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Allelic diversity of high-molecular-weight glutenin protein subunits in natural populations of *Dasypyrum villosum* (L.) Candargy

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Abstract. *Dasypyrum villosum* (L.) Candargy (2n = 14, V genome) is a wild, allogamous, diploid grass species that is a potential genetic resource for wheat improvement. The diversity of high-molecular-weight (HMW) glutenin subunits of the seed storage proteins of this species was examined in populations sampled in their natural habitats in Italy and Yugoslavia where the species is widely distributed. The results of selfed progeny tests confirmed that the allelic variation of HMW-glutenin subunits in *D. villosum* is controlled by a single locus (*Glu-V1*). Fourteen alleles at *Glu-V1* were found among 982 individuals representing 12 populations from Italy and two from Yugoslavia, with a mean of seven alleles per population. Among the 14 *Glu-V1* alleles, one produced no HMW-glutenin subunits, ten coded for a single subunit, and three for two subunits. The mobilities of all the subunits in SDS-PAGE gels were greater than that of reference subunit 7 of *Triticum aestivum* cv Chinese Spring. Eight of the alleles were relatively abundant (mean frequency over all populations ranged from 0.08 to 0.17) and distributed widely among the 14 populations (8 to 14); five of the alleles were rare (0.003 to 0.021) and found in only 1 to 5 populations. The frequencies of two alleles could not be individually estimated because of the similar electrophoretic mobility of their subunits. The multiple-allelic diversity at *Glu-V1* was high (H_e ranged from 0.700 to 0.857) but similar from population to population. Overall, about 7% of the total allelic variation was distributed among populations (G_{st} = 0.072), and more than 90% within populations. Whether the allelic variation at *Glu-V1* is subject to natural selection is unknown, but the discovery of the homozygous null *Glu-V1* alleles in the present study may be useful in pursuing this question. The multiple-allelic diversity in *Glu-V1* presents the plant breeder with an opportunity to evaluate and select the most useful alleles for transfer to wheat. The importance of an evaluation genetic diversity in a wild species before interspecific gene transfers are attempted is well illustrated in this study.

Key words: Triticeae – Poaceae – Wheat breeding – Genetic diversity – Multiple alleles – Seed storage protein

Communicated by G. E. Hart

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Introduction

Dasypyrum villosum (L.) Candargy (formerly known as *Haynaldia villosa* Schur) is an allogamous annual species (2n = 2x = 14, V genome) in the tribe Triticeae of the grass family Poaceae. It is distributed in West Asia and the Mediterranean regions. The *D. villosum* genome is distantly related to the A, B, and D genomes of common wheat, but hybrids between tetraploid (*Triticum turgidum* L. cv durum) and hexaploid (*T. aestivum* L.) wheats and *D. villosum* have been produced and several *D. villosum* chromosomes have been added individually to wheat (Sears 1953; Liu et al. 1983; Jan et al. 1986; Blanco et al. 1987). It appears, therefore, that genes of this species could be integrated into wheat chromosomes. Phenotypic evaluations have revealed potentially useful genes for wheat improvement, including resistance to powdery mildew caused by *Erysiphe graminis* (De Pace et al. 1988) and root-infecting fungi (Scott 1981), as well as to *Septoria tritici*, barley yellow dwarf virus, and salinity (G.-Y.

Zhong and C. O. Qualset, unpublished results). Direct use of the synthesized allohexaploid (AABBVV) as a forage crop is under investigation (De Pace et al. 1990).

D. villosum is also a reservoir for genic diversity for endosperm (seed) storage proteins (Montebove et al. 1987; Shewry et al. 1987, 1991; Blanco et al. 1991). Of particular interest with respect to potential value for wheat improvement are the high-molecular-weight glutenin (HMW-glu) subunits since these are associated with breadmaking quality in wheat (Payne et al. 1981; Payne 1987). Montebove et al. (1987) showed that a locus *Glu-V1* exists on chromosome 1V of *D. villosum*, apparently orthologous to the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci of hexaploid wheat. Subunits having a molecular weight of approximately 95,000 in *D. villosum* migrated in a sodium dodecylsulfate-polyacrylamide gel (SDS-PAGE) to the same region as the subunits controlled by *Glu-B1* in wheat. On this basis these authors suggested that the V genome was more closely related to the B than the A and D genomes of hexaploid wheat.

Although allelic variation in *Glu* is high in domesticated wheat, even more novel variation of HMW-glu subunits has been found in the wild progenitors and relatives of wheat (Lawrence and Shepherd 1980; Law and Payne 1983; Nevo and Payne 1987; Lagudah and Halloran 1988; Levy and Feldman 1988; Fernàndez-Calvìn and Orellana 1990). Hence these species may provide alternative genetic resources for improvement in the breadmaking quality of hexaploid wheat (Lagudah et al. 1987; Rogers et al. 1987).

De Pace et al. (1988) demonstrated variation in the size of single subunits controlled by *Glu-V1*, but the extent of allelic variation in natural populations is not known. In the present study natural populations from Italy and Yugoslavia were sampled and we report extensive variation in the HMW-glu subunits found singly in *D. villosum* and also show that alleles at *Glu-V1* produce two subunits comparable to the pairs of HMW-glu subunits coded by *Glu-B1* in wheat. In addition to the potential practical value of this information, storage protein loci provide important data concerning the evolutionary history of populations and for the study of population dynamics (Gepts 1990). This has been particularly useful in other species of the Triticeae, including wild barley, *Hordeum spontaneum* (Nevo et al. 1983), and wild tetraploid wheat, *Triticum turgidum* var. *dicoccoides* (Nevo and Payne 1987; Levy and Feldman 1988).

Materials and methods

Genetic materials

D. villosum populations were sampled by taking several spikes from each of ten or more plants from their native habitats in Italy

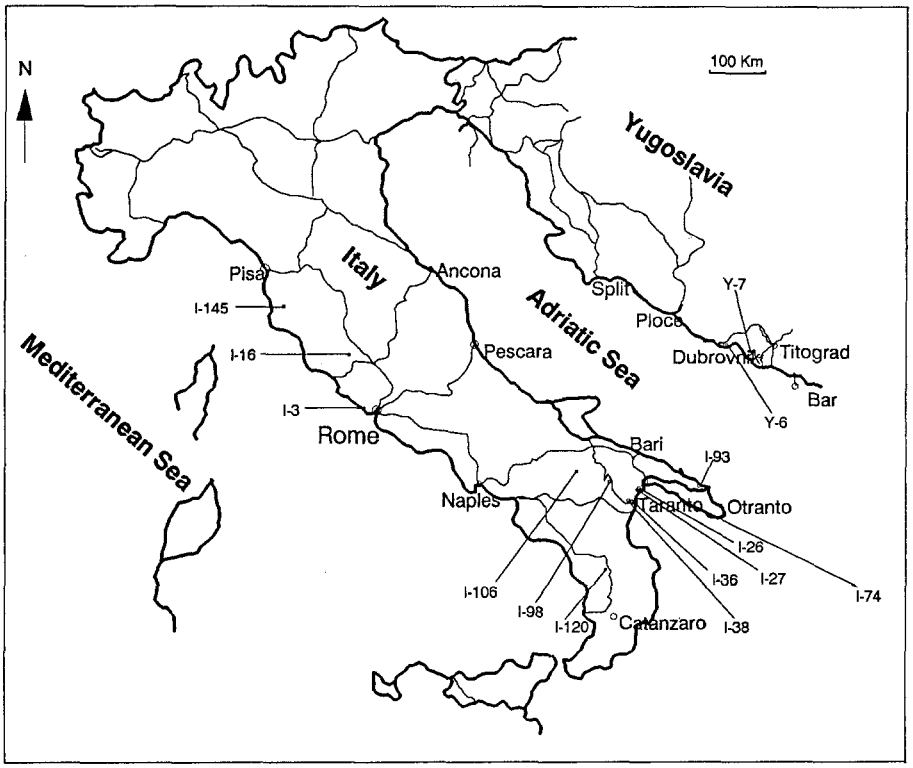

Fig. 1. Collection sites in Italy and Yugoslavia of 14 *Dasypyrum villosum* populations

(P. E. McGuire, C. De Pace, and C. O. Qualset, unpublished data) and Yugoslavia (Qualset et al. 1984). *D. villosum* is a predominantly outcrossing species (De Pace 1987); therefore seeds obtained from the same plant are collectively called a half-sib family. All the plants sampled at a site are said to represent a population. Seeds (referred as S_0 seeds) from random plants from 12 natural populations in Italy and two in Yugoslavia (Fig. 1) were used in this study. Five or more families, each with five or more seeds, were investigated in each population.

Allelic segregation patterns of HMW-glu subunits were determined from the progeny of spikes which were bagged preanthesis. Selfed seeds (referred as S_1 seeds) were produced on 33 S_0 plants grown from S_0 seeds of five populations in a field at the University of California Agronomy Farm near Davis.

SDS-PAGE electrophoresis

A modified Laemmli's system was used for SDS-PAGE according to Fullington et al. (1983). Samples were analyzed several times to establish the relative mobilities of the HMW-glu subunits. The subunits were named using the system of Payne and Lawrence (1983). The gene for HMW-glu in *D. villosum* was designated as *Glu-V1* (Montebove et al. 1987); therefore, the allele '*a*' of the locus coding for a unique glutenin subunit(s) is represented as *Glu-V1a*, with subsequently identified alleles as *b*, *c*, and so on. Subunits expressed as bands on the electrophoregrams were numbered sequentially from 71 onward from the highest to lowest molecular weight based on mobility in the polyacrylamide gel. The number 71 was taken arbitrarily as a starting point to avoid common identification of potentially different subunits listed by Payne and Lawrence (1983), since subunit homoeologies between *D. villosum* and common wheat could not be established. A common wheat variety *Triticum aestivum* cv Chinese Spring was used as the reference genotype.

Statistical methods

Because several *Glu-V1* alleles existed in each population assayed, estimation of the maternal allelic compositions of half-sibs and the determination of allele frequencies requires larger sample sizes per family than could be studied and evaluated by extension of the triallelic model as developed by Brown and Allard (1970). Instead, in our study the numbers of different *Glu-V1* alleles observed for each family in each population were enumerated. The relative frequency x_{ik} of allele k in population i was defined as

$$x_{ik} = \frac{\sum_j f_{ijk}}{\sum_k \sum_j f_{ijk}},$$

where f_{ijk} is 1 (or 0) if the kth allele is present (or absent) in the jth half-sib family of the ith population.

Based on the estimates of allele frequencies at the *Glu-V1* locus, several parameters expressing genetic diversity among and within populations were assessed according to the methods of Nei (1975). For $i = 1, 2, \ldots, s$ populations, the gene identity J_i for the ith population is calculated as

$$J_i = \sum_k x_{ik}^2.$$

Then gene diversity (H_{ei}) for the ith population is given as $H_{ei} = 1 - J_i$. Similarly, gene identity over all populations (J_t) is expressed as

$$J_t = \sum_k \left(\sum_i w_i x_{ik} \right)^2,$$

where w_i is the sample weight for the ith population and defined as $\sum_k \sum_j f_{ijk} / \sum_i \sum_k \sum_j f_{ijk}$. The gene diversity over all populations (H_t) can be obtained by $H_t = 1 - J_t$. H_t can be analysed into its components: $H_t = H_s + D_{st}$. H_s and D_{st} are the average gene diversities within and among populations, respectively. H_s is estimated as

$$H_s = \sum_i w_i H_{ei}$$

and $D_{st} = H_t - H_s$.

Then the relative magnitude of genic differentiation among populations, G_{st}, is estimated as D_{st}/H_t. The interpopulational gene diversity relative to the intrapopulational gene diversity (R_{st}) is given as $R_{st} = s D_{st}/(s-1)H_s$.

The coefficient of normalized genetic identity was estimated as

$$I_{i'} = \frac{J_{ii'}}{\sqrt{J_i J_{i'}}},$$

where $I_{i'}$, is the coefficient of normalized genetic identity between population i and population i', and

$$J_{ii'} = \sum_k x_{ik} x_{i'k}.$$

Results

Single-locus segregation pattern

The SDS-PAGE electrophoregrams of HMW-glu extracted from the selfed seed (S_1) of three S_0 plants of *D. villosum* from population Y-6 are presented in Fig. 2 as an example of the selfed progeny test for study of the genetic control of HMW glutenins. The electrophoretic patterns of HMW glutenins were codominantly expressed. One-hundred and seventy S_1 seeds from 33 S_0 plants of five populations, with a mean

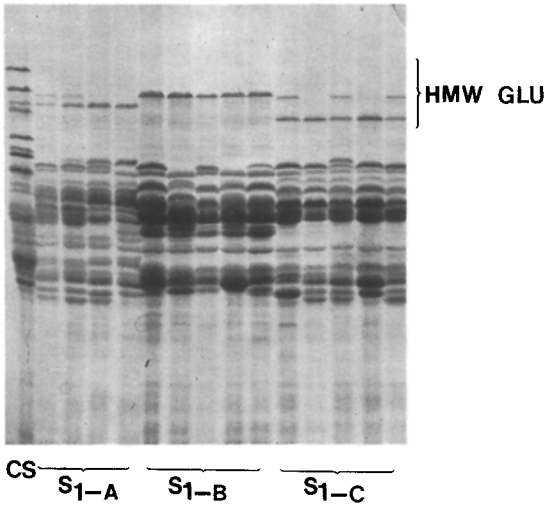

Fig. 2. SDS-PAGE electrophoregrams of total storage proteins extracted from 4, 5, and 5 S_1 progeny seeds of *Dasypyrum villosum* families A, B, and C from population Y-6. CS is a Chinese Spring wheat reference standard

of five selfed seeds per plant, were assayed. As inferred from the segregation patterns of selfed seeds, 13 S_0 plants were homozygous and 20 were heterozygous at *Glu-V1*. Of the 20 S_0 heterozygous plants, four had null alleles for which heterozygosity of the selfed seeds could not be determined after one selfing generation.

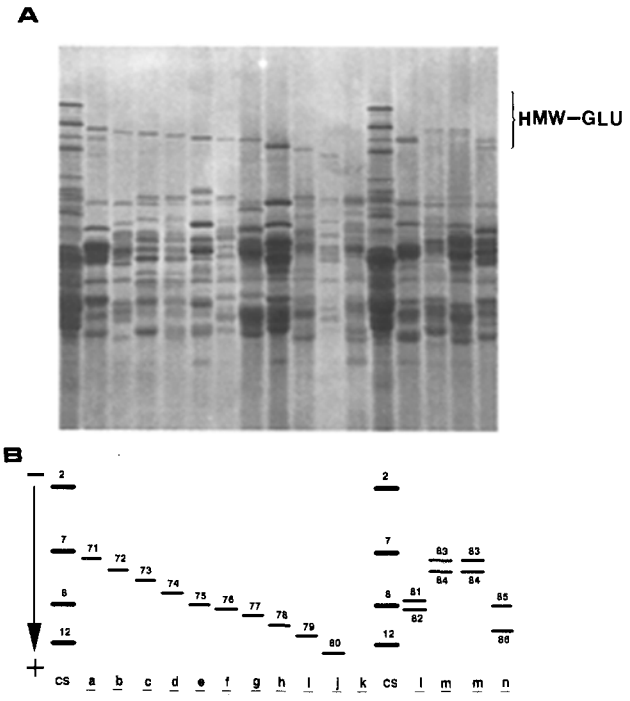

Fig. 3. **A** SDS-PAGE electrophoregrams of total storage proteins extracted from Chinese Spring (*CS*) and *Dasypyrum villosum* individuals having different HMW-glutenin alleles. **B** HMW-glutenin subunit alleles and subunits are identified by the small letters and numbers, respectively

The segregation results for 80 S_1 progeny from 16 heterozygous S_0 plants showed 38 homozygous and 42 heterozygous ($P > 0.5$ for 1:1 segregation), suggesting that a single locus, or several tightly-linked loci, produce the same type of HMW-glu subunits in *D. villosum*. Simple inheritance of HMW-glu subunit variation was also reported in the diploid species *Triticum tauschii* (Lagudah and Halloran 1988). Montebove et al. (1987), using the disomic addition lines produced by Sears (1953), mapped the HMW-glu locus to chromosome 1V of *D. villosum*.

Allelic diversity

Fourteen alleles coding for HMW-glu subunits were found among 14 natural populations of *D. villosum*. These alleles were inferred from the segregation patterns of the half-sib progenies. The SDS-PAGE electrophoregrams of the glutenin subunits coded by each allele are presented in Fig. 3 along with the designations of each allele and the corresponding subunit(s). Among the 14 alleles observed at *Glu-V1*, one produced no HMW-glu subunit (*k*), ten coded for a single HMW-glu subunit, (alleles *a* to *j* for subunits 71 to 80, respectively), and three coded for two subunits (alleles *l*, *m*, and *n* for subunits 81, 82, 83, 84, and 85, 86). The mobilities of all the subunits coded by *D. villosum* alleles were greater than that of subunit 7 of Chinese Spring (Fig. 3). Molecular weight comparisons of the glutenin alleles of *D. villosum* with those of common wheat were not made. Some alleles in *D. villosum* evidently migrated to different positions than the presently known HMW-glu subunits of wheat. Nine *D. villosum* HMW-glu subunits, each coded by different *Glu-V1* alleles (*a* to *i*), had relative mobilities within the

Table 1. Distributions of *Glu-V1* alleles among 122 families of 14 *D. villosum* populations

Population identity	Number of families with *Glu-V1* allele													No. of alleles	Total no. families	Mean no. seeds per family
	a	*b*	*c*	*d*	*e+f*	*g*	*h*	*i*	*j*	*k*	*l*	*m*	*n*			
I-3	2	5	2	1	0	5	5	0	0	1	0	0	0	7	6	8.8
I-16	6	5	1	0	2	5	1	2	2	0	0	0	0	8	7	10.3
I-26	13	5	9	0	6	4	7	3	0	3	0	1	1	10	15	7.3
I-27	4	5	5	0	4	2	0	6	0	6	0	0	0	7	8	10.0
I-36	3	3	5	0	3	1	2	4	0	0	0	0	1	8	9	5.6
I-38	6	11	2	0	3	2	5	3	0	7	0	0	0	8	12	10.3
I-74	4	7	1	0	3	1	1	0	0	7	0	0	3	8	8	8.4
I-93	0	3	4	0	2	1	3	0	0	4	0	0	1	7	7	5.4
I-98	9	7	2	0	0	4	6	1	0	3	3	0	0	8	10	10.0
I-106	3	4	2	0	0	2	0	2	0	3	0	0	2	7	5	7.8
I-120	0	2	4	0	5	0	0	5	0	4	0	0	0	5	6	7.7
I-145	4	0	8	0	0	14	0	1	0	5	0	0	0	5	14	6.7
Y-6	7	8	2	2	1	0	0	2	1	1	0	0	0	8	10	5.2
Y-7	5	0	1	0	4	1	0	3	1	0	0	0	0	6	5	11.4

Table 2. *Glu-V1* allele frequencies and diversity (H_e) in 14 populations of *D. villosum*[a]

Population identity	*Glu-V1* allele														
	N[b]	*a*	*b*	*c*	*d*	*e*+*f*	*g*	*h*	*i*	*j*	*k*	*l*	*m*	*n*	H_e
I-3	21	0.10	0.24	0.10	0.05	0.00	0.24	0.24	0.00	0.00	0.05	0.00	0.00	0.00	0.802
I-16	24	0.25	0.21	0.04	0.00	0.08	0.21	0.04	0.08	0.08	0.00	0.00	0.00	0.00	0.827
I-26	52	0.25	0.09	0.17	0.00	0.11	0.08	0.13	0.06	0.00	0.06	0.00	0.02	0.02	0.857
I-27	32	0.13	0.16	0.16	0.00	0.13	0.06	0.00	0.19	0.00	0.19	0.00	0.00	0.00	0.839
I-36	22	0.14	0.14	0.23	0.00	0.14	0.05	0.09	0.18	0.00	0.00	0.00	0.00	0.05	0.843
I-38	39	0.15	0.28	0.05	0.00	0.08	0.05	0.13	0.08	0.00	0.18	0.00	0.00	0.00	0.832
I-74	27	0.15	0.26	0.04	0.00	0.11	0.04	0.04	0.00	0.00	0.26	0.00	0.00	0.11	0.813
I-93	18	0.00	0.17	0.22	0.00	0.11	0.06	0.17	0.00	0.00	0.22	0.00	0.00	0.06	0.826
I-98	35	0.26	0.20	0.06	0.00	0.00	0.11	0.17	0.03	0.00	0.09	0.09	0.00	0.00	0.831
I-106	18	0.17	0.22	0.11	0.00	0.00	0.11	0.00	0.11	0.00	0.17	0.00	0.00	0.11	0.845
I-120	20	0.00	0.10	0.20	0.00	0.25	0.00	0.00	0.25	0.00	0.20	0.00	0.00	0.00	0.785
I-145	32	0.13	0.00	0.25	0.00	0.00	0.44	0.00	0.03	0.00	0.16	0.00	0.00	0.00	0.700
Y-6	24	0.29	0.33	0.08	0.08	0.04	0.00	0.00	0.08	0.04	0.04	0.00	0.00	0.00	0.783
Y-7	15	0.33	0.00	0.07	0.00	0.27	0.07	0.00	0.20	0.07	0.00	0.00	0.00	0.00	0.764
Weighted mean[c]		0.174	0.171	0.126	0.008	0.087	0.111	0.079	0.087	0.011	0.116	0.008	0.003	0.021	0.814

[a] Most frequent allele in a population underlined

[b] $\sum_k \sum_j f_{ijk}$

[c] $\sum_i (\sum_k \sum_j f_{ijk}) x_{ik} / \sum_i \sum_k \sum_j f_{ijk}$

Table 3. Analysis of allelic diversity in *Glu-V1* within and among 14 populations of *D. villosum* from Italy and Yugoslavia[a]

Source	No. populations	No. seeds	H_t	H_s	D_{st}	G_{st}	R_{st}
Italy	12	873	0.877	0.819	0.058	0.066	0.077
Yugoslavia	2	109	0.818	0.775	0.043	0.053	0.111
Overall	14	982	0.877	0.814	0.063	0.072	0.083

[a] See text for identification of symbols

range of subunits 7 and 12 of Chinese Spring. There are only three wheat HMW-glu alleles (*Glu-B1a*, *Glu-B1e*, and *Glu-B1k*) each coding for a single HMW-glu subunit known to migrate to this region. In addition, subunit 80, coded by *Glu-V1j* in *D. villosum*, had a relative mobility greater than subunit 12 of Chinese Spring. Such a HMW-glu subunit has not been observed in common wheat.

Population distribution of alleles

The allelic distribution in half-sib families for each population (Table 1) revealed 5 to 10 alleles (mean = 7) in each population. The numbers of families showing the *Glu-V1* alleles *e* and *f* were pooled because the relative mobilities of subunits 75 and 76 were very similar and not always discernible. *Glu-V1c* was found in all 14 populations and alleles *a*, *b*, *e* + *f*, *g*, *i*, and *k* were observed in ten or more populations. In contrast, alleles *l* and *m* were each found in only one population. Alleles *a* and *b* had the highest mean frequencies over all populations (Table 2). *Glu-V1c* was the third most common allele, followed by alleles *k* and *g*. The within-population gene diversities (H_e), also shown in Table 2, were high but similar from population to population.

Additional characterization of the diversity in *D. villosum* for the *Glu-V1* locus is presented in Table 3. The total allelic diversity within each country (H_t) was high and most of the allelic variation was distributed within populations (H_s) rather than among populations (D_{st}). The genic diversity among populations was similar for the Italian and Yugoslavian populations, being only about 7 and 5% of the total genic diversity (G_{st}), respectively. Taken together for populations from both countries, about 7% of the total allelic variation was distributed among populations and more than 90% within populations.

The coefficients of normalized genetic identity (Nei 1975) for each pair of populations (Table 4) gave further evidence about the degree of genetic differentiation of *D. villosum* populations at the *Glu-V1* locus. The mean value of the genetic identity between populations was 0.641 with a range of 0.242 to 0.903, indicating variation in interpopulation differentiation. The high identity coefficient between I-38 and I-74 (I = 0.903) indicated that these two populations share most of the alleles at approximately the same frequency, as is evident in the Table 2. Population Y-7, on the other hand, was dissimilar to I-93 (I = 0.242) and these two populations had only three alleles in common (Table 2).

The 14 populations were grouped according to their geographic origins (1, central Italy; 2, southern Italy; and 3, Yugoslavia). When the mean genetic identities were computed pair-wise within these groups, the

Table 4. Coefficients of normalized genetic identity ($I_{ii'}$) between 14 populations of *D. villosum* from Italy and Yugoslaiva

Population identity	I-3	I-16	I-26	I-27	I-36	I-38	I-74	I-93	I-98	I-106	I-120	I-145	Y-6	Y-7
I-16	0.752													
I-26	0.696	0.789												
I-27	0.510	0.666	0.765											
I-36	0.590	0.685	0.867	0.836										
I-38	0.763	0.745	0.755	0.822	0.689									
I-74	0.594	0.629	0.649	0.774	0.543	0.903								
I-93	0.696	0.421	0.672	0.729	0.672	0.772	0.766							
I-98	0.831	0.830	0.842	0.637	0.638	0.855	0.720	0.595						
I-106	0.663	0.764	0.733	0.856	0.712	0.856	0.871	0.683	0.778					
I-120	0.262	0.358	0.559	0.892	0.762	0.600	0.569	0.688	0.304	0.576				
I-145	0.625	0.602	0.590	0.542	0.475	0.379	0.376	0.513	0.502	0.600	0.351			
Y-6	0.589	0.815	0.721	0.701	0.677	0.822	0.731	0.448	0.793	0.798	0.403	0.263		
Y-7	0.264	0.707	0.773	0.672	0.726	0.472	0.404	0.242	0.520	0.491	0.586	0.365	0.578	
Mean	0.537	0.603	0.670	0.710	0.729	0.696	0.713	0.664	0.618	0.670	0.691	0.560	0.473	0.596

values for the two groups of Italian populations were 0.66 and 0.72, both larger than the estimate for the Yugoslavian groups (0.58). Intergroup identities (0.57, 0.60, and 0.58 for pairs of groups 1 with 2 and 3, 2 with 1 and 3, and 3 with 1 and 2, respectively) were about equal in magnitude, but two of them were lower than their intragroup identities. The identity coefficient for the two Yugoslavian populations was about the same as the intergroup value, indicating that these two populations had differentiated genetically, at least as measured by this single multiallelic locus.

Discussion

The allelic diversity at the *Glu-V1* locus of *Dasypyrum villosum* demonstrated here, with 14 alleles, is one of the highest reported in diploid plants. Of these alleles eight could be classified as common by the 0.05 frequency rule (0.09 to 0.17), and five as rare. Two alleles, *e* and *f*, could not be independently assayed because of a similar molecular weight of subunits and a very similar migration distance of the proteins in the SDS-PAGE gel. The rare alleles were indeed observed at low frequencies (0.003 to 0.021) and the mechanisms for maintenance of these alleles in natural populations deserves further study.

The high level of allelic diversity of HMW-glu subunits of *D. villosum* contrasts with that of three isozyme loci (De Pace 1987) where a maximum of three alleles was found for isozymes of glutamate-oxaloacetate-transaminase (GOT-2 and GOT-3) and esterase (EST-F) in Italian populations. Similar contrasting results were also reported from natural populations of tetraploid wild wheat *T. turgidum* var. *dicoccoides*, a selfing species, in which the mean number of alleles per locus per population was 2.5 (1.0 to 5.5) for HMW-glu and 1.33 (1.2 to 1.46) for isozymes (Nevo et al. 1982; Nevo and Payne 1987). High levels of polymorphism of the storage proteins were also found in *Hordeum spontaneum* (Nevo et al. 1983) and *Phaseolus vulgaris* (Gepts 1990). These observations suggest that variation is not uniformly distributed among loci, as also reported for isozymes in maize (Doebley et al. 1985). Nevo and Payne (1987) and Levy and Feldman (1988) suggested that HMW-glu subunits may have selective values in their natural habitats since storage proteins provide amino acids valuable to the establishment of young seedlings. Levy and Feldman (1988) did not find individuals lacking HMW-glu subunits in wild tetraploid wheat in their study, nor have such individuals been observed in previous studies of allelic variation of glutenin subunits in natural populations. In contrast, in the *D. villosum* populations studied here the homozygous null allele was found at an average frequency of 0.12 in 11 of 14 populations surveyed and was predominant in three of them. This suggests that the null allele in *D. villosum* may not be at a selective disadvantage in natural populations. The discovery of the presence of homozygous null alleles of HMW-glu subunits in this diploid species may be useful for studying the evolutionary significance of allelic variation in seed storage proteins.

Although the level of allelic diversity in HMW-glu of *D. villosum* in this study was higher than that for the isozymes examined by De Pace (1987), the distribution patterns of variation among and within populations were quite similar for HMW-glu and isozymes. The inter-population relative to intra-population (R_{st}) allelic variation of HMW-glu was 8% in the present study and similar to estimates (10%) for isozymes (De Pace 1987). Low levels of population differentiation in *D. villosum* could be attributed to the wind-pollinated and predominantly outcrossed breeding system of this

species, as found also in weedy rye (*Secale cereale* L.) populations (Sun and Corke 1992) and other predominantly outcrossing species (Brown 1979).

The average identity statistics (mean 0.641 with range 0.242 to 0.903) between *D. villosum* populations were much lower than that (0.956) found in isozymes for outcrossing species (Brown 1979). This may be largely the result of the within-population allelic richness of *Glu-V1* relative to that of most isozymes. A wide range in estimates of identity statistics based on allelic variation of HMW-glu was also observed by Nevo and Payne (1987) in populations of the selfing species *T. turgidum* var. *dicoccoides* (mean, 0.357; range, 0 to 0.983). They also reported that the correlation of glutenin diversity with geographical distance between populations was very low and nonsignificant, but significant correlations were found between the frequencies of specific glutenin alleles and physical (climate and soil) and biotic (vegetation) variables in *T. turgidum* var. *dicoccoides*. In a similar study with this species, Levy and Feldman (1988) and Levy et al. (1988) found significant correlations between the glutenin subunits and environmental parameters. They also observed that geographically close populations tended to have similar alleles. The present study showed similar results in that some geographically closer populations shared more genetic identity than geographically more distant populations, although this was not a generalized result.

Most of the glutenin alleles in the B and D genomes of common wheat code for two subunits, although a small number of alleles code for a single subunit (Payne and Lawrence 1983). The reverse was found in *D. villosum*. Among the 14 *Glu-V1* alleles, only three were found to code for two subunits and these were extremely rare alleles. These unique HMW-glu alleles of *D. villosum* may serve as alternative genetic resources for the improvement of breadmaking quality in wheat. For example, in common wheat, a significant amount of the variation of breadmaking quality can be associated with allelic variation of HMW glutenins (Payne et al. 1981; Rousset et al. 1992). In a preliminary study (unpublished results) this predictive relationship was confirmed for *D. villosum*. Dough mixing and baking quality predicted by an SDS-sedimentation test [method of Mansur et al. (1990) with 0.5 g whole meal flour] showed that a plant homozygous for the null allele (*kk*) had the lowest SDS-sedimentation value (19.0 ± 1 mm) while a heterozygous plant for the null allele (*ak*) showed a higher SDS-sedimentation value (54.5 ± 4.5), but still lower than plants homozygous *aa* (68.5 ± 2.5). This suggests the existence of a relationship of specific alleles to SDS-sedimentation values and, by inference, on breadmaking quality in *D. villosum*. Further elucidation of such correlations for other *Glu-V1* alleles will aid in identifying desirable *Glu-V1* alleles that may be transferred to wheat for the improvement of breadmaking quality, although the effects of various *Glu-V1* alleles on wheat quality should be ultimately evaluated in a wheat background.

Wild relatives of crop plants certainly provide valuable genetic resources for crop improvement. In this study intraspecific genetic diversity at a single locus of practical importance illustrated the value of assessing genetic diversity in wild populations so that specific gene alleles may be chosen for transfer to wheat or other crop plants.

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