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Distribution of genetic variability in a durum wheat world collection *

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Summary. A durum wheat world collection of 349 entries has been used to study the amount and distribution of genetic variability based on isoenzymatic characters involving a minimum of 13 loci. Genetic variability has been studied in a hierarchical fashion: between origins and within origins, further divided into between entries per origin and within entries. Factorial analysis of correspondences and chi-square distance were the basic statistical tools. The effect of domestication is deduced by comparing isozymic frequencies between wild emmer and durum wheat. It involves changes in frequencies mainly towards the accumulation of "null" alleles. The richest origins of genetic variation for durum wheat were Iran, Mexico, Ethiopia, Egypt and Afghanistan. Generally, between-entry variability was larger than the within-entry component. Exceptions were the accessions from Mexico, Greece, Argentina and Cyprus. The relationships between origins were greatly affected by their within-variability, the logic in the grouping is mostly along geographical or political lines. Egypt might be considered a microcenter of diversity for durum wheat within the Mediterranean center, although it is certainly related to Ethiopia (included in the Abisinic center). Mexico has become a new microcenter of diversity, quite likely man-made, and is distant from other centers of durum wheat diversity as far as gene frequency is concerned.

Key words: Germplasm collection – Crop evolution – *Triticum turgidum* L. – Isozymes – Variability distribution

Introduction

To measure genetic variability and study its pattern of distribution are essential tasks in germplasm conservation, if genetic erosion is to be effectively controlled. In that context, the application of gel electrophoresis to population genetics allows the estimation of both between- and within-population variability.

It is common knowledge that despite the high number of different wheat varieties, modern agronomic practices during the last 100 years have reduced the genetic diversity of advanced wheat cultivars. These became increasingly homogeneous genetically and, hence, vulnerable to new disease and adverse climatic changes. On the other hand, survey responses of plant breeders on the genetic diversity in major farm crops has revealed that the genetic base of the elite germplasm pool is wider and provides more useful diversity than is generally thought (Duvick 1984).

Plant breeding programs depend on the availability of large germplasm collections representing diverse gene pools. These collections are an invaluable source of parental strains for hybridization and subsequent development of improved varieties. The time-consuming process of a breeding program makes the choice of parents a critical step. Genetic diversity among parentals is considered an important factor for obtaining heterotic hybrids (Ghadery et al. 1984); therefore, a previous knowledge of the genetic variability of a crop is very useful to diminish the number of entries in the initial stages (screening and crossing) of the breeding program. Fortunately, germplasm collections have been established for many crop species; however, they generally contain such a large number of entries that it is now a major concern of gene bank managers and breeders, since desirable materials cannot be easily evaluated or located in such large collec-

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tions (Holden 1984). The study of genetic variability distribution in a crop species is a first step towards gene conservation and germplasm characterization, both of which are necessary to fill future needs in plant breeding and genetic engineering.

Wild emmer wheat, *Triticum turgidum* var. dicocoides, is the progenitor of tetraploid cultivated emmer *Triticum turgidum* var. dicoccum, which resulted after the accumulation of some mutations in durum wheat *T. turgidum* var. durum due to man's action (Feldman 1976). Diversity for quantitative spike characters in a world collection of durum wheat was recently studied (Spagnoletti and Qualset 1987). Their study used a large germplasm collection investigating the phenotypic variability of a sample of agronomic traits. However, a study on the distribution and nature of genetic variability using characters with known genetic control is still needed.

The purpose of the present paper is to study the amount and distribution of genetic variability based on isozymatic characters of a durum wheat world-wide germplasm collection, and to compare the results with previous studies, mainly those of variability in *T. turgidum* var. dicoccoides and *T. turgidum* var. carthlicum.

Material and methods

The base material was a world collection of 349 entries of durum wheat from the C.N.R. in Bari, Italy. One kernel per entry was assayed by horizontal polyacrylamide gel slab electrophoresis, following the methods described by Benito and Pérez de la Vega (1979) and Asins and Pérez de la Vega (1985b). The enzymatic systems examined were cathodal peroxidases of dry kernel, embryo plus scutellum and endosperm, and alkaline phosphatases of dry endosperm. Dry seeds of *T. aestivum* cv. Chinese Spring were always used as a control in the electrophoresis.

The nomenclature used for the isoenzymes and their corresponding loci is described in Asins and Pérez de la Vega (1985a, b), where the inheritance of these traits is also described.

Genetic variability has been studied in a hierarchical fashion as follows: (1) between origins, mostly countries; and (2) within origins; further subdivided into: (a) between entries per origin, and (b) within entries.

To comparatively study the contribution of the within-entry variability relative to the total variability found in the country of origin, a random sample of 101 entries from the world collection was analyzed, assaying nine kernels per entry. In this study, only embryo plus scutellum and endosperm cathodal peroxidases were analyzed. Hence, two sets of data were used throughout the study, each one with a different purpose. One, that using 349 entries, was aimed at having a better representation of the origin variability by using as many entries per origin as possible given the autogamous nature of the crop; another used less entries but with nine kernels per entry, in order to obtain an estimation of the within-entry variability. When the first set of data was analyzed to obtain an estimation of the between-entry variability, the original observations (0's and 1's) were used, whereas for the study at the origin level, the values used in the computations were those obtained by summing up all the original observations for each origin. Similarly, computations for the second set of data were based either on the observations at the kernel level when studying the within-entry variability (0's and 1's) or by summing them up when studying the between-entry variability (resulting in values in the 0–9 range).

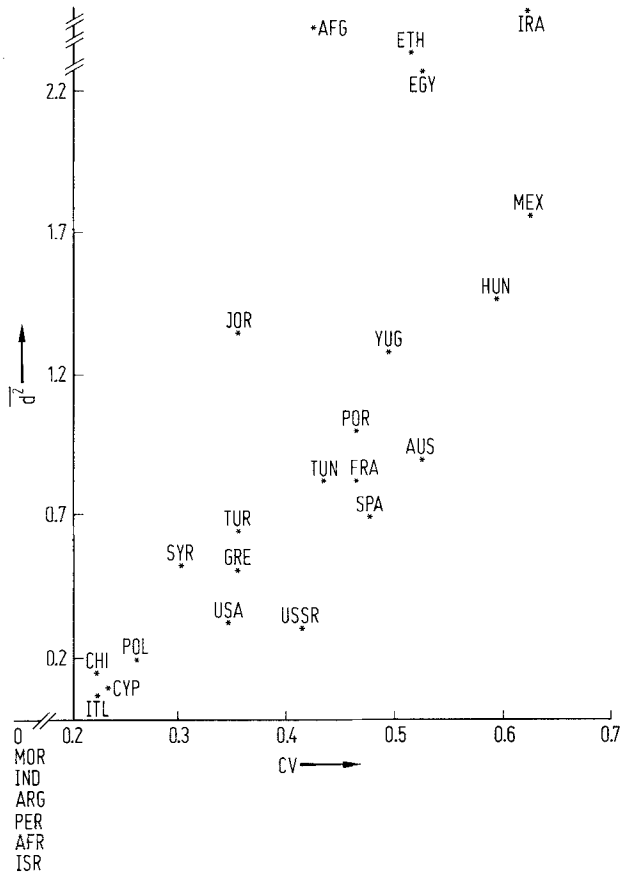

Fig. 1. Within origin variability of Table 2 data. Origins named by their first three letters

Since gene frequencies cannot be estimated from these isozyme data (every loci involves an active allele and a "null" allele), the statistical methodology (Asins and Carbonell 1986a, 1987) used to measure variability in the above hierarchical distribution was as follows:

(1) Factorial analysis of correspondences (Benzecri and Benzecri 1980) using data obtained by summing up all values in each origin. Dendrograms were based on the chi-square distance of Benzecri (1970) and the aggregation method was that of Lance and Williams (1967).

(2) Number of polymorphic loci and coefficient of variation of the mean isozymatic frequency, and mean chi-square distance obtained by averaging all chi-square distances between kernels from a given origin ($\bar{d}^2_{wo}$) as measures of the total variability within that origin.

(a) Mean of the chi-square distances between entries per origin using the first set of original data ($\bar{d}^2$) or data obtained by summing up all values of the kernels of a given entry ($\bar{d}^2_{be}$).

(b) Mean of the chi-square distances between kernels of a given entry; for a given origin, by its overall mean ($\bar{d}^2_{we}$).

When $\bar{d}^2_{we}$ was available, we consider the difference $\bar{d}^2_{wo} - \bar{d}^2_{we}$ to be a better estimate of the between-entry variability than $\bar{d}^2_{be}$.

Table 1. Peroxidase and alkaline phosphatase isozymic frequencies for those origins having more than one entry

Origin	*N*	Cathodal peroxidases								Alk. phosphatatase			
		a_1	a_2	d_2	*e*	*f*	*c*	*d*	4	3	4	5	7
Hungary	3	0	0.67	0.97	0.33	0	0.67	0.67	0.67	1	1	1	0
Poland	2	0	1	0.50	0	0	0	1	1	1	1	1	0
Australia	5	0	0.60	1	0.40	0	0.40	0.80	0.80	1	1	1	0
India	2	0	0	1	1	0	1	1	1	1	1	1	0
Afghanistan	2	0	0.50	1	0.50	0	0.50	1	1	1	1	1	0.50
USA	2	0	1	1	0	0	1	0.50	0.50	1	1	1	0
Argentina	2	0	1	1	0	0	1	1	1	1	1	1	0
China	2	0	1	0.50	0	0	1	1	1	1	1	1	0
Peru	2	0	1	1	0	0	1	1	1	1	1	1	0
Africa	2	0	1	1	0	0	1	1	1	1	1	1	0
Greece	4	0	0.75	0.50	0.25	0	1	1	1	1	1	1	0
Cyprus	3	0	1	1	0	0	0.33	1	1	1	1	1	0
Israel	2	0	1	0	0	0	1	1	1	1	1	1	0
Jordan	9	0	1	0.78	0	0	0.72	1	1	1	0.89	1	0.22
Egypt	7	0.14	0.43	0.71	0.43	0	0.29	1	1	1	1	1	0
Italy	8	0	1	1	0	0	0.75	1	1	1	1	1	0
Morroco	2	0	1	1	0	0	1	1	1	1	1	1	0
Iran	3	0	0.67	1	0.33	0.33	0.67	0.67	0.67	1	0.67	1	0
France	3	0	0.67	0.67	0.33	0	0.33	1	1	1	1	1	0
Portugal	53	0.04	0.72	0.70	0.28	0	0.72	0.92	0.92	1	0.98	1	0
Turkey	81	0	0.90	0.89	0.11	0	0.84	0.99	0.99	1	0.85	0.98	0.06
Syria	3	0	0.67	1	0.33	0	1	1	1	1	1	1	0
Ethiopia	20	0.25	0.75	0.65	0.05	0	0.45	0.95	0.95	1	0.95	1	0.05
USSR	30	0	0.97	0.87	0.03	0	0.93	0.73	0.70	1	0.97	0.97	0
Spain	14	0	0.71	0.79	0.36	0	0.50	1	1	1	0.93	0.93	0
Mexico	3	0	0.67	0.67	0.33	0	0.33	0.67	0.67	1	1	1	0
Yugoslavia	2	0	0.50	0.50	0.50	0	0.50	1	1	1	1	1	0
Tunisia	19	0	0.84	0.89	0.16	0	0.74	0.89	0.89	1	0.95	1	0.05
Mean freq.		0.01	0.80	0.80	0.22	0.01	0.73	0.91	0.91	1	0.98	0.99	0.02
Mean varianc.		0.01	0.11	0.10	0.11	0.01	0.10	0.04	0.04	0	0.02	0.01	0.02
Coef. variat.		10	0.37	0.35	1.36	10	0.43	0.22	0.22	0	0.14	0.05	7.08

Results

The peroxidase and alkaline phosphatase isozymic frequencies for those origins having more than one entry as well as the number of entries per origin (*N*) are shown in Table 1; isozymes a_1, a_2, d_2, *e* and *f* belong to embryo plus scutellum and *c*, *d* and *4* to endosperm. The overall mean, mean variance and coefficient of variation of the isozymatic frequency per locus are also shown in Table 1. No new isozyme has been found other than what was already reported in previously published work on wheat variability (Asins and Carbonell 1986 b); however, some isozymes commonly found in the wild emmer *T. turgidum* var. dicoccoides were not so common here (isozymes a_1 and *e*). Conversely, isozyme a_2 has become very characteristic of durum wheat.

The frequency of "null" alleles is much lower for isozymes of the endosperm than for those of the embryo plus scutellum. For endosperm, presence of "null" alleles mostly affects locus Phos 7, an isozyme quite frequent in the wild emmer group (Asins 1983) that is fixed in the hexaploid wheat cultivars (Salinas et al. 1982). Isophosphatase 3 is present in all entries.

For each origin the overall mean of the isozymatic frequency ($\bar{p}$), its coefficient of variation (CV), the mean variance ($\overline{var}$), the number of polymorphic loci (NPL) and the mean between-entry chi-square distance ($\bar{d}^2$) are shown in Table 2. A graphic representation of within-origin variability of data found in Table 2 is depicted in Fig. 1 as a function of the coefficient of variation of the mean isozymic frequencies (X axis) and the mean chi-square distance between all entries of a given origin (Y axis). Figures 2 and 3 show the dendrograms for isozymes and origins with more than one entry. The first three factors of the correspondence analysis accounted for 41.47%, 22.81% and 17.99% of the total variance, respectively. These factors were mostly related to isozymes *f*, a_1 and *e*, respectively.

The study based on 101 entries is summarized in Table 3, where *N* is the number of entries, $\bar{p}$ the overall mean of the isoenzymatic frequency, $\overline{var}$ its mean variance, CV its coefficient of variation, and $\bar{d}^2_{we}$, $\bar{d}^2_{be}$ and $\bar{d}^2_{wo}$

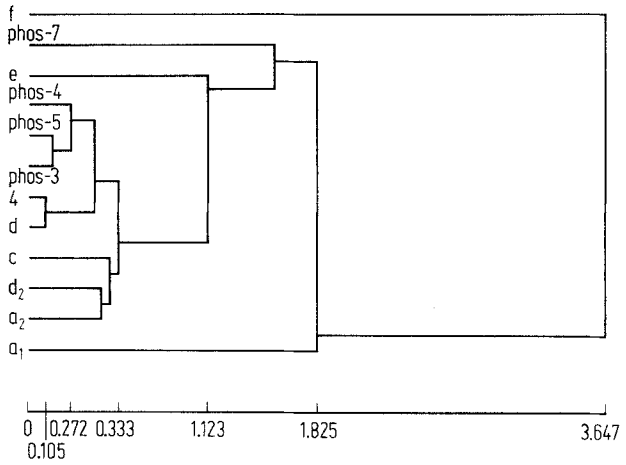

Fig. 2. Dendrogram for peroxidase and alkaline phosphatase isozymes

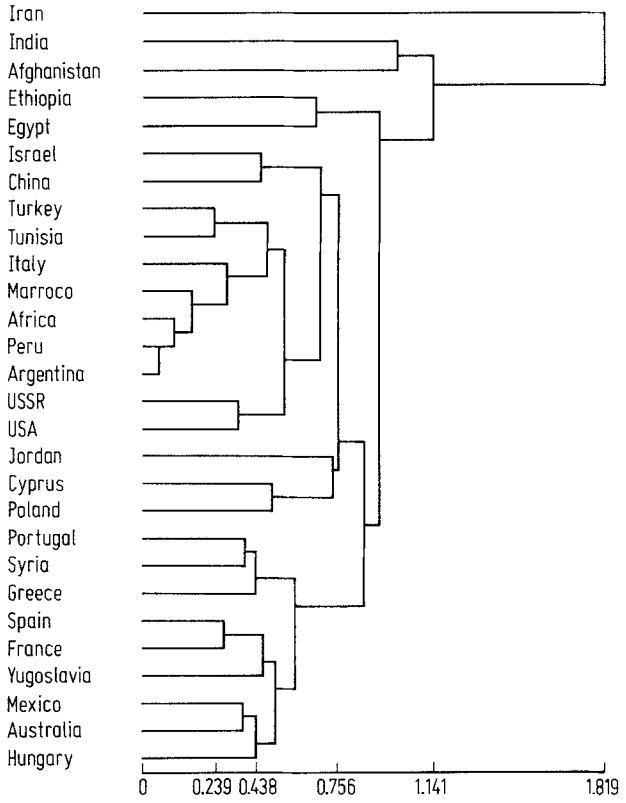

Fig. 3. Dendrogram for origins with more than one entry

Table 2. Within-origin variability

Origin	NPL	$\bar{p}$	$\overline{var}$	CV	$\overline{d^2}$
Hungary	6	0.56	0.11	0.59	1.48
Poland	1	0.54	0.02	0.26	0.21
Australia	5	0.58	0.09	0.52	0.91
India	0	0.67	0	0	0
Afghanistan	4	0.67	0.08	0.42	3.58
USA	2	0.58	0.04	0.34	0.34
Argentina	0	0.67	0	0	0
China	1	0.63	0.02	0.22	0.16
Peru	0	0.67	0	0	0
Africa	0	0.67	0	0	0
Greece	3	0.63	0.05	0.35	0.52
Cyprus	1	0.61	0.02	0.23	0.12
Israel	0	0.58	0	0	0
Jordan	4	0.64	0.05	0.35	1.36
Egypt	5	0.58	0.09	0.52	2.38
Italy	1	0.65	0.02	0.22	0.07
Morroco	0	0.67	0	0	0
Iran	7	0.58	0.13	0.62	19.02
France	4	0.58	0.07	0.46	0.84
Portugal	8	0.61	0.08	0.46	1.01
Turkey	9	0.63	0.05	0.35	0.66
Syria	2	0.67	0.04	0.30	0.54
Ethiopia	9	0.59	0.09	0.51	2.82
USSR	8	0.60	0.06	0.41	0.32
Spain	6	0.60	0.08	0.47	0.71
Mexico	6	0.53	0.11	0.62	1.87
Yugoslavia	4	0.58	0.08	0.49	1.28
Tunisia	8	0.62	0.07	0.43	0.83

Table 3. Genetic variability distribution based on a sample of 101 entries

Origin	N	$\bar{p}$	$\overline{var}$	CV	$\overline{d^2_{we}}$	$\overline{d^2_{be}}$	$\overline{d^2_{wo}}$
Greece	3	0.53	0.09	0.57	4.97	4.97	7.51
Ethiopia	5	0.51	0.11	0.65	2.14	4.08	5.16
Mexico	2	0.22	0.09	1.36	2.14	1.33	3.02
Egypt	4	0.45	0.10	0.70	0.02	1.28	1.01
Portugal	22	0.51	0.09	0.60	0.12	0.78	0.86
Tunisia	4	0.52	0.07	0.51	0.19	0.77	0.85
USSR	6	0.53	0.05	0.43	0.01	0.47	0.41
Turkey	25	0.53	0.05	0.43	0.08	1.50	0.40
Argentina	2	0.59	0.02	0.24	0.17	0.23	0.27
Italy	4	0.56	0.02	0.25	0.13	0.11	0.18
Spain	6	0.56	0.01	0.22	0.08	0.11	0.15
Israel	2	0.49	0.03	0.35	0.03	0.24	0.15
Cyprus	2	0.53	0.02	0.27	0.09	0.01	0.10
Morroco	2	0.56	0	0	0	0	0
Peru	2	0.56	0	0	0	0	0

are the corresponding mean distances, as already defined. Origins represented by only one entry were excluded: Germany, Australia, Poland, Iran, Syria, Jordan, France, Algeria, Hungary and Yugoslavia. From these origins, only Germany and Australia showed within-entry variability. A graphical representation of the distribution of genetic variability is shown in Fig. 4, where the Y axis is the mean chi-square distance between all kernels of a given origin and the length of the bars represent the difference between the total variation (measured by the mean between kernel distances) and the within-component. If this difference is smaller than the within-component, a broken line instead of a solid one is used.

With this set of data, the first two factors of the correspondence analysis accounted for 48.36% and 31.77% of the total variance. Hence, the representation

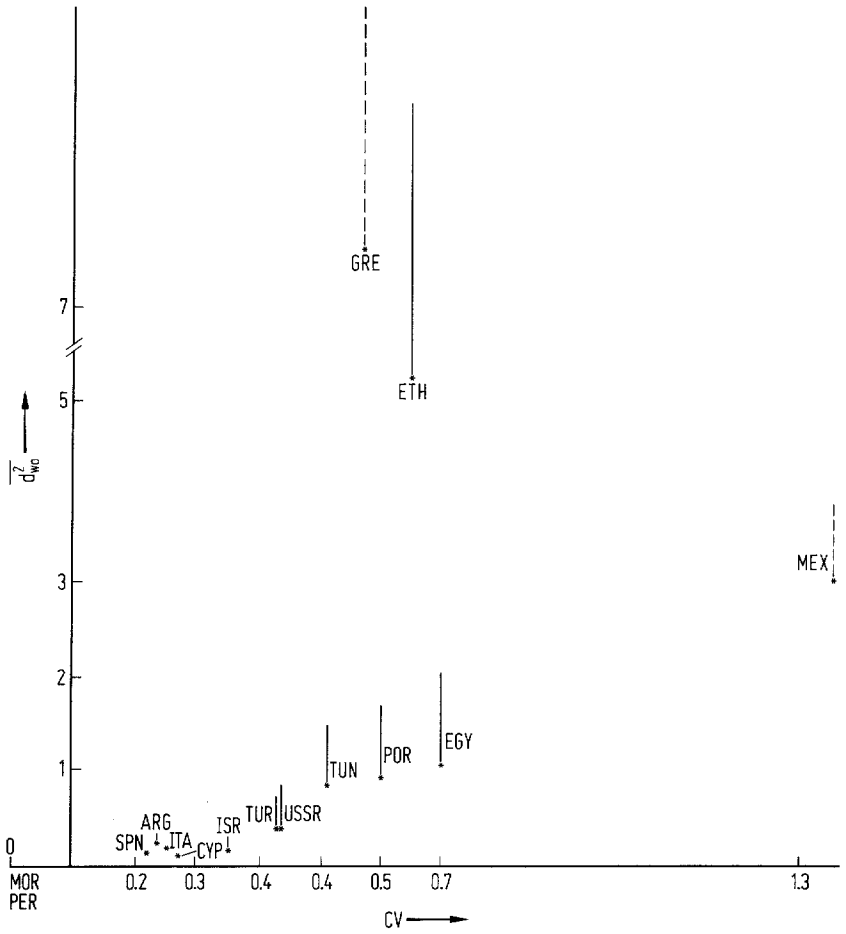

Fig. 4. Distribution of genetic variability for Table 3 data

using two factors is quite informative of the inter-origin variability distribution and is shown in Fig. 5. The first factor is related to isozyme *f* and Iran and the second factor to the isozyme a_1 and Ethiopia. The point where Turkey is located also represents the following origins: Spain, Italy, Egypt, USSR, Tunisia, Cyprus, Morocco, Syria, Jordan, Poland, Australia, Argentina and Peru.

Discussion

The durum wheat collection used here is less extensive than that used in previously reported work (Spagnoletti and Qualset 1987); however, it came from the same germplasm institution and the number of entries per origin are proportional between collections. Therefore, our study might be considered a random sample of the original durum wheat collection. The loci used do not represent a random sample – the enzymatic systems screened in this study involved a minimum of 13 loci and the peroxidase system includes a minimum of nine loci. Dry kernel peroxidases have been shown to be good genetic markers to distinguish between wheat species (Asins et al. 1981).

The durum wheat collection as a cultivated species

Three very rare isozymes were found in *T. turgidum* var. durum: a_1, *f* and *7*. This explains their great involvement in the first factors of the correspondence analysis. Their mean frequencies are almost identical to their mean variances (see Table 1). Isozymes a_1 and *7* are common in *T. turgidum* var. dicoccoides (the wild emmer progenitor of durum wheat); *f* is quite abundant in *T. turgidum* var. carthlicum (Asins 1983), sometimes named *T. persicum* because of its area of origin, Iran (Feldman 1976). The isozyme d_1 was only observed in the within-entry variability study in Turkey. This extremely rare isozyme has also been observed in the wild emmer (Asins and Pérez de la Vega 1985a).

Consequently, by comparing isozyme frequencies between wild emmer and durum wheat, the effect of domestication can be deduced. According to the present data, domestication has caused isozyme frequencies to change. The direction of the change is mainly to decrease them, i.e. accumulation of "null" alleles for the isoenzymatic loci under consideration. The smallest mean isoenzymatic frequency corresponds to Mexico, where the most

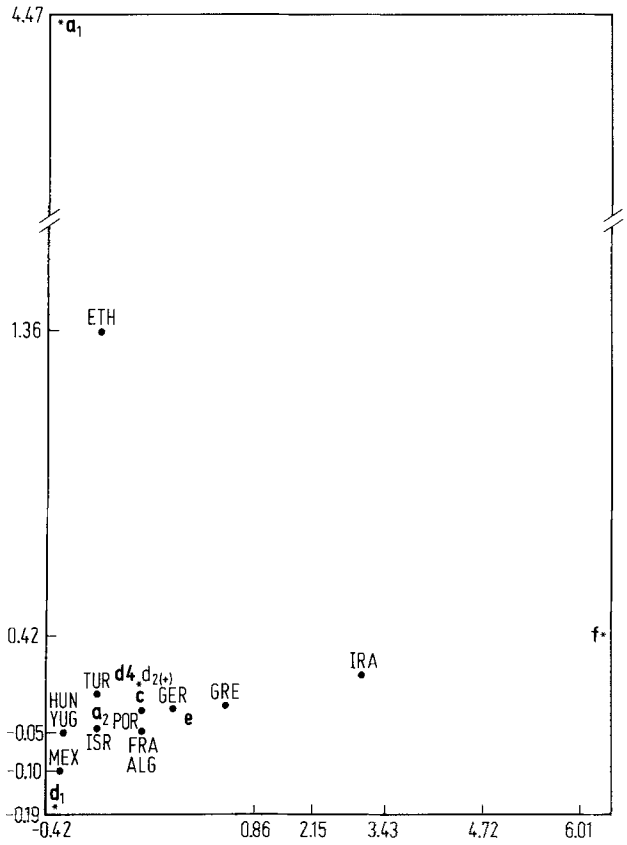

Fig. 5. Representation in the first two factors (X axis is the first factor) of the correspondence analysis for origins and isozymes using 101 entries

intensive durum wheat breeding programs are being developed (CIMMYT, Centro Internacional de Mejoramiento de Maiz y Trigo). Regarding peroxidases this small frequency may be, in part, due to the better quality found in pasta from low peroxidase activity cultivars (Kobrehel et al. 1972). Conversely, isozyme a_2 has greatly increased its frequency. Although loci involving isozymes a_2 and e are closely linked (Asins and Pérez de la Vega 1985a), their frequencies evolved in opposite directions. The other linkage groups involve isozymes whose frequency distribution has not changed (peroxidases d, 4 and phosphatases 3, 4, 5). These data explain the dendrogram of Fig. 2.

Plant domestication has been an ongoing evolutionary process throughout the history of mankind. During this process of domestication in different environments with varying selection pressure (including farming techniques), rapid evolution with continental change has taken place. As Bekele (1985) points out, such a continual genetic change of domesticates coincides with genetic changes in their progenitors and parasites (pests as well as pathogens). Because of this complex genetic build-up, differences between wild and corresponding cultivated species are difficult to interpret. But as Darwin (1970) first noted, when individuals of the same variety of our older cultivated plants are compared, they generally differ more from each other than do individuals of any one species or variety in a state of nature. He concluded that this great variability is due to the fact that our domestic productions have been raised under conditions of life not so uniform as those to which parent species had been exposed in nature. Over all the causes of change the accumulative action of selection whether applied methodically and quickly or unconsciously and slowly, have been the origin of our domestic races of animals and plants.

Within the limitation of the sample size, we have found *T. turgidum* var. durum genetic differentiation among entries to be generally greater than that of its wild progenitor *T. turgidum* var. dicoccoides. For the latter, a distance of 0.15 with a range 0.00–0.30 has been reported (Asins and Carbonell 1986a) using almost the same methodologies as in the present paper. The mean of the square root of the mean chi-square distance per origin for the durum wheat collection is 0.85 and its range 0.00–4.36 (see Table 2). It is therefore important to point out the great genetic diversity we found in durum wheat, as also was the case with the phenotypic one previously reported (Spagnoletti and Qualset 1987) and that affecting other major farm crops (Duvick 1984).

Distribution of genetic variability in Triticum turgidum var durum

Among origins, genetic variability varies in amount (here measured by the coefficient of variation or by the mean chi-square distance between kernels per origin), nature (difference in frequencies at many loci or by the presence of rare alleles), and distribution (measured as between- vs. within-entry variation), see Figs. 1 and 4 and Table 3. Quite clearly, Iran and Mexico are the richest origins of genetic variability for durum wheat; however, Ethiopia, Egypt and Afghanistan, showed a similar amount of genetic variability as Iran, this due to the existence of rare alleles rather than to gene frequencies per se.

The following low variabilities are surprising: that of Israel, because domestication took place in the Near East Fertile Crescent, and those of Italy and Cyprus because the Mediterranean basin is one the main growing areas, of durum wheat (Feldman 1976). Our records do not distinguish between the category of the entry, i.e., single-spike derivatives of landraces, landraces, breeding lines, etc., so identification is difficult. This problem has also been pointed out by Spagnoletti and Qualset (1987) in a durum wheat collection.

When within-entry variability is considered in addition to between-entry variability, some countries showed a large within-entry variability, namely, Greece, Mexico

and Ethiopia. Generally, the between-component was larger than the within-component, as expected in an autogamous species. There were four exceptions to this general rule: Mexico, Greece, Argentina and, to a lesser extent, Cyprus (Fig. 4). It seems possible that some entries were actually F_n's segregating generations; however, this finding needs further investigation to identify the possible causes of this phenomenon.

The distribution of genetic variability among origins is closely related to durum wheat history. *T. turgidum* var. dicoccum (cultivated emmer) occurs in prehistoric villages of the Near East (Iran, the plains of Mesopotamia, Syria, Israel and Jordan) as early as 7500 B.C. It was transferred to the lowlands of Mesopotamia in the sixth millenium B.C., and during the fifth and fourth millenium to Egypt, the Mediterranean basin, Europe, Central Asia and India. It was taken to Ethiopia some 5,000 years ago. In all these regions, cultivated emmer remained the principal cereal until the first millenium when it was replaced by the more advanced free-threshing tetraploid form, *T. turgidum* var. durum (emmer's derivative). Emmer is still grown on a limited scale in Ethiopia, Iran, Transcaucasia, eastern Turkey and the Balkans (Feldman 1976).

It is quite plausible that gene flow from emmer to durum wheat has occurred in these areas and explains the great diversity found in Iran, Ethiopia, Egypt and Afghanistan. This hypothesis is supported by the presence, in these areas only, of isoenzymes a_1, *f*, and *7* that are characteristic of the wild emmer (Asins and Carbonell 1986b). In addition, Afghanistan has also been reported to have a wide range of variation (Spagnoletti and Qualset 1987). Our results correspond to the centers of genetic diversity described by Vavilov (1951): Near East (primary center), which includes Asia Minor, Transcaucasia, Iran and the Turkestan highlands; Central Asia (secondary), which includes some regions of India, USSR and Afghanistan; Mediterranean (secondary), which according our results would mainly involve Egypt, Yugoslavia, Tunisia, France, Spain and Greece, and shows in general much less genetic variability. Our results support the idea that Egypt should be considered as a microcenter of diversity for durum wheat. The Abisinic secondary center would mainly include Ethiopia. It is worth pointing out that, similar to other crops such as *Glicine max* or *Citrus ssp.* which have their maximum production areas outside their centers of diversity, durum wheat has developed an interesting microcenter of diversity in Mexico.

The relationships we have found between origins (Figs. 3 and 5) are greatly affected by their within-variability, consequently countries that showed a large variability do not group easily (their grouping distance is large). When within-variability was used to characterize the origin, different groupings were found as compared to the dendrogram, in which only the between-entry variability characterized the origin (Fig. 3 and 5). The latter representation, involving more entries per origin, should be more realistic since between-entry is generally greater than within-variability in these species; however, there are origins with a larger within-entry variability and origins represented in the world collection by only one entry. This causes the countries to group differently when the within-entry variability is considered.

The logic in the groupings follows geographical or political lines for the most part. This is the case for groups Italy-Spain, (France-Algeria)-Germany and Hungary-Yugoslavia (data not shown here). Therefore, our results suggest that for the study of the pattern of variability distribution among countries, not only concerning the relative amount but also the differential characteristics (alleles and gene frequency differences), within-entry variability should also be studied even if one should decrease the number of entries per origin in some origins. These hierarchical studies of genetic variability distribution in germplasm conservation or plant evolution in general, even in "autogamous" species, are always needed (see Brown 1978, Bekele 1985, Asins and Carbonell 1986a, 1987).

The classification of countries of origin according to their continental and subcontinental geographical position, as used for durum wheat by Jain et al. (1975), or according to centers of diversity by Spagnoletti and Qualset (1987) does not correspond exactly with the grouping of origins for the isozyme characters of durum wheat found in the present study. However, there are some coincidences with the latter, for example, the grouping of USA and USSR. As was observed in the above mentioned papers, regional and political boundaries seem to have played an important role in the evolution of this important crop.

The results reported here represent to the best of our knowledge the first study on the distribution of genetic diversity based on isoenzyme frequencies in a durum wheat world collection. Although some countries of origin have shown a large within-entry variability, the between-entry component is the most important one, particularly for some centers of diversity such as the Near East, Central Asia and Abisinia, where rare alleles previously reported in the wild emmer have been found. Egypt might be considered a microcenter of diversity within the Mediterranean center, although certainly related to Ethiopia of the Abisinic center. Mexico has become a new microcenter of diversity, quite likely manmade and, as far as gene frequencies are concerned, distant from other centers of diversity.

The possibility of choosing entries from those origins of maximum genetic variability that indicate differences due to their gene pools facilitates the initial step in the research of a plant breeder or plant scientist – screening for desired characteristics.

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References

Asins MJ (1983) Genetic and phylogenetic studies in diploid and tetraploid species of genus *Triticum* by the analysis of peroxidase and phosphatase isozymes. Universidad Complutense, Madrid

Asins MJ, Carbonell EA (1986a) A comparative study on variability and phylogeny of Triticum species. 1. Intraspecific variability. Theor Appl Genet 72:551–558

Asins MJ, Carbonell EA (1986b) A comparative study on variability and phylogeny of Triticum species. 2. Interspecific relationships. Theor Appl Genet 72:559–568

Asins MJ, Carbonell EA (1987) Concepts involved in measuring genetic variability and its importance in conservation of plant genetic resources. Evolutionary Trends in Plants 1:51–62

Asins MJ, Perez de la Vega M (1985a) The inheritance of tetraploid wheat seed peroxidases. Theor Appl Genet 71:61–67

Asins MJ, Pérez de la Vega M (1985b) Inheritance of endosperm phosphatases in durum wheat. Z Pflanzenzücht 95:319–324

Asins MJ, Benito C, Pérez de la Vega M (1981) Endosperm peroxidase electrophoresis patterns to distinguish tetraploid from hexaploid wheats. Euphytica 30:389–392

Bekele E (1985) The biology of cereal land race populations. Hereditas 103:119–134

Benito C, Pérez de la Vega M (1979) The chromosomal location of peroxidase isozymes of the wheat kernel. Theor Appl Genet 55:73–76

Benzecri JP (1970) Distance distributionelle et metrique chi-deux en analyse factorielle des correspondances. Laboratoire de Statistique Math., Paris

Benzecri JP, Benzecri F (1980) Practique de l'analyse des données. 1. Analyse des correspondences. Exposé elementaire. Dunod, Paris

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

Darwin C (1970) The origin of species (1859). In: Appleman P (ed) Darwin. Norton and Company, New York, pp 98–199

Duvick DN (1984) Genetic diversity in major farm crops on the farm and in reserve. Econ Bot 38:161–178

Feldman M (1976) Wheats. In: Simmonds NW (ed) Evolution of crop plants. Longman, London, pp 120–128

Ghaderi A, Adams MW, Nassib AM (1984) Relationship between genetic distance and heterosis for yield and morphological traits in dry edible bean and faba bean. Crop Sci 24:37–43

Holden JHW (1984) The second ten years. In: Holden JHW, Williams JT (eds) Crop genetic resources: Conservation and evaluation. Allen and Unwin, Winchester/MA, pp 276–285

Jain SK, Qualset CO, Bhatt GM, Wu KK (1975) Geographical patterns of phenotypic diversity in a world collection of durum wheats. Crop Sci 15:700–704

Kobrehel K, Laignelet B, Feillet P (1972) Relation entre les activités peroxidasiques et polyphenoloxydasiques des bles durs et la brunissement des pâtes alimentaires. CR Séances Acad Agric Fr 14:1099–1106

Lance GN, Williams WT (1967) Mixed-data classificatory programs. 1. Agglomerative system. Aust Comp J 1:15–20

Salinas J, Pérez de la Vega M, Benito C (1982) Identification of hexaploid wheat cultivars based on isozyme patterns. J Sci Food Agric 33:221–226

Spagnoletti Zeuli PL, Qualset CO (1987) Geographical diversity for quantitative spike characters in a world collection of durum wheat. Crop Sci 27:235–241

Vavilov NI (1951) Phytogeographic basis of plant breeding. The origin, variation, immunity and breeding of cultivated plants. Chronica Bot 13:1–366