a relative value ranging from 1 (warm habitat) to 6 (cold habitat)

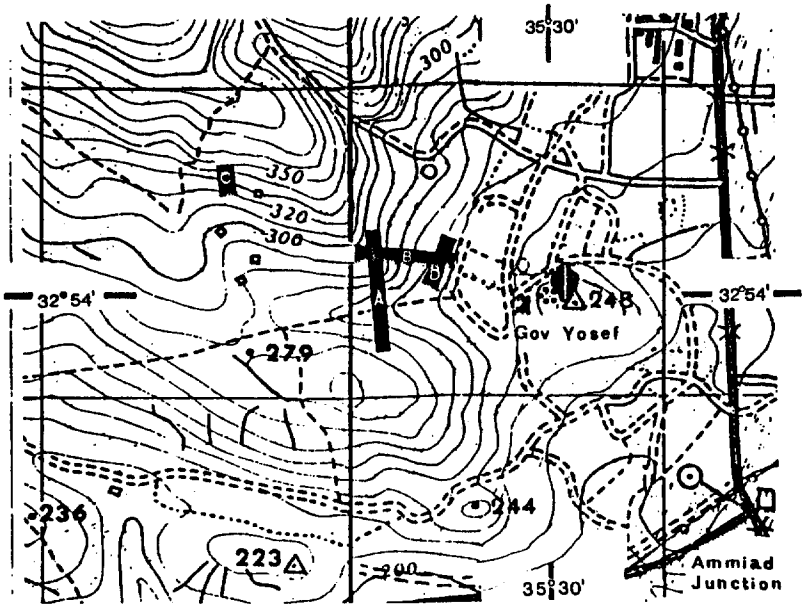

Fig. 2. General area (1:23720) of the Ammi'ad site, showing transects *A, B, C* and *D* (obtained from Anikster 1986)

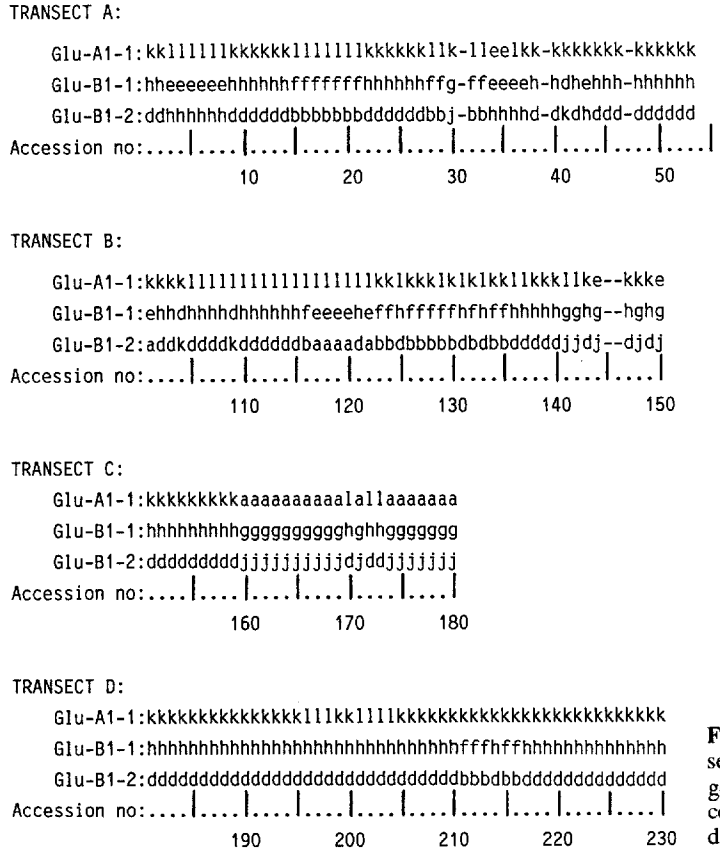

Fig. 3. Distribution of HMW glutenin alleles along transects *A, B, C* and *D* at Ammi'ad, for the HMW glutenin genes *Glu-A1-1, Glu-B1-1* and *Glu-B1-2*. Var. *dicoccoides* accession numbers are *indicated*. The alleles of each gene are described in Table 2

other transects. Transect D more or less followed the bottom level of a valley.

Plants of each transect were collected at intervals of 2–7 m, depending on the presence of var. *dicoccoides*. An accession number was ascribed to each plant, corresponding to the order of collection along the transects (Fig. 3).

Extraction and fractionation of HMW glutenins

In accordance with Galili and Feldman (1983), endosperm protein subunits were extracted from mature kernels collected from the wild, using 8 m*M* Al-lactate, followed by a sample buffer solution (consisting of 10% glycerol, 3% SDS, 5% 2-mer-

Table 2. Gene clusters (*Glu-A1* and *Glu-B1*), genes (*Glu-A1-1, Glu-A1-2, Glu-B1-1* and *Glu-B1-2*) and alleles coding for the HMW glutenins or var. *dicoccoides*. The MW (kDa) of the corresponding subunits is given

Glu-A1				*Glu-B1*			
Glu-A1-1		*Glu-A1-2*		*Glu-B1-1*		*Glu-B1-2*	
allele	MW	allele	MW	allele	MW	allele	MW
a	(null)	a	(null)	a	(null)	a	(null)
b	103.5	b	71.5	b	93.0	b	82.0
c	104.0	c	75.5	c	94.0	c	83.0
d	104.5	d	76.0	d	94.5	d	84.0
e	105.0			e	95.0	e	85.0
f	105.5			f	96.0	f	86.0
g	106.0			g	97.0	g	87.0
h	107.0			h	99.0	h	88.0
i	107.5			i	99.5	i	88.5
j	108.0					j	89.5
k	108.5					k	90.5
l	109.5						
m	114.0						

Table 3. Sorting of 26 populations of var. *dicoccoides* into three levels of intra-population variation of the HMW glutenin genes: *low* (one allele), *medium* (two alleles) and *high* (three to four alleles)

Gene	1 allele	2 alleles	3–4 alleles
Glu-A1-1	1, 4, 10, 11, 13, 15, 21, 22, 25	2, 7, 12, 14, 16, 17, 24, 26	3, 5, 6, 8, 9
Glu-A1-2	1, 4, 8 to 26	2, 3, 5, 6, 7	
Glu-B1-1	2, 4, 7, 10, 11, 12 13, 14, 15, 16, 21 22, 24, 25	1, 3, 5, 9, 17	6, 8, 26
Glu-B1-2	2, 4, 7, 10, 11, 12, 13, 15, 16, 21, 22, 25	1, 14, 17, 24	3, 5, 6, 8, 9, 26

captoethanol and 66 m*M* Tris-HCl, pH 6.8). Fractionation was carried out in SDS PAGE of 7%–12% acrylamide gradients. The samples were run on 13 cm long gels for 4 h at a constant voltage of 150 volts.

Estimation of molecular weight (MW)

The MW of various HMW glutenin subunits was estimated by comparison to the following protein markers (Pharmacia) with the indicated MW: phosphorylase-B (94,000), bovine serum albumin (67,000), ovalbumin (43,000) and carbonic anhydrase (30,000). Samples of the cv CS were run in each gel for comparison; the MWs of its HMW glutenins were previously described (Galili and Feldman 1983). The high-resolution, one-dimensional SDS PAGE enabled us to distinguish differences in MW as low as 500. Such differences were confirmed by several gel runs.

Alleles of each gene were determined based on the MW of the subunits they encode for (Levy et al. 1987). The various alleles of each gene, as well as the MW of the subunit they encode for are indicated in Table 2. The "a" allele of each gene corresponds to a "null" allele.

Results

Polymorphic vs. *uniform populations*

Populations were sorted according to the number of alleles of each gene within a population (Table 3). Uniform populations, with one allele per gene, like populations 4, 10, 11, 13, 15, 21, 22 and 25, were mostly marginal, and in most cases monomorphic at all loci. Populations with a wide variation, carrying 3–4 alleles per gene, like 3, 5, 6, 8, 9 and 26, were characteristically at the center of distribution of var. *dicoccoides,* and were polymorphic at all loci, except *Glu-A1-2,* which is usually inactive in var. *dicoccoides* (unpublished data). Polymorphic populations were found in cool and hot habitats, in terra rossa or basaltic soil, and at low and high altitudes. Similarly, monomorphic populations were found in a wide spectrum of habitats (Table 1). Therefore, intra-population variation could not be predicted by ecological factors.

Geographical distribution of alleles

Alleles varied in their distribution among the populations studied (Table 4). Some alleles were rare and unique to specific populations, like alleles d, f, g, h and m of *Glu-A1-1.* Rare alleles of *Glu-A1-1,* as well as of other genes, were found both in central and in marginal populations. Other alleles were very widespread, like *Glu-B1-2h* or *Glu-A1-1j,* which were found in very different habitats (Table 4). Geographically close populations (Fig. 1) tended to have similar alleles: in *Glu-A1-1,* null subunit occurred in populations 1, 3, 4, 5 and 7; allele e occurred in populations 3, 5 and 7; and allele i occurred in populations 11 and 12. In *Glu-A1-2,* allele c

Table 4. Frequency (%) of alleles of each of the HMW glutenin genes *Glu-A1-1*, *Glu-A1-2*, *Glu-B1-1* and *Glu-B1-2* in the 21 populations studied

Population	*Glu-A1-1*														*Glu-A1-2*				*Glu-B1-1*									*Glu-B1-2*									
	a	b	c	d	e	f	g	h	i	j	k	l	m		a	b	c	d	a	b	c	d	e	f	g	h	i	a	b	c	d	e	f	g	h	i	j	k
1	100														100								64		35											65		35	
2					84							16			16		84							100						100									
3	10				52	38									10		90					7	93						3						93			3
4	100														100										100					100								
5	57				35					4		4			64		36						93		7				4		4				93			
6			5							62	29	5			71	29				29			67		5				5	5		62			29			
7	73				27										73		27						100												100			
8				2						28		69			100				15	2				39	13		30			39					48		13	
9		69								8	17	6			100					14							86	36					13	14	36		
10			100												100						100												100					
11									100						100												100								100			
12									13		87				100												100								100			
14								91		9					100												100								9			91
15							100											100									100								100			
16												94	6		100									100									100					
17	18									82					100									47		53								47			53	
21										100					100												100								100			
22											100				100					100															100			
24										69		31			100									100					69						31			
25										100					100								100									100						
26		45								55					100								52			41	7	3			41				55			
Total no. of populations	6	2	2	1	4	1	1	1	2	10	4	7	1		20	1	4	1	1	4	1	1	7	5	5	2	8	6	4	1	1	2	1	3	15	1	3	2
Allelic frequency out of all populations	17	5	5	<1	8	2	5	4	5	25	11	11	<1		83	1	11	5	1	7	5	<1	27	18	7	4	30	6	12	<1	2	8	5	8	49	2	5	4

Table 5. Correlation coefficients between the MW of subunits encoded by the three HMW glutenin genes *Glu-A1-1, Glu-B1-1* and *Glu-B1-2,* and ecogeographical parameters (ecogeographical parameters were described in Table 1)

	Glu-A1-1	*Glu-B1-1*	*Glu-B1-2*	Altitude	Longitude	Latitude	Temperature (annual av)
Glu-B1-1	0.04	–					
Glu-B1-2	−0.12	0.13	–				
Altitude	0.37*	0.06	0.11	–			
Longitude	−0.04	0.12	0.15	−0.32*	–		
Latitude	0.13	0.01	0.25	0.11	0.58*	–	
Temperature (annual av)	0.41*	0.02	−0.02	0.85*	−0.40*	−0.10	
Rainfall (annual av)	0.33*	0.01	0.19	0.90*	−0.13	0.39*	0.70*

* Significant at a 1% level of significance

Table 6. Average MW of the subunits encoded by *Glu-A1-1, Glu-B1-1* and *Glu-B1-2* in var. *dicoccoides* populations arranged in four altitude transects. The altitude (m) along each transect is *indicated*

Transect 1				
Populations		03	05	08
(Altitude)		(25)	(220)	(650)
Glu-A1-1		105.2	105.6	108.7
Glu-B1-1		94.9	95.2	97.7
Glu-B1-2		88.2	87.9	85.8
Transect 2				
Populations		15	14	21
(Altitude)		(500)	(640)	(750)
Glu-A1-1		106.0	107.1	108.0
Glu-B1-1		99.5	99.5	99.5
Glu-B1-2		88.0	90.3	88.0
Transect 3				
Populations	07	16	17	24
(Altitude)	(150)	(950)	(1,100)	(1,575)
Glu-A1-1	105.0	109.9	108.0	108.5
Glu-B1-1	95.0	96.0	97.5	96.0
Glu-B1-2	88.0	87.0	88.3	88.0
Transect 4				
Populations		10	12	11
(Altitude)		(450)	(750)	(800)
Glu-A1-1		104.0	107.5	107.5
Glu-B1-1		94.0	99.5	99.5
Glu-B1-2		86.0	88.0	88.0

occurred in populations 3, 5 and 7. In *Glu-B1-1,* allele i occurred in populations 11 and 12 and in populations 14, 15 and 21; allele e occurred in populations 1, 2, 5 and 7. In *Glu-B1-2,* allele g occurred in populations 16 and 17 and allele h occurred in populations 1, 3, 5, 7, 8 and 9 or in 11 and 12 or in 14, 15 and 21. Although there is a general trend for alleles to form geographical clusters, some geographically close populations may have different alleles, like populations 4 and 25.

Distribution of alleles along transects in the Ammi'ad population

The distribution of the various HMW glutenin alleles of each gene along the transects is shown in Fig. 3. The order of the alleles along the transects corresponds to the order of collection of the accessions. *Glu-A1-2* was omitted, being usually inactive in var. *dicoccoides* (unpublished data) and in the material collected here. Some alleles, such as *Glu-A1-1k, Glu-A1-1l, Glu-B1-1h, Glu-B1- 1f, Glu-B1-2d* and *Glu-B1-2b* were widespread, while others were specific to certain transects, such as *Glu-B1-2h* to transect A, and *Glu-A1-1a* to transect C. The distribution of alleles along the transects was characteristically clustered; for example, allele *Glu-A1-1l* was found uninterruptedly from accession 15 to 21; allele *Glu-B1-1e* from accession 117 to 120; and allele *Glu-A1-1a* from accession 160 to 169. In most cases a specific allele of *Glu-B1-1* tended to occur together with a specific allele of *Glu-B1-2,* except for *Glu-B1-1e* which occurred either with *Glu-B1-2a* or *Glu-B2-2h.* This is probably due to the close linkage between these two genes (Payne et al. 1983). Although specific alleles of *Glu-A1-1* tended to occur with specific alleles of *Glu-B1-1* and *Glu-B1-2,* there are several "recombinant types": for example, *Glu-A1-1k* occurred either with *Glu-B1-1h* or *Glu-B1-1f* or *Glu-B1-1d; Glu-A1-1l* occurred either with *Glu-B1-1e, Glu-B1-1f* or *Glu-B1-1h.*

Relationship between the size of HMW glutenins and ecological conditions

The correlations between the MW of subunits encoded by the three HMW glutenin genes of all populations, and the ecogeographical parameters (Table 1) are shown in Table 5; correlations between the ecogeographical parameters are also indicated. Null alleles of each gene were omitted from the analysis. The MW of subunits encoded by *Glu-A1-1* was significantly cor-

related with altitude, temperature and rainfall, i.e., elevated, cool and rainy habitats were occupied by populations whose *Glu-A1-1* subunits had a high MW. Note that altitude, temperature and rainfall were significantly intercorrelated. Because of the tendency for regional clustering of alleles, the above findings were confirmed on a regional basis along four "altitude transects", since altitude was the most accurately determined parameter. The average MW of subunits encoded by *Glu-A1-1, Glu-B1-1* and *Glu-B1-2* in populations along these altitude transects is presented in Table 6. In all transects, subunits encoded by *Glu-A1-1* had a lower MW in populations of low altitude, whereas elevated populations were characterized by subunits of a higher MW. The same trend was observed in subunits encoded by *Glu-B1-1,* but not in subunits encoded by *Glu-B1-2.*

Discussion

Predicting the variability of the HMW glutenins

For all the HMW glutenin loci studied, marginal populations were less polymorphic than central ones in accord with Vavilov's theory that centers of distribution are also centers of variation. The narrow variation of marginal populations might result from a "double" founder effect: a) the founder effect of the first settler that colonized this new location, and b) a recurrent founder effect i.e., marginal populations, having a non-optimal level of adaptation, fluctuating much stronger than central populations. We observed that several marginal populations disappeared in one year and regenerated one or two years later with a very limited number of plants – the new founders. It is assumed that such fluctuations inhibit the establishment of wide genetic variability.

Clustering of alleles

Our data on the distribution of HMW glutenin alleles show a strong trend of clustering, both at a regional level (comparisons between populations) and within one population (at Ammi'ad along the transects). This clustering might be explained by two main models: 1) clusters result from neutral factors, such as founder effects in a given micro- or regional environment, resulting in temporary clusters along the transects due to gene flow, which is known to occur in var. *dicoccoides* (Golenberg 1986); 2) a given HMW glutenin allele confers to each accession of var. *dicoccoides* a higher adaptative value at a certain micro- or regional environment – in this case, clustering reflects a response to selective pressures.

The distribution of some alleles at Ammi'ad, such as *Glu-A1-1a* (Fig. 3), provides a strong indication that HMW glutenins are under selection pressures. This allele is not only confined to transect C, which is removed only 500 m from all other transects, but it is also abundant there, and therefore must have been present in this transect for a long period. Yet, despite its abundance and the evidence of recombinations among HMW glutenins, and considering the possibility of gene flow, this allele is absent from all other transects. These findings strongly indicate the adaptative value of this allele.

Correlation with ecological parameters

Since several alleles were specific either to certain regions, populations, or transects, the approach of correlating the frequency of alleles with ecological conditions could not be adopted. A more suitable parameter to be correlated with ecological traits was the MW of the HMW glutenin subunits encoded by the different alleles, which included all alleles, even the unique ones. The positive correlation of the MW of *Glu-A1-1* of all populations with temperature, rainfall and altitude (Table 5), and at a regional level with altitude (Table 6), indicates that at least one feature of the HMW glutenins, their size, is under selection pressure. This correlation excludes the possibility that the clustering of alleles, as found in this work, is due to a linkage of presumably neutral HMW glutenin genes with another unknown adapted gene, as suggested by Thomson (1977). Although it is difficult to point out the selective pressure of altitude *per se,* it might be that altitude, which is correlated to rainfall, temperature and radiation, reflects an integration of several parameters.

The *Glu-A1-1* gene showed the strongest relationship with ecological variation and was therefore of particular interest. It was also the most polymorphic HMW glutenin gene (Levy et al. 1988) and was strongly subjected to genetic inactivation (diploidization) as a result of cultivation (Feldman et al. 1986). It might be that among the HMW glutenin genes, *Glu-A1-1* is under the strongest selection pressure.

Possible selective value of HMW glutenins

Several other lines of evidence indicate the selective value of the HMW glutenin genes.

Interspecific variation. Closely related species might have different electrophoretic patterns of their seed storage proteins (SSP) (Levy et al. 1988). Based on conservative interspecific differences, Ladizinsky (1983) suggested that SSP are an excellent object for phylogenetic studies. Had the SSP not been subjected to selection pressures, their specific migration pattern would not have been so highly conserved, but would have been modified and confounded through mutation. This species-specificity suggests the involvement of these proteins in speciation.

Non-random and massive silencing under cultivation. It was previously shown (Feldman et al. 1986) that silencing

of the HMW glutenin genes was non-random, affecting genes of the *Glu-A1* rather than of the *Glu-B1* locus. Moreover, silencing occurred massively as a result of selection pressures during cultivation. Such a phenomenon is unlikely to occur in neutral genes.

Incomplete silencing. In all the accessions of var. *dicoccoides* studied, in 263 lines of var *durum* and in various accessions of diploid species studied in our laboratory (unpublished data), as well as in various reports in literature, no line was found to completely lack the HMW glutenin fraction; the smallest number of HMW glutenins subunits found was one. Had the function of the HMW glutenins been limited to providing amino acids for the developing seedling, one might expect to find lines with zero HMW glutenin subunits, as this function could as well be met by subunits of another fraction.

Indications for other functions of HMW glutenins. Mutants were characterized in maize and barley (high-lysine mutants) in which alterations occurred in the SSP structural gene(s), or in the amount of SSP synthesized. In these mutants, there was a reduction of 10%–90% in the accumulation of zein classes 19 and 22 kDa (Soave and Salamini 1983) and in the B and C hordeins (Shewry et al. 1980). Moreover, Kreis et al. (1983) found that the high-lysine barley mutant Riso 56 lacked several major components of the B hordeins; in this mutant at least 85 kilo base pairs of DNA were deleted from the *Hor-2* locus. Both the maize and barley high-lysine mutants had poor agronomical performances, and often had shrunken seeds or opaque endosperm. Thus, it might be that SSP interact with factors related to starch accumulation or seed development, either directly or indirectly through their packaging into protein bodies.

Role in packing. Pernollet and Mosse (1983) suggested in their "maximal packing" hypothesis that SSP structure is under strong selection pressures for a maximal packing within protein bodies, and that the repetitive sequences found in SSP genes are important for the secondary structure of the protein. This hypothesis is supported by the findings of Thompson et al. (1985) that allelic variation in HMW glutenins results from differences in the number of a 27 base pairs repeat. Yet, this variation did not affect the secondary structure. Although this hypothesis does not explain selective aspects such as speciation and seed development, it might represent an additional level on which selection acts.

The understanding of SSP functions could shed light on evolutionary processes related to these proteins, and be of great value for plant breeding.

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