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Relationships among tetraploid wheat (*Triticum turgidum* L.) landrace populations revealed by isozyme markers and agronomic traits

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Abstract Diversity and relationships among ten tetraploid wheat landrace populations, collected from different localities in the central highlands of Ethiopia, were studied using isozyme markers and agronomic traits. This type of analysis in crop species is fundamental for designing optimal germ plasm collection, management practices and for developing an index for parental selection. The populations differed in allelic frequencies. Gene-diversity estimates showed that the populations encompass an appreciable amount of variation. However, differentiation between them was low, as was also confirmed by the presence of gene flow. Much of the diversity (85%), was attributable to the within-population level. The genetic distances were mostly small with the exception of those between a few pairs of populations. Thus, the relationships discerned among the populations were more of a similarity nature which could be ascribed to sharing a common ancestral population and/or adaptation to similar climatic conditions. The pattern of genetic divergence appeared to be independent of geographic distance. Considerable divergence in the agronomic traits was observed for certain populations. Cluster analyses of the isozyme and agronomic data produced different patterns and memberships of groupings. This lack of agreement could be ascribed to the different forces of evolution acting on isozyme markers and agronomic traits since agronomic traits, are the prime target of artificial selection. The clustering based on agronomic traits resulted in grouping together populations with similar agronomic performance. The results of this study suggest that taking more samples within a locality or population would be a better approach to capture the range of variation in the landrace populations of the central highlands of Ethiopia.

Key words *Triticum turgidum* · Landrace populations · Gene diversity · Genetic distance · Agronomic divergence · Relationships

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Introduction

Tetraploid wheat (*Triticum turgidum* L.) is the predominant wheat species grown in Ethiopia since ancient times and is believed to have accumulated a wide range of diversity as a consequence of considerable natural selection. Harlan (1971) noted that Ethiopia is a center of diversity for this wheat species. The main distributional range of the species covers areas between 1800 to 2800 m above sea level and its constituents are largely landraces harbouring variations in agro-morphological characteristics (Tesemma and Belay 1991). Anderson (1961) also observed that wheat fields in Ethiopia consist of mixtures of various types where introgression and the appearance of new types is likely to be enhanced. Landraces of crop plants hold a central position in genetic resources (Brown and Munday 1982) and are geographically and ecologically distinctive populations which are genetically diverse both between and within populations (Brown 1978). The study of the distribution of genetic variability in a crop species is of importance in conservation, as well as in the characterization (Asins and Carbonell 1989) and sampling of genetic resources (Brown 1978). The advent of isozyme electrophoresis has resulted in markers that have wide application in the characterization of plant germ plasm (Kahler and Lay 1985) and in the estimation of genetic variability in populations (Rebordinos and Perez de la Vega 1990).

Genetic distances within crop species are measures of the average genetic divergence between populations and

provide an index for parental selection and a structure for the stratified sampling of populations (Souza and Sorrells 1991b). The analysis of overall patterns of genetic diversity (Murphy et al. 1986) and relationships among germ plasm accessions (Souza and Sorrells 1991a) facilitates the selection of parents with diverse genetic background. Moreover, Peeters and Martinelli (1989) pointed out that hierarchical cluster analysis highlights the nature of relationships between any type of samples described by any type of descriptors which could serve as a basis for the selection of parental types with high potentials for segregation. In addition to markers of a qualitative nature, quantitative agronomic traits have been utilized to assess relationships among germ plasms (Souza and Sorrells 1991a) and cultivars (Cross 1994). The study of relationships among populations using quantitative characters is based on the assumption that the differences in the characters reflect their genetic divergence (Souza and Sorrells 1991a).

A previous study on morphological diversity involving seven of these tetraploid wheat landrace populations has established that the populations are composed of diverse forms (Tesfaye et al. 1991). However, information on the genetic structure and relationships of these populations is not available and this sort of information would provide a basis for planning and conducting future collections and the efficient utilization of them as genetic resources. The objectives of the present research were thus to study the pattern of genetic variation in ten populations originating from the central highlands of Ethiopia and to assess their relationships using isozyme markers and agronomic characters.

Materials and methods

Diversity and relationships among ten tetraploid wheat landrace populations collected from different localities in the central highlands of Ethiopia were studied based on isozymes and agronomic traits. The populations studied were: Ambo1 (A1), Ambo2 (A2), Ambo3 (A3), Ambo4 (A4), Bichena1 (B1), Bichena2 (B2), Bichena3 (B3), Kotu1 (K1), Kotu2 (2) and Cheffe Donsa (CDSA). The names of the populations refer to their localities of origin and they were sampled as described in Tesfaye et al. (1991). The regions in which the localities are situated are: Ambo, Bichena, Kotu and Cheffe Donsa. These cover an altitudinal range of 2200–2500 m above sea level, which is refered to as the central highland. Seeds were planted in pots filled with soil which were kept under uniform conditions of light and temperature in the greenhouse. Leaves of 7-day-old seedlings were used as sources of the enzymes assayed and each population in the assay was represented by 40 plants. The extraction and electrophoresis conditions are as described in Tsegaye and Tesemma (1995). At the end of electrophoresis, the gels were sliced and the middle and lower slices were stained. The enzyme systems assayed were: aconitate hydratase (ACO, E.C. 4.2.1.3), esterase (EST, E.C. 3.1.1.2), cathodal peroxidase (PRX, E.C. 1.11.1.7), malate dehydrogenase (MDH, E.C. 1.1.1.37) and phosphogluconate dehydrogenase (PGD, E.C. 1.1.1.44).

The staining solutions for aconitase, esterase and cathodal peroxidase are given in Tsegaye and Tesemma (1995). Malate dehydrogenase and phosphogluconate dehydrogenase were stained with slight modifications of the procedure of Brown et al. (1978). Following staining, the gels were incubated until the appearance of bands which were immediately scored. Only bands that had clear resolution and could be scored without ambiguity were considered. The inheritance of aconitase, esterase and cathodal peroxidase, and the designation of loci, are reported in Tsegaye and Tesemma (1995). For the remainder, the interpretation of zymograms was based on inference from the study of Nevo and Beiles (1989) in the tetraploid progenitor of cultivated wheat, wild emmer wheat. Letters were used to designate alleles of each locus. In cathodal peroxidase, the expressed allele was named as active (a), and the non-expressed as null (n).

Each population was split into component morphotypes which were evaluated in replicated trials for agronomic traits, and the data for each population were thus based on the average values of its morphotypes.

The agronomic traits considered were: days to heading, days to maturity, grain-filling period (days), plant height, tiller number, number of kernels/spike, number of spikelets/spike, number of kernels/spikelet, 1000-kernel weight, biological yield, grain yield/plant and harvest index. These traits had intermediate to high heritability values.

Genetic distances between all pairs of populations were calculated according to the unbiased method of Nei (1978). Gene-diversity estimates and an hierarchical analysis of gene diversity were made in order to sub-divide the total genetic diversity (Ht) into its components, i.e. among and within populations, in order to gain an estimate of the proportion of genetic diversity attributable to the different levels of structure based on the methods of Nei (1973). Euclidean distances were used for the agronomic traits and these coefficients were computed on standardized values of the traits so that all the traits become equally important in determining these distances (Manly 1986). The patterns of relationships between the populations were further examined by performing hierarchical cluster analyses using the genetic distance coefficients for the isozyme markers and the Euclidean distance coefficients for the agronomic characters. The clustering was based on the unweighted pair group method with arithmetic averages (UPGMA) using the program Numerical Taxonomy and Multivariate Analysis System, NTSYS (Rohlf 1993). Phenograms were produced from the clusters.

Results

A total of 18 alleles were detected at the nine polymorphic loci assayed. The frequencies of alleles determined, based on 40 individuals, are presented in Table 1. This sample size is regarded as sufficient for a self-pollinating species. The alleles *Pgd-1a, Aco-2b* and *Mdh-1b* appeared to be fixed in the populations since their frequencies were ≥98%. The other alleles of these loci occurred in more than one population with frequencies of <10% and could be considered rare and widespread. All alleles of *Aco-1*, *Est-3*, *Per-1*, *Per-2 and Per-3* could be described as having a common and widespread occurrence (Brown 1978). Null alleles were detected only in loci *Per-1* and *Per-3* and their frequencies, averaged over all populations, were 0.745 and 0.536 respectively. The degree of polymorphism varied from population to population, with populations Kotu2 and Kotu1 having a higher polymorphism at all loci. Of the loci studied, five, on average, had high levels of polymorphism (P>0.10) in the populations.

The gene diversity value averaged over all loci and populations was 0.216. The mean gene diversity (H) varied from 0.146–0.283, and the higher diversities observed were in the populations Ambo4=0.287, Ambo3=0.260, Bichena2=0.251 and Kotu2=0.232 (Table 2). On the other hand, the populations Ambo1=0.146, Kotu1=0.162 and Bichena1=0.178 had relatively low levels of diversity. This is an indication of the fact that the populations have con-

Table 1 Allele frequencies at nine isozyme loci in landrace populations of *T. turgidum*

Locus	Allele	Populations										
		A1	A2	A3	A4	B1	B2	B3	K1	K2	CDSA	X[a]
Aco-1	a	1.000	0.470	0.460	0.490	0.000	0.800	0.960	0.710	0.830	1.000	0.672
	b	0.000	0.530	0.540	0.510	1.000	0.200	0.040	0.290	0.170	0.000	0.328
Aco-2	a	0.060	0.000	0.000	0.030	0.000	0.000	0.000	0.090	0.030	0.000	0.021
	b	0.940	1.000	1.000	0.970	1.000	1.000	1.000	0.910	0.970	1.000	0.979
Est-3	a	0.770	0.730	0.190	0.480	0.440	0.570	0.610	0.060	0.470	0.300	0.462
	b	0.230	0.270	0.810	0.520	0.560	0.430	0.390	0.940	0.530	0.700	0.538
Mdh-1	a	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.050	0.000	0.008
	b	0.990	1.000	1.000	1.000	1.000	1.000	1.000	0.980	0.950	1.000	0.992
Mdh-2	a	0.980	0.970	1.000	0.980	1.000	0.970	1.000	0.890	0.940	1.000	0.973
	b	0.020	0.030	0.000	0.020	0.000	0.030	0.000	0.110	0.060	0.000	0.027
Per-1	a	0.000	0.000	0.480	0.430	0.500	0.270	0.230	0.090	0.150	0.400	0.255
	n	1.000	1.000	0.520	0.570	0.500	0.730	0.770	0.910	0.850	0.600	0.745
Per-2	a	0.600	0.580	0.460	0.490	0.280	0.500	0.320	0.820	0.450	0.470	0.497
	b	0.400	0.420	0.540	0.510	0.720	0.500	0.680	0.180	0.550	0.530	0.503
Per-3	a	0.810	0.370	0.590	0.460	0.880	0.470	0.340	0.000	0.200	0.520	0.464
	n	0.190	0.630	0.410	0.540	0.120	0.530	0.660	1.000	0.800	0.480	0.536
Pgd-1	a	1.000	1.000	0.970	1.000	1.000	1.000	0.920	0.960	1.000	1.000	0.985
	b	0.000	0.000	0.030	0.000	0.000	0.000	0.080	0.040	0.000	0.000	0.015

[a] X = mean frequencies of alleles over all the populations

Table 2 Gene diversity in the tetraploid wheat landrace populations

Locus	Population									
	A1	A2	A3	A4	B1	B2	B3	K1	K2	CDSA
Aco-1	0.000	0.498	0.497	0.500	0.000	0.320	0.077	0.412	0.282	0.000
Aco-2	0.113	0.000	0.000	0.058	0.000	0.000	0.000	0.164	0.058	0.000
Est-3	0.354	0.394	0.308	0.499	0.493	0.476	0.476	0.113	0.498	0.420
Mdh-1	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.039	0.095	0.000
Mdh-2	0.040	0.058	0.000	0.039	0.000	0.058	0.000	0.196	0.113	0.000
Per-1	0.000	0.000	0.499	0.490	0.500	0.394	0.354	0.164	0.255	0.480
Per-2	0.480	0.487	0.497	0.500	0.403	0.500	0.435	0.295	0.495	0.498
Per-3	0.308	0.466	0.484	0.497	0.211	0.498	0.449	0.000	0.320	0.499
Pgd-1	0.000	0.000	0.058	0.000	0.000	0.000	0.153	0.077	0.000	0.000
H[a]	0.146	0.211	0.260	0.283	0.178	0.251	0.215	0.162	0.235	0.211

[a] H = average gene diversity over all loci

siderable and variable levels of diversity. The most heterozygous loci were *Est-3*, *Per-2* and *Per-3*. The high level of diversity found in this study was in line with expectation since an outcrossing level of up to 3.5% was estimated in these landraces (Tsegaye 1996). These isozyme diversity values are, however, much lower than the morphological diversity values reported in Tesfaye et al. (1991).

The distribution of genetic variation at the various levels of structure for each locus is summarized in Table 3. The average total genetic diversity (Ht) was=0.273 and the range was 0.016–0.500. Five loci, *Per-2*, *Per-3*, *Est-3* *Aco-1* and *Per-1*, exhibited marked diversity, while the rest had values that were below the average. The mean within-population component of diversity (Hs) was 0.216 with a range of 0.015–0.459. The values of the loci *Per-2*, *Est-3*, *Per-3*, *Per-1* and *Aco-1* were above the average. The measure of interpopulational diversity (Dst), was on average 0.057, ranging from 0.001 to 0.182. The mean relative coefficient of gene differentiation (G_{st}) was 0.146 with a range of 0.024–0.413. This reveals that the interpopulational component accounted for almost 15% of the total diversity while 85% of the total was due to the within-population component. This finding is in agreement with the results of Tsegaye et al. (1994) where much of the diversity was due to the within-component, but is in disagreement with the morphological diversity results of Tesfaye et al. (1991) where the between-population component of diversity was larger. The highest differentiation coefficient was displayed by the locus *Aco-1*, followed by *Per-3*. Since G_{st} is equivalent to Wright's between-population differentiation coefficient, F_{st} (Nei 1973), the average number of migrants (Nm) between any pair of populations was estimated according to Slatkin and Barton (1989). This estimate was 1.460 suggesting the occurrence of gene flow

which may be sufficient to prevent any differentiation of the populations.

Genetic distance values computed for all possible pairs of populations are given in Table 4. The distances between pairs of populations were variable, ranging from 0.024 to 0.309, with an overall mean of 0.103. The highest genetic divergence values were displayed by the pairs Bichena1 and Kotu1 (D=0.309), followed by that for the pairs Ambo1 and Bichena1 (D=0.228) and Bichena1 and Cheffe Donsa (D=0.224), which are geographically separated. The lowest degree of genetic dissimilarity was between Bichena3 and Kotu2 (D=0.024), which also originated from areas that are geographically distant. Mostly, the divergence values were small and there appeared no marked trend in relation to geographic distance.

The Euclidean distance values (d), which reflect divergences for agronomic traits, are given in Table 5. The values ranged from 2.371 to 7.352 with a mean of 4.691. The highest values were between geographically distant populations (Ambo4 and Kotu2=7.512, Ambo4 and Cheffe Donsa=7.352). The lowest distance values included pairs both from the same and different regions, which is an indication of the absence of association between divergence and geographic distance. Some of the agronomic divergence values indicate the possibility of having used distantly related parents.

The results of cluster analysis in the form of dendrograms, illustrating population relationships for both the isozymes and agronomic characters, are presented in Fig. 1A and B respectively. Clustering of the populations on the basis of their genetic distances produced six groups. The largest of these groups comprised the populations Bichena2, Bichena3, Kotu2 and Cheffe Donsa. In the next largest cluster are the geographically proximal populations of Ambo3 and Ambo4. The remaining clusters included a single population each. With the exception of a single cluster, the clustering did not reflect the geographical proximity of the populations. Clustering based on the similarity of agronomic traits produced three major groups. The largest cluster contained five populations (Ambo1, Ambo3. Cheffe Donsa, Bichena1 and Bichena3). The second largest cluster comprised Ambo2, Bichena2 Ambo4 and Kotu1. In general the grouping was also not consistent with the distance of origin of the populations. One population, Kotu2, belonged to a single cluster. The clusters resulting from isozyme markers were different, both in pattern and composition, from those formed by agronomic traits. The

Table 3 Hierarchical analysis of gene diversity in the landrace populations

Locus	Level			
	H_t	H_s	D_{st}	G_{st}
Aco-1	0.441	0.259	0.182	0.413
Aco-2	0.041	0.040	0.001	0.024
Est-3	0.497	0.405	0.092	0.185
Mdh-1	0.016	0.015	0.001	0.062
Mdh-2	0.053	0.050	0.003	0.057
Per-1	0.380	0.314	0.066	0.174
Per-2	0.500	0.459	0.041	0.082
Per-3	0.498	0.373	0.125	0.251
Pgd-1	0.030	0.028	0.002	0.067
Mean	0.273	0.216	0.057	0.146

H_t = total gene diversity
H_s = gene diversity within population
D_{st} = gene diversity between populations
G_{st} = coefficient of gene differentiation

Table 4 Coefficients of genetic distance (D) between the populations

Population	A2	A3	A4	B1	B2	B3	K1	K2	CDSA
A1	0.076	0.146	0.104	0.228	0.057	0.063	0.202	0.086	0.110
A2		0.098	0.048	0.145	0.052	0.065	0.116	0.050	0.140
A3			0.025	0.067	0.068	0.096	0.119	0.085	0.089
A4				0.079	0.039	0.058	0.111	0.051	0.086
B1					0.161	0.213	0.309	0.215	0.224
B2						0.031	0.115	0.036	0.071
B3							0.124	0.024	0.069
K1								0.066	0.138
K2									0.077

Table 5 Euclidean distances (d) based on standardized values of the agronomic traits between pairs of the populations

Population	A2	A3	A4	B1	B2	B3	K1	K2	CDSA
A1	3.505	2.793	6.212	3.567	4.544	3.003	4.771	5.069	3.148
A2		4.665	4.101	5.131	2.925	4.463	3.423	6.743	5.261
A3			6.394	4.707	4.595	2.884	5.066	2.877	3.261
A4				6.410	3.785	6.253	2.371	7.517	7.352
B1					6.410	2.824	5.523	5.477	3.753
B2						5.496	2.825	6.419	6.015
B3							5.327	3.934	3.486
K1								6.205	5.952
K2									4.654

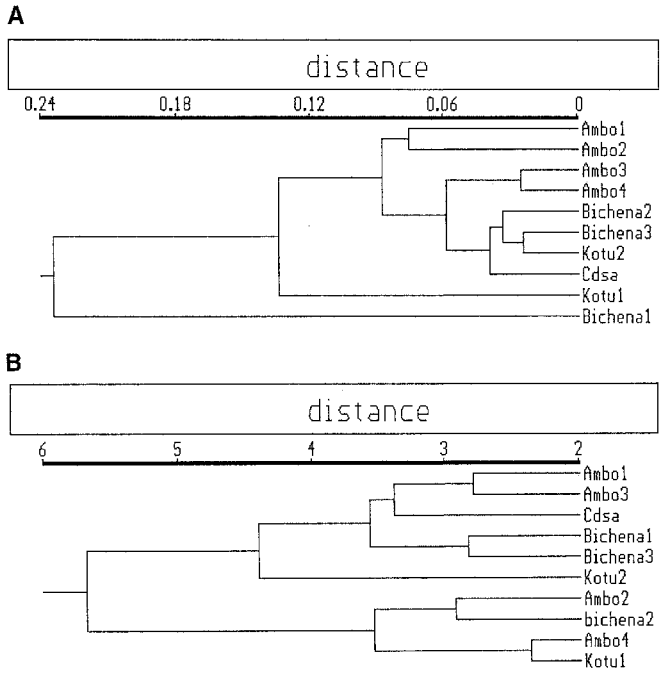

Fig. 1 A, B Phenogram generated based on the unweighted pair-group method with arithmetic averages (UPGMA) analysis of genetic distance (A) and Euclidean distance (B)

isozyme data highlighted Bichena1 and Kotu1 as the most distinct from the rest of the populations and from themselves, whereas the agronomic data did not depict such distinctiveness. Other combinations of populations were contained in distinctly different clusters for the agronomic data. Kotu1 had the highest seed yield followed by members of the largest cluster (data not shown). Ambo4 and Kotu1, which clustered together, were the lowest yielders. A similar picture was observed when compared in terms of maturity; Kotu2 being the earliest maturing followed by members of the largest cluster. The comparatively late ones also clustered together. Based on this observation it appears that the clustering provided an insight into the adaptation and agronomic performance of the populations.

Discussion

Information on genetic structure and relationships can be used to gain insight into population divergence, which is an important step towards an exploitation of genetic resources for hybridization breeding. In the present case the populations' differences were expressed in the frequencies of alleles. The occurrence of most of the alleles can be considered as common and widespread. The gene diversity values demonstrated the variability of the populations, and populations like Ambo4, Ambo3, and Bichena2 had relatively higher levels of diversity and clearly are more important sources of variation. The amount of diversity found in this study is comparable with that reported for a number of predominantly self-pollinating species (Brown 1978) and higher than that found by Nevo and Beiles (1989) in the wild emmer wheat (*Triticum dicoccoides*). Moreover, Asins and Carbonell (1989) have noted high isozyme variation in the durum-wheat collections of Ethiopian origin which they included in their study. The origin of this level of diversity was ascribed to the high degree of outcrossing observed in these landraces.

The nature of relationships among the populations as revealed by their genetic distances largely involved similarities, with the exception of some pairs which displayed divergence. This is further corroborated by a relatively low degree of differentiation, and evidence of gene flow. The most plausible explanations for the comparatively low genetic distances between the populations is that they have probably descended from a common ancestral population and have adapted to similar climatic and edaphic variables in the central highlands of Ethiopia. A practical implication of this is that a method of sampling more within a population or locality would be adequate to preserve the genetic variation.

The agronomic distance values, which are assumed to reflect the genetic diversity of the loci controlling these characters, indicated the possibility of selecting parents that have a diverse genetic background from these populations and the prospect of obtaining broad segregation for the characters.

The results of cluster analysis, which is a useful method to summarize genetic affinities, showed different patterns of clustering for isozyme and agronomic traits. The isozyme data resulted in six groups, whereas the agronomic data produced three major groups. A similar result was obtained by Cross (1994). The lack of concordance between isozyme and agronomic data indicate the influence of different evolutionary forces on the two categories of descriptors. Agronomic traits are the primary target of artificial selection, and traits like maturity and tillering capacity have significant adaptive value under the growing conditions obtaining at the site of origin of the populations. It is worth noting that clustering based on agronomic traits reflected the agronomic performance of the populations and could serve as a guide in predicting their segregation potential and adaptation.

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