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Wheat storage proteins: glutenin DNA diversity in wild emmer wheat, *Triticum dicoccoids*, in Israel and Turkey. 3. Environmental correlates and allozymic associations

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Abstract The diversity of high-molecular-weight (HMW) and low-molecular-weight (LMW) glutenin subunits in the tetraploid wild progenitor of wheat, *Triticum dicoccoides*, was studied at the DNA level by the polymerase chain reaction (PCR). The DNA diversity of HMW and LMW glutenins was shown to be correlated to environmental physical and biotic factors (climate, soil and pathogen resistance) and to allozyme variation. We conclude that glutenin DNA diversity is nonrandomly distributed and could be more optimally sampled in nature for future breeding programmes to improve bread quality.

Key words Glutenin DNA polymorphism · Environmental influence · Disease resistance · Allozymic variation · Natural selection

Introduction

Glutenin and gliadin prolamin storage proteins comprise most of the wheat grain endosperm. Glutenin consists of approximately 20% high-molecular-weight (HMW) glutenin subunits and 80% low-molecular-weight (LMW) subunits. The biochemistry and genetics of endosperm proteins in bread wheat have been extensively studied (e.g. Kasarda et al. 1976; Konzak 1977; Payne et al. 1980, 1981a,b, 1982, 1983, 1984; Galili and Feldman 1983a,b,c, 1985; Nevo and Payne 1987; Levy and Feldman 1987, 1988; Levy et al. 1988; Gepts 1990; Felsenburg et al. 1991) due to their importance in bread baking (Wall 1979). During the last 15 years we have explored the genetics of wild emmer wheat, the progenitor of all cultivated wheats, as promising resources for wheat improvement. Many agriculturally important traits have been studied (Nevo 1983, 1986, 1987, 1988, 1993a), including the diversity of high molecular weight glutenin at the protein level across the wild emmer range in Israel (Nevo and Payne 1987).

The diversity of HMW glutenin subunits in the tetraploid wild progenitor of wheat, *Triticum dicoccoides*, was studied electrophoretically in 231 individuals representing 12 populations of wild emmer from Israel (Nevo and Payne 1987). The results showed that (1) the two HMW glutenin loci, *Glu-A1* and *Glu-B1*, are rich in variation, having 12 and 15 alleles, respectively; (2) genetic variation in HMW glutenin subunits is often severely restricted in individual populations, supporting an island population genetic model; (3) there are significant correlations between glutenin diversity and the frequencies of specific glutenin alleles and physical (climate and soil) and biotic (vegetation) variables. Our results suggested that: (1) at least part of the glutenin polymorphisms in wild emmer can be accounted for by environmental factors, and (2) the endosperm of wild emmer contains many allelic variants of glutenin storage proteins that are not present in bread wheat, and these could be utilized in breeding varieties with improved bread-making qualities.

In a complementary paper in this issue (Pagnotta et al. 1995), we present a report on glutenin genetic diversity detected by the polymerase chain reaction (PCR). Two pairs of primers were used in the PCR in amplifying the DNA tracts coding the high- and the low-molecular-weight glutenin subunits (LMW glutenins in *T. dicoccoides* were not studied at the protein level by Nevo and Payne 1987). The DNA analyses revealed great diversity between and within populations, indicating the high values of this germ plasm for future breeding programmes to improve protein quality in wheat.

In the present article, we show that the diversity detected at the DNA level by PCR is associated with the environment (climate and soil variation), with glutenin allozymic diversity and with biotic factors of disease

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resistance. These associations suggest that glutenin diveristy, also at the DNA level, is nonrandom and oriented by natural selection as an adaptive environmental strategy. Furthermore, it can be utilized in agriculture for improving bread quality.

Materials and methods

Ecological and genetic background

Wild tetraploid emmer wheat, *Triticum dicoccoides*, is the immediate progenitor of most cultivated wheats, and is distributed over the Near East Fertile Crescent (Harlan and Zohary, 1966). Its center of distribution is in the drainage area of the Upper Jordan Valley in Israel, where it grows as an annual in steppe-like herbaceous formations, and in the *Quercus ithaburensis* park forest belt. Its ecological background has been described by Zohary (1969, 1970) and its ecological genetics by Nevo et al. (1982) and Nevo and Beiles (1989). A general review appears in Nevo (1995).

Sampling

Individual plants of *T. dicoccoides* were collected at random from 25 populations from Israel (24) and Turkey (1) during the period 1979–1987 across the major ecogeographical regions of wild emmer in Israel and in the 1 representative population in Turkey. The localities appear in Fig. 1 of Pagnotta et al. (1995, this volume), and their ecogeographical background appears in Table A(see results) or Table 1 of Nevo and Beiles (1989). The ecogeographic data is mainly derived from the Atlas of Israel (1970). We correlated the PCR results with 3 geographic, 18 climatic and 3 soil dummy variables and tested the seeds collected originally in the field (and propagated at the Institute of Evolution) for 42–50 gene loci (Nevo et al. 1982; Nevo and Beiles 1989). We also conducted diverse tests on samples of these genotypes, including tests for disease resistance [powdery mildew and leaf rust (Moseman et al. 1984, 1985; Nevo et al. 1985), stripe rust (Nevo et al. 1986) and stem rust (Nevo et al. 1991a)]. In the study presented here we analysed the data set of 249 plants belonging to 25 populations, out of the 37 populations reported in Nevo and Beiles (1989), for glutenin DNA diversity by PCR on the HMW and LMW glutenin subunits reported in our complementary paper (Pagnotta et al. 1995). We correlated the DNA glutenin diversity reported by Pagnotta et al. (1995) with other sets of data (glutenin diversity at the protein level, allozymes and disease resistances) involving the same genotypes.

Statistical analysis

Spearman rank correlations were computed between all variables. Stepwise multiple regression analysis (SPSS 1990) was employed to determine whether environmental factors were associated with frequencies of PCR bands of LMW and HMW glutenin subunits and their patterns, i.e. a series of bands of LMW and/or HMW characterizing genotypes (see Pagnotta et al. 1995). Principal component analysis was conducted on environmental factors which were then correlated with PCR glutenin bands and patterns. Levels of significance: * = $P < 0.05$;** = $P < 0.01$;*** $P < 0.001$, in all analyses.

Results

The full set of Tables A–F – ecological background, correlations, multiple regression and association with allozymes – can be received from the authors upon request. Any reference in the text to a lettered table (i.e. Table B) is to one of the retrieved tables.

The pattern of variation of glutenin PCR providing the following correlations appears in Pagnotta et al. (1995), which also includes genetic distances between populations and genetic differentiation within and between populations (Gst analysis).

Environmental correlates of PCR glutenin polymorphism

Correlations among LMW and HMW PCR glutenin bands and pattern frequencies with environmental variables

Some of both of the LMW and HMW PCR glutenin band and pattern frequencies are significantly correlated (r_s = 0.410* – 0.694***) with geographic, climatic (temperature and water availability factors) and soil variables. By chance we expected one significant correlation, on average, for each band or pattern. We found that HMW band 1780 showed 9 significant correlations and that the LMW 890 and 650 bands displayed 4 significant correlations each. Clearly, some of the frequencies increase (e.g. LMW band 650 increases mainly eastwards) or decrease (e.g. HMW 1780) with aridity. Likewise, the patterns have parallel trends. Each of the patterns LMW-16 and HMW-7 had 7 significant correlations.

We extracted principle component factors from different groups of ecogeographical variables (given in Table A or Table 1 of Nevo and Beiles 1989). These were correlated with band and pattern frequencies. The diversity of a PCR glutenin band and/or pattern is explained by geographic or climatic factors, either of temperature or water availability, or of both. The detailed correlation matrix appears in Table B.

Multiple regression analysis

A test of the best predictors of LMW and HMW PCR band and pattern glutenin frequencies (those that occured in at least 3 populations) in 23 populations was conducted by stepwise multiple regression analysis (MR). The MR employed the PCR variables as dependent variables and the geographic, climatic and edaphic variables as independent variables. Soil was used as 3 dummy variables of basalt (Bs), terra-rossa (TR) and rendzina (Rz). Temperature, water availability and soil variables in combination accounted for a significant proportion of the variation in PCR glutenin frequencies. For example a 3-variable combination consisting of soil type (Bs), August temperature (Ta) and daily temperature difference (Tdd) significantly explained 64% of the LMW 650 band diversity. Likewise, the frequency variance of HMW pattern-1 was explained by a 3-variable combination of seasonal temperature difference (Td), humidity at 14:00 (Hu-14) and January mean tempera-

ture (Tj); $R^2 = 0.535^{**}$. In summary the variation in 25 out of 30 bands and patterns was significantly explained by a combination of 3 or fewer variables (see Table C).

Associations between DNA PCR bands and patterns of HMW and LMW glutenins with HMW protein alleles

Extensive and strong associates were found between DNA PCR bands and patterns and HMW allozymic alleles. Only the strongest associations that remained significant or nearly so, after the Bonferroni Correction for multiple testing, are given in retrieved Table D. DNA and protein glutenin levels are associated even between HMW protein and LMW DNA PCR. For example: a positive association of *Gly-A1*^{1} with LMW 1054 ($\chi_1^2 = 15.508$, $P = 0.00008$) and *Glu-B1*^{8} with LMW band 650 ($P = 0.00010$, Fisher exact test).

Associations between DNA PCR bands and patterns with allozyme alleles of 18 polymorphic loci

Extensive and strong associations were also found between DNA PCR bands and patterns and allozymic at 18 polymorphic loci (Table E). There are 88 associations in Table E involving 22 loci. Four loci (*Aat-2a, Adh-1A, Adh-1B, Pept-2*) had no associations, while *Est-5A* had 27 significant associations. Six loci had 7–11 associations: *Est-4B*(11), *Nadh-1A*(10), *6Pgi-2*(9), *Mdh-1A* and *Pgi-1A*(8) and *Gluc*(7). Twenty-six associations were more significant then $P < 0.000005$; 6 involved *Nadh-1A;* 5 involved *Est-5A*; 3 with *Est-4B*; 2 with *Hk* and *6Pgd-2*; and a single association in additional loci.

The most associated patterns are number 7 of LMW glutenin (9) and number 18 of HMW glutenin (6). The "associated" bands (the numbers of associations are in parentheses) are : 1180(22), 1054(10), 831(10) of LMW glutenin while 2070 and 1740 of HMW glutenin participated only in 7 associations each. However, among the 26 most significant associations, 5 involved band 650 of LMW glutenin. Among those 26 associations 19 were with bands and only 7 were with patterns.

Likewise, genetic indices of the allozymes, *A* (allele diversity), *P*-1% and *P*-5% (polymorphism) and H_e (genetic diversity), showed Spearman rank correlations with 3 patterns (pattern 1 of LMW glutenins and patterns 3 and 10 of HMW glutenins, Table F). Pattern 10 of the HMW glutenins was correlated with *A*, *P*-1%, *P*-5% and H_e ($r_s = 0.409^*, 0.435^*, 0.463^*$ and 0.476^*, respectively).

Notably, associations were also found between glutenin DNA diversity (Table 1) and disease resistance genes to powdery mildew and leaf, stripe and stem rusts.

Discussion

The HMW and LMW glutenin subunits are important multiallellic gene families of storage proteins whose extensive polymorphism provides ample evidence for evolutionary theory and precious material for wheat breeding, primarily for baking quality. The high level of polymorphism at both the protein (Nevo and Payne 1987) and DNA (Pagnotta et al. 1995) levels provides useful material for (1) studying adaptations to different habitats and assessing the relative importance of

Table 1 Spearman rank correlations of glutenin PCR bands and patterns of wild wheat (*Triticum dicoccoides*) in Israel, with disease resistance. The test was conducted with 7 patterns and 7 bands of PCR of low-weight glutenins, and 4 patterns and 6 bands of high-weight glutenins. According to the Bonferroni correction for multiple testing we regard $P < 0.007$ as representing the 0.05 significance level for low-weight glutenin and $P < 0.0125$ and $P < 0.0083$ for patterns and bands of high-weight glutenins, respectively. Near-significant results appear in parenthesis. Sample sizes: $n = 54$ for resistance to powdery mildew and leaf rust, $n = 43$ for stripe (= yellow) rust and $n = 32$ for stem rust (*low*) Low-weight glutenin band, *High* high-weight glutenin band, *Patt* band pattern, *rs* resistance)

PCR	Powdery mildew		Leaf rust		Stripe rust (adults)		Stripe rust (seedling)		Stem rust	
	rs	*P*	rs	*P*	rs	*P*	rs	*P*	rs	*P*
Patt-1 Low	0.428	0.001	–		–		–		–	
Patt-2 Low	−0.383	0.004	–		–		–		–	
Patt-3 Low	0.444	0.001	–		–		–		–	
Patt-5 Low	−0.391	0.004	–		–		–		–	
Low-1156	–		–		–		0.450	0.003	–	
Low-1105	(−0.349)	0.010	–		–		–		–	
Low-831	(−0.359)	0.008	–		–		–		–	
Patt-2 High	–		–		(0.352)	0.021	(0.354)	0.023	–	
Patt-4 High	–		–		–		–		0.502	0.003
High-1600	–		–		–		–		0.520	0.002
Standardized to population mean disease resistance										
Patt-3 Low	–		−0.440	0.001						
Low-1156	–		−0.370	0.006						
Patt-3 High	–		(−0.359)	0.008						

the evolutionary forces involved in differentiation and (2) providing informative molecular markers for gene mapping. Practically, these subunits play a fundamental role in baking quality and the processing of foods such as chapatis and noodles. The genetic diversity at the protein level of HMW glutenin and its environmental correlates has been described in a previous paper (Nevo and Payne 1987), and a complementary paper describing DNA detected by PCR (Pagnotta et al. 1995, this vo-lume) presents the data for the correlations and associations described here.

In our protein-glutenin analysis we have identified three major features characterizing HMW glutenin in Israel: (1) extensive allozymic diversity: the two HMW glutenin loci, *Glu-A1* and *Glu-B1*, displayed a rich diversity, with 12 and 15 alleles, respectively; (2) extreme population differentiation displaying an island population genetic model; and (3) significant correlation with ecological factors (climate and soil parameters) and biotic (vegetation) variables. These results suggest that natural selection is a major determining evolutionary differentiation factor and that *T. dicoccoides* harbours many new glutenin alleles not found in wheat cultivars that could be used in improving breadmaking quality.

The complementary study of glutenin genetic diversity at the DNA level (detected by PCR) (Pagnotta et al. 1995, this volume) corroborated and extended the protein glutenin patterns into the DNA level, incorporating also LMW glutenin, which was not studied by us at the protein level. The major features now found at the DNA level are: (1) extensive PCR diversity, both within and between populations; (2) extensive population differentiation, both micro- and macrogeographically; (3) significant correlations with physical (climate and soil) and biotic (resistance to pathogens) environments. Ecological factors, rather than geographic distance, determine glutenin differentiation both at the protein and DNA levels, which display adaptive landscapes, as predicted theoretically by the environmental theory of genetic differentiation (Nevo 1988) and negating the neutral theory of molecular evolution (Kimura 1983). Importantly, the physical and biotic patterns displayed at the DNA level parallel those observed at the protein level.

Macrogeographic patterns appear to extend into microgeographic patterns. The aridity index, or climatic natural selection, plays a major role in glutenin differentiation at the DNA level, which is then translated into protein differentiation. The ecological-genetic factor (Nevo 1993b) is the key to understanding glutenin differentiation in wild emmer wheat, as is also true for both allozymic (Nevo 1988) and DNA differentiation in general (Nevo 1991), both within and between populations. This suggests that macrogeographic differentiation reflects on a larger scale, differentiation found microgeographically (see details in Nevo 1988, 1993a,b; Nevo et al. 1991b; and for a microgeographic glutenin study see Felsenburg et al. 1991).

Utilization of wild emmer wheat for glutenin diversity in bread making quality

Wild emmer wheat, the tetraploid progenitor of hexaploid wheats, harbours rich potential genetic resources for wheat improvement (Nevo 1983, 1988, 1993a), including glutenins (Nevo and Payne 1987). The idea to exploit the wild genetic resources of wild relatives of crop plants was largely developed by Vavilov and his school and has been elaborated upon by many investigators (e.g. Harlan 1976; Frankel and Bennett 1970; Frankel and Hawkes 1975; Frankel and Soule' 1980; Plucknett et al. 1983).

The potential genetic resources of wild emmer include disease-resistant genes against viruses (wheat soil-borne mosaic virus) and fungi (powdery mildew, yellow or stripe rust and stem rust), genes resistant against salt and herbicides and genes elevating protein quantity and quality, amino acid levels, amylases, heat production and photosynthetic yields, among others (see Nevo 1983, 1988, 1993a). Tapping these genes into commercial cultivars (e.g. powdery mildew, Reader and Miller 1991) is just beginning, and yellow rust resistance and high protein level will follow soon. But even these are just the beginning. Most of the genetic resources of wild emmer wheat (as well as other *Triticum* and *Aegilops* species) are yet untapped and await exploitation, including the LMW and HMW glutenins described here.

Glutenins, like other wheat grain proteins, play a key role in food processing, such as the manufacture of bread, biscuits, breakfast cereals, and pasta products (Payne and Rhodes 1982). A major effort of plant breeders is to develop elite bread wheats with improved breadmaking quality. Significant associations have been found for certain HMW subunits of glutenin and breadmaking quality (Payne et al. 1981b), which have since been confirmed (Moonen et al. 1982) and expanded (Payne et al. 1984). Dough strength is the limiting factor in the breadmaking process in western European wheats. This character is controlled by the elasticity of glutenin, which in turn is determined by the specific composition of its LMW and HMW subunits.

One approach to improving the quality of wheat cultivars for bread making is by utilizing genes from (1) landraces of primitive agriculture (Payne et al. 1984) and (2) the wild relatives of bread wheat (Law and Payne 1983). Wild emmer could provide a host of genetic variants of the endosperm storage proteins for improving breadmaking quality (Nevo and Payne 1987, Felsenburg et al. 1991; Pagnotta et al. 1995), as it does for other agronomic traits (Nevo 1983; Feldman 1979). The range of allelic variation in the glutenin loci of wild emmer is remarkable, and all of it could be readily transferred to bread wheat for testing by plant breeders.

Future challenges of crop improvemnt can be dramatically advanced by effectively utilizing the immense resources of genetic diversity unravelled by molecular biology in natural populations of the progenitors. Widespread exploration, evaluation, conservation (both in-

situ and ex-situ) and utilization of the rich unravelled genetic resources could be advanced by classical breeding and modern biotechnology, including the mapping, cloning and transformation of economically important major genes (reviewed in Nevo 1995). Population genetics and ecology, primarily at the molecular level of proteins and DNA nuclear and extranuclear genomes, relate genetic diversity, at both the single and multilocus genetic levels, to organismal evolutionary biology. The latter provides the basis for understanding environmental adaptations and the theoretical and empirical framework for crop improvement by old and new methods. A large number of glutenin alleles at both the protein and DNA levels have been found in wild emmer wheat to be intimately linked to the environment. These provide an invaluable resource for improving wheat cultivars and bread quality and quantity in an increasingly populated and starving world.

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