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A comparative study on variability and phylogeny of *Triticum* species

2. Interspecific relationships

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Summary. Interspecific relationship studies between A, S and D genome diploid species, and between AAGG and AABB allotetraploid species of the genus *Triticum* were conducted using isoenzymatic characters located in dry mature seeds. Data was analyzed by the factorial analysis of correspondences, and dendograms were obtained by two different genetic distances. The discussion of results was based on the limitations of the study, intraspecific variability differences, isoperoxidase frequency differences and chromosomal location of peroxidases in *T. aestivum* cv. 'Chinese Spring'. The closest relationship was found between 'dicoccoides' and 'carthlicum'. Relationships found between *T. turgidum* L. and *T. timopheevvi* Zhuk., both allotetraploid species and 'boeoticum'; this species and *speltoides; tauschi* and *searsii,* and the last two species with 'bicorne', are discussed at the phylogenetic level.

Key words: *Triticum* – Isozymes – Phylogeny – Allopolyploids – Genetic distances

Introduction

It has been postulated that the A and D genomes of polyploid wheats have been derived from Einkorn wheat and *Ae. squarrosa* (*T. tauschii*), respectively. The source of the B genome is as yet unknown and depending on the characters under study, several species have been proposed as donors: *T. speltoides, T. bicorne, T. urartu, T. searsii, T. sharonensis* and *T. longissimum.* Concerning the source of the G genome, only two species have been proposed as donors – *Ae. speltoides* and *Ae. aucheri* – both of which are most likely conspecific. All these species, except for *T. urartu,* belong to the sitopsis section and have an S or modified S genome (see Tsunewaki and Ogihara 1983 for a list of references on the reported donors of *Triticum* A, B, D and G genomes).

A considerable number of gel electrophoretic studies have been carried out on the wheat group. Most of them used endosperm storage proteins, although in a few cases diploids were compared to one another. The fact that seed protein patterns prove to be very complex and not easily deciphered adds a large handicap to evolutionary studies. When soluble enzymes are used, this handicap is overcome provided their genetic control is known. Studies using deciphered soluble enzymes are usually limited to characterizing enzymes in cultivated wheats and their progenitors, and studies are few where the objective is just the progenitors of cultivated wheats (Brody and Mendlinger 1980).

Intraspecific variability in the *Triticum* species that are most likely involved in the origin of *T. timopheevii* (AAGG) and dinkel wheats (AABBDD) has been previously reported (Asins and Carbonell 1986). It is the objective of the present paper to study the relationships among these species based on their patterns of genetic variation, genetic markers and genetic distances using dry kernel isoenzymatic characters.

Material and methods

The species and the number of lines or populations per taxon are shown in Table 1. The nomenclature described by Morris and Sears (1967) was followed. The populations were kindly

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Table 1. Species and subspecies studied

Species[a]	Varietal			No. of populations
	Genomes[b]	Group	Symbol	
T. monococcum L.	AA	'monococcum'	M	9
		'urartu'	U	12
		'boeoticum'	B	17
T. sharonensis Eig	S^lS^l		R	11
T. bicorne Forsk.	S^bS^b		C	19
T. speltoides (tausch) Gren.	SS		S	19
T. longissimum (Schweinf. & Muschli.) Bowden	S^lS^l		L	24
T. searsii Feld. & Kis.	S^sS^s		E	5
T. tauschii (Coss) Schmal.	DD		H	13
T. timopheevii (Zhuk.) Zhuk	AAGG	'araraticum'	A	12
		'timopheevii'	T	7
T. turgidum L.	AABB	'dicoccoides'	D	19
		'carthlicum'	P	5

[a] Following Morris and Sears (1967), and Brody and Mendlinger (1980)
[b] Following Sears and Feldman (1981)

supplied by B.L. Johnson, C.O. Qualset, M. Tanaka, T. Mello-Sampayo, M. Feldman, E. Sanchez-Monge, the CNR (Italy), the NI Vavilov (USSR), the NIAVT (Hungary), and the BGRC (Federal Republic of Germany).

Data from two enzymatic systems, the peroxidases of embryo plus scutellum (CPX_{E+S}), and endosperm (CPX_{Ed}), and the alkaline phosphatases of endosperm (Aph) were used (Asins and Carbonell 1986). The electrophoretic and staining methods as well as the way variables were defined have also been previously described in part 1 (Asins and Carbonell 1986).

Data was analyzed by the factorial analysis of correspondences as described by Benzecri and Benzecri (1980). This analysis could be considered as a principal components analysis of contingency tables, i.e., when the observed values correspond to binary or absolute frequency data (Jacquard 1974). Among other advantages, this method allows the simultaneous representation of variables (columns of the contingency table) and species (rows). Hence, a correspondence between columns and rows can be established in order to better interprete the results. Two types of distances between species were used, the Jaccard coefficient of similarity (Jaccard 1908) and the chi-square distance of Benzecri (1970). The definition and justification of the use of the chi-square distance is found in part 1. The clustering method was that of Lance and Williams (1967).

Results

Peroxidase isoenzymatic characters as markers

The observed relative mobilities and their absolute frequencies per species are shown in Table 2.

CPX_{E+S}. There were three very generalized mobilities over the species: 0.54, 1.00 and 0.82.

0.54 (e). This mobility is specially characteristic of 'urartu', *tauschii* and both allotetraploid species.

1.00 (a_2). It was found in the same linkage group as e (Asins and Pérez de la Vega 1985) and has not been observed in samples from *urartu*, 'dicoccoides' or *timopheevii.* It is very characteristic of 'boeoticum', 'araraticum' and the *sitopsis* section species.

0.82 (d_1). It has been found in a line of 'dicoccoides', in a different linkage group to that of e (Asins and Pérez de la Vega 1986). Isoenzyme d_1 has been observed in *T. turgidum* L. durum and *T. aestivum* but always at a very low staining intensity (Asins et al. 1981), therefore, neither its inheritance nor linkage group are available from durum or common wheats. This mobility has not been observed in our samples from *urartu, searsii* and *T. turgidum* ssp., while it is characteristic of *monococcum, tauschii* and the *sitopsis* section species.

The isozyme of $Rm = 0.68$ (d_2) is characteristic of all classical *sitopsis* section species except *searsii.* Due to its chromosomal location, it could be considered as a B genome marker. The linkage group to which it belongs in *T. turgidum* depends on the subspecies. From crosses involving durum wheats it showed an independent inheritance from e and f but when a line of *dicoccoides* was involved it did not show independent inheritance from e and f (Asíns and Pérez de la Vega 1985). Hence, it is undetermined whether or not the same donor diploid species is responsible for the three isoenzymes.

Allotetraploids did not show any mobility that was not observed in at least one of the diploid species.

Table 2. CPX isozyme frequencies per subspecies or species

	Rm	(1)	(2)	Species												
				M	B	U	E	H	D	P	A	T	R	C	S	L
E+S	1.14	a_1							6				1	1	1	
	1.07			3								1			6	6
	1.00	a_2	3D	3	14		5	2		1	8		8	12	8	11
	0.89				1						9	1	2		3	8
	0.82	d_1		4	2			8			5	1	3	9	9	10
	0.75						4						1	1	1	3
	0.68	d_2	3B						7		3	1	5	13	10	8
	0.61														2	3
	0.54	e	3D[a]		3	12		5	14	5	11	5	1	6	3	6
	0.43													1		1
	0.36	f	3D			1										
	0.29															2
Ed	1.04	a^-	7D				5	13					2	13	1	12
	0.96	b^-							1		3		8	8	7	6
	0.89	c	4B		6				12	5		1				
	0.82											2				
	0.75	d	7D	9	12	12			19	5	7	1		1	9	2
	0.68												8		7	
	0.61	4			2				19	4	4	6	5		6	4
	0.54										2	3				
	0.25														1	
	0.43														3	

(1) Following nomenclature by Benito et al. (1981); ($^-$) not observed in durum wheats (Asins et al. 1981)
(2) Chromosomal location in 'Chinese Spring' (Benito and Pérez de la Vega 1979)
[a] Just partially related

Moreover, their most characteristic mobility, 0.54, was shown by species from both the A and S genomic groups.

CPX_{Ed}. 0.75 (d). This was the most generalized mobility. It has not been found in *searsii, tauschii* or *sharonensis* while was characteristics of diploid species of the A genome, *T. turgidum, T. timopheevii* 'araraticum' and *T. speltoides.*

0.61 (4). It is quite generalized and characteristic of *T. turgidum.* It could be considered a modification of the isoenzyme d in *T. turgidum* L. (Asíns and Pérez de la Vega 1985). It has not been observed in our samples from *monococcum,* 'urartu', *searsii, tauschii* or *bicorne.*

1.04 (a). It can be considered as a biochemical marker of *searsii* and *tauschii.* It has not been found in durum wheats (Asins et al. 1981) nor in our samples from the A genome diploids and allotetraploids. It is somehow characteristic of *bicorne.*

0.96. It is characteristic of diploids of the S genome (except *searsii*). In addition to them it has only been observed in *dicoccoides* and *araraticum.*

It is important to point out that *timopheevii* and *araraticum* showed mobilities not found in any sample from the diploids under study.

Factorial analyses of correspondences

Only those values of CPX where the sum of the contribution of first and second factors accounted for more that 50% of the total variance will be considered.

CPX_{E+S}. Eleven factors were extracted for this group of characters. The first and second factors accounted for 51.25% of the total variance. The first factor (33.75%) is related to the band of Rm = 0.36 and with *urartu.* The second factor (17.50%) is related with the band of Rm = 0.75 and *T. searsii.* Figure 1 depicts the characters and species for the first two factors. Two groups were clearly distinguished: one, on the positive part of the first factor and within a narrow range of the second factor where mobilities of 1.14 and 0.54 and the allotetraploid species were found. The second main group, mostly on the negative side of the first factor and at a higher interval than the second one included the species of the *sitopsis* section. The subspecies of *T. monococcum* were very distant from one another. *Spel-*

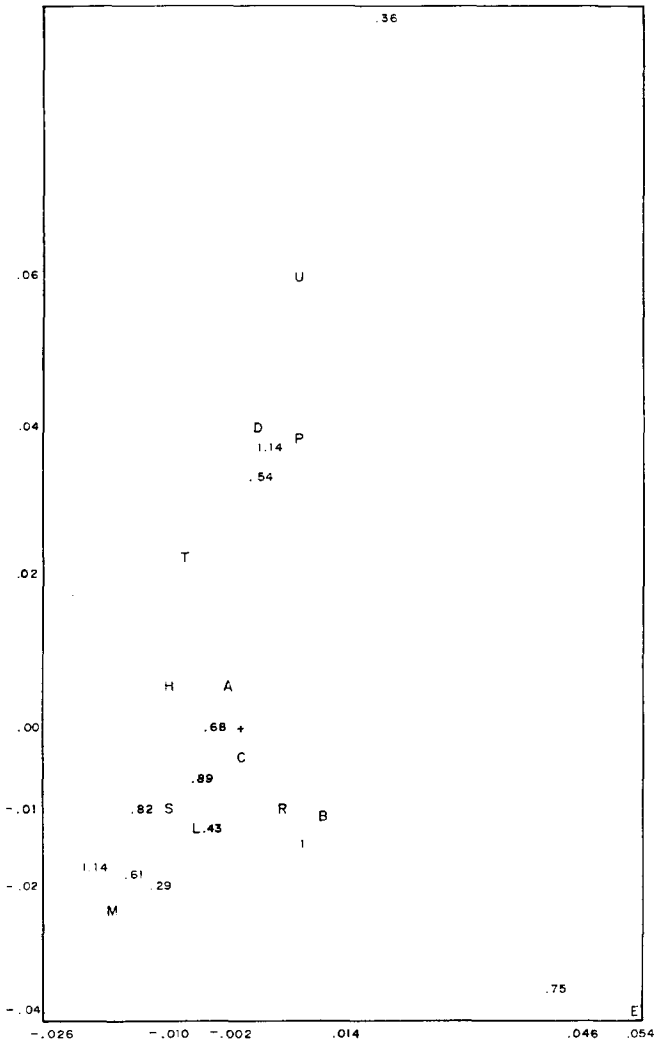

Fig. 1. Simultaneous representation of species and CPX_{E+S} variables

toides, bicorne, longissimum and *sharonensis* formed quite a compact group. Distances between them are small and all fall between *speltoides* and *longissimum.*

CPX_{Ed}. Nine factors were extracted – the first and second ones were responsible for 38.49% and 20.32% of the total variance, respectively. The representation of characters and species by these two factors is shown in Fig. 2. The first factor is related to mobility 1.04, and *searsii* and *tauschii,* the second factor is closely related with mobilities 0.54 and 0.82, and *timopheevii.* Disregarding these species and characters, three compact groups can be clearly distinguished. One, located to the negative side of the first factor, is formed by *sharonensis, longissimum* and *bicorne.* The last two species are related to *tauschii* and *searsii* because of band 1.04, and *sharonensis* with *longissimum* because of band 0.68. The second group, related to the first one by band 0.89, is formed by 'boeoticum', *speltoides,* 'dicoccoides' and 'carthlicum'. Band 0.75, which represents the main characteristic of this group, acts as a bridge with the third group formed by 'urartu' and 'monococcum'. Therefore, as far as this enzymatic system is concerned there is a close relationship among the subspecies of *T. monococcum,* and between *searsii* and *T. tauchii,* while *speltoides, longissimum, sharonensis* and *bicorne* are somehow distant from one another as are 'timopheevii' and 'araraticum'.

Interspecific genetic distances and dendograms

CPX_{E+S}. Dendograms and grouping distances using the chi-square distance are shown in Fig. 3. There were two main branches, one containing *speltoides, longissimum, bicorne* and *sharonensis,* and another formed by the allotetraploid species. The subspecies of *T. monococcum* were disperse, and *searsii* was the most distantly related species.

A dendogram obtained using the Jaccard coefficient of similarity (Fig. 4), only matches the previous one for *bicorne, longissimum, speltoides* and *sharonensis.*

CPX_{Ed}. Three main branches were obtained by the chi-square distance (Fig. 5): one is formed by *tauschii, searsii, bicorne, longissimum* and *sharonensis;* another by 'carthlicum', 'dicoccoides', 'boeoticum' and *speltoides;* and finally another by 'urartu' and 'monococcum' somehow related with the previous one. A dendogram using Jaccard's is shown in Fig. 6.

CPX system. Considering the CPX enzymatic system as a whole, three branches were obtained using the chi-square distance (Fig. 7). One, formed by *sharonensis, speltoides, bicorne* and *longissimum,* is related with the next branch formed by 'carthlicum', 'dicoccoides', 'boeoticum' and 'araraticum'. The third one was formed by 'urartu' and 'monococcum'.

CPX-APh. When all data was pooled, a dendogram by the chi-square distance again showed three branches (Fig. 8). One formed by *tauschii* and *searsii,* a complex group including the allotetraploids (though *araraticum* and *timopheevii* are far away), and the classical sitopsis section. The third branch included the *T. monococcum* subspecies as a compact group.

Discussion

Assumptions and limitations

As discussed in part 1, before attempting to study the taxa, one must take into consideration all the limita-

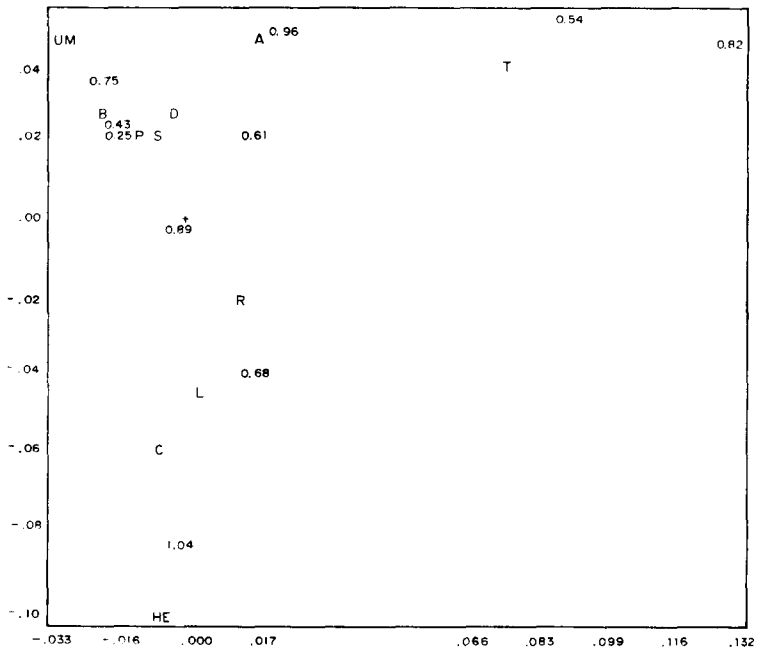

Fig. 2. Simultaneous representation of species and CPX_{Ed} variables

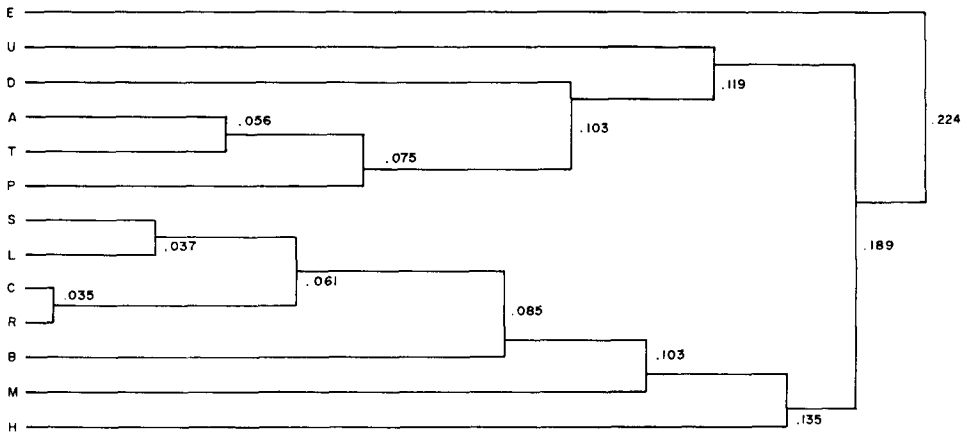

Fig. 3. Dendogram for species by chi-square distance, based on CPX_{E+S} variables. Distances reported here are the square root of the corresponding d^2

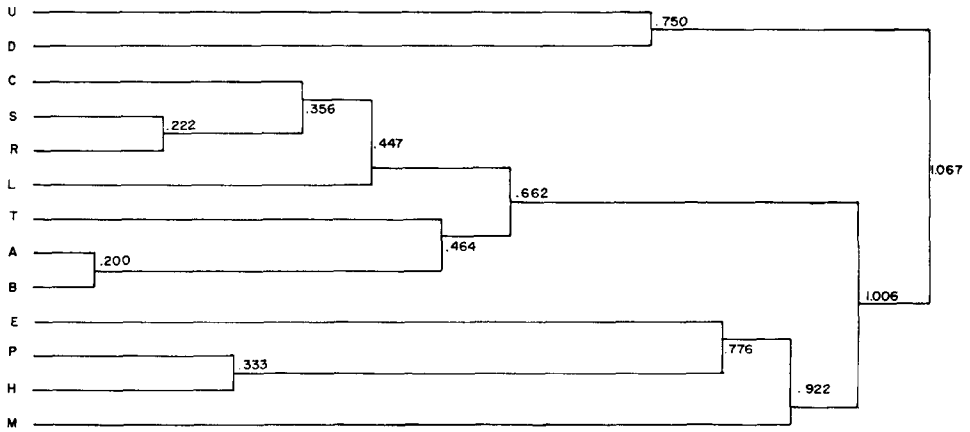

Fig. 4. Dendogram for species by the complement to unity of the Jaccard coefficient of similarity (based on CPX_{E+S})

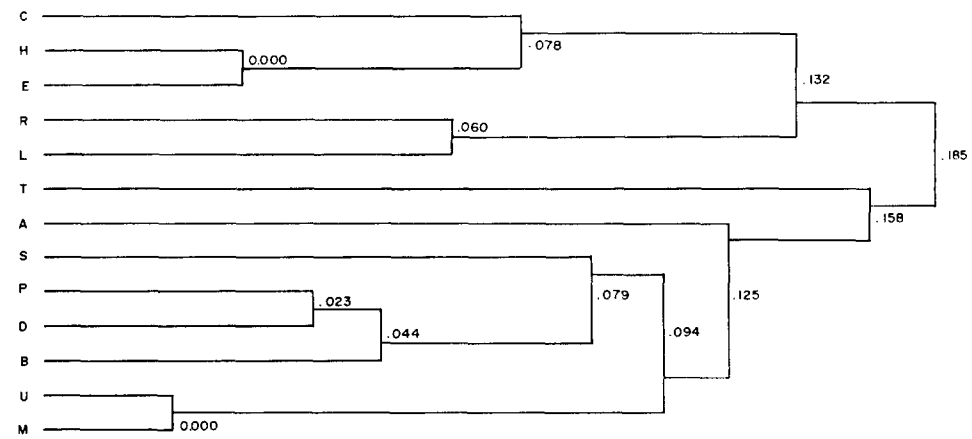

Fig. 5. Dendogram for species by chi-square distance, based on CPX_{Ed} variables. Distances reported here are the square root of the corresponding d^2

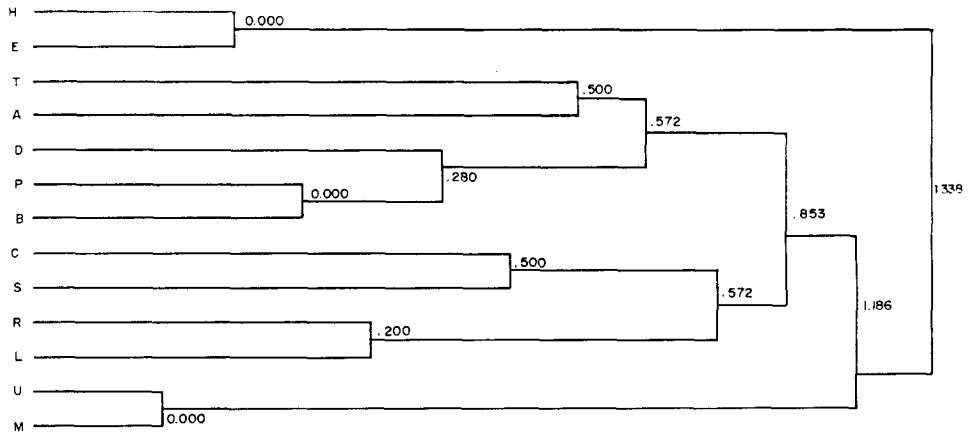

Fig. 6. Dendogram for species by the complement to unity ot the Jaccard coefficient of similarity (based on CPX_{Ed})

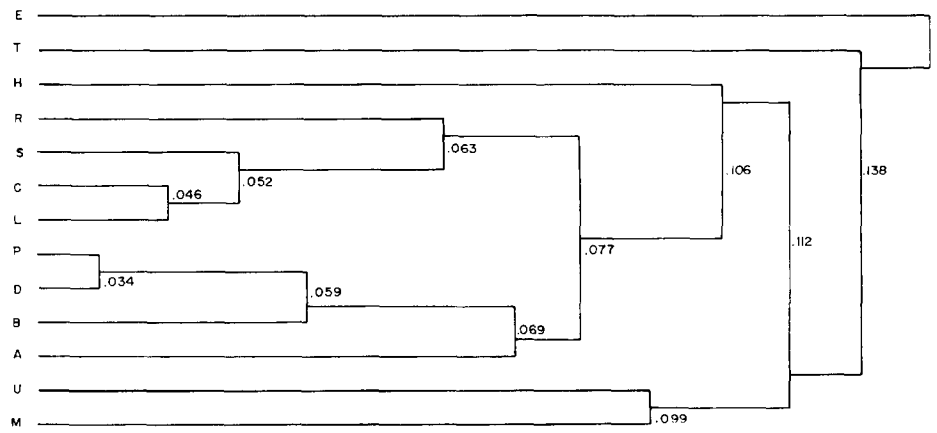

Fig. 7. Dendogram for species by chi-square distance, based on CPX variables. Distances here reported are the square root of the corresponding d^2

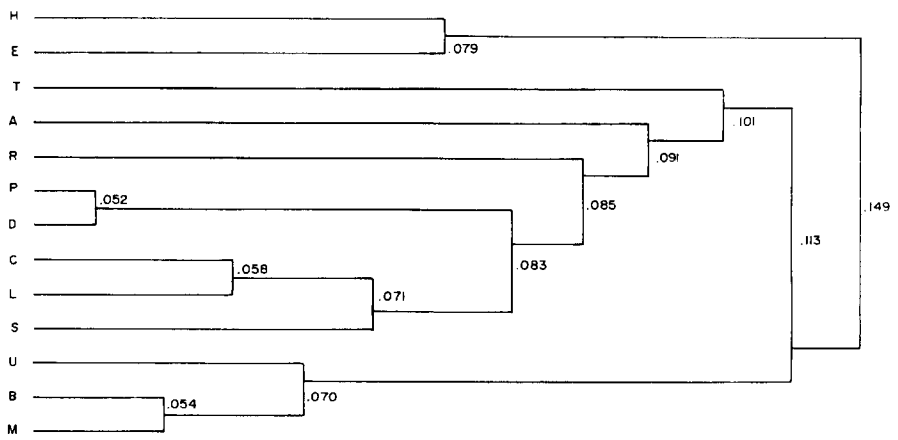

Fig. 8. Dendogram for species by chi-square distance, based on all variables as a whole. Distances here reported are the square root of the corresponding d^2

tions involved; i.e., sample size (number of population per taxon, number of loci, etc.) and its representativeness. Characters are not representative but they are well known in *T. aestivum* and *T. turgidum,* therefore, though inferences to the whole genome should be regarded with caution, they could be useful at the comparison level to provide suggestions or hypotheses to be tested in further critical studies. In order to properly and deeply discuss the results concerning interspecific relationships, data and methodology should be carefully weighed.

Data from CPX variables are very useful because each of these variables are supposed to be single locus controlled and CPX_{Ed} loci are independent from those of CPX_{E+S}. Furthermore, some CPX bands or isozymes could be considered as genomic markers. On the other hand, data obtained from Aph variables provided isoenzymatic patterns that can only be used as supplemental information to CPX data.

As observed from our results, dendograms using chi-square distances are in better agreement with results from factorial analysis than those from the Jaccard coefficient of similarity. Both methods must then be evaluated for their usefulness.

If differences among species are mainly due to the presence or absence of variables (binary data), distances using Jaccard's coefficients are informative enough. If frequential data at variables are also important, then chi-square distances are much more useful because they extract more information from the data.

As shown in part 1, intraspecific variability was mainly due to the intrapopulational component for CPX_{E+S}; thus chi-square distances are more informative than those of Jaccard. On the other hand, CPX_{Ed} species showed low intraspecific variability, differences arising mainly from the presence or absence of variables. Thus, distances here based on Jaccard's coefficients are informative enough.

Dendograms obtained by the Jaccard coefficient of similarity have no evolutionary meaning from the second unions onward because genetic distances under this method do not have the transitive property while those by chi-square do. Hence, the latter ones may be informative on the existence of different evolutionary branches and their relationships at the evolutionary level, whereas the former ones can only be informative about which species show proportionally the largest number of common variables with one specific species (preferably variables could be interpreted as genes).

Interspecific relationships within genome groups

D genome group. From our data, *T. tauschii* as well as *T. searsii* should be included in this genome group. Both species showed the same enzymatic pattern for CPX_{Ed} and Aph. They were found to be fixed for both enzymatic patterns and therefore also have the CPX_{Ed} D genome marker (isoenzyme a, Rm = 1.04).

A genome group. These species showed in general the same property of low intrapopulational variability as the group above. However, sometimes this variability was high (see part 1) like, for instance, in *urartu* and *monococcum* for CPX_{E+S} while for CPX_{Ed} both species were fixed. Though they followed the same intraspecific scheme, their genetic distance was found to be very high for CPX_{E+S} whereas for CPX_{Ed} they appeared to be closely related due to isoenzyme d (Rm = 0.75). Hence, differences among these species seem to be due to their intraspecific variability which is mainly caused by the V_i component.

The species with most polymorphic loci was 'boeoticum' (wild); therefore, it could be considered as the origin from which, 'urartu' (wild) and 'monococcum' (cultivated) forms arose. The important differences between them on polymorphic loci might be due to such reproductive isolating barriers as has been found

between 'urartu' and 'boeoticum' (Johnson and Dhaliwal 1976).

S genome group. It should be comprised of *speltoides, bicorne, longissimum* and *sharonensis;* i.e., the *sitopsis* section species with the exception of *searsii.* All showed high intraspecific variability, especially *speltoides, longissium* and *sharonensis* (see part 1), due mainly to the V_w component for CPX. This might be the reason why the genetic distances among them as species were quite low in spite of high intraspecific variation: i.e., differences are mainly frequental and not due to the presence or absence of characteristic (very frequent) variables.

Three CPX_{E+S} isoenzymes were very highly represented in these species: the B genome marker for this system, d_2 (Rm = 0.68); the a_2 (Rm = 1.00); and e (Rm = 0.54). This fact makes them appear very closely related due to CPX_{E+S} loci. On the other hand, the frequency distribution among CPX_{Ed} variables is quite different though the isoenzyme of Rm = 0.96 seems to be a S genome marker.

T. speltoides showed the largest number of polymorphic loci, therefore it just may be the original species. The closest related form to it among all S genome species was *longissimum. Sharonensis* appeared closely associated to *longissimum,* mainly due to having the CPX_{Ed} isoenzyme of Rm = 0.68. It is important to point out here that most taxonomists and cytogeneticists of the S group consider *sharonensis* to be a variety of *longissimum* (Kihara 1954; Roy 1959; Bowden 1959; Morris and Sears 1967; Mac Key 1968). *Bicorne,* on the other hand, shows an association to both *sharonensis* (CPX_{E+S}), and both of the abovementioned species (CPX_{Ed}), although it is more associated with *searsii* and *tauschii* because of isoenzyme a (Rm = 1.04) (see Fig. 5).

Differences concerning a reciprocal translocation between *sharonensis* and *longissimum,* and between the latter and *bicorne* have already been reported (Kihara 1954; Tanaka 1955; Kimber 1961, respectively) while the F_1 hybrid of a biotype of *sharonensis* and *bicorne* showed fairly regular chromosome pairing with 6 to 7 bivalents (Tanaka 1955). Hence, it seems likely that similarities between these two species should be due to a common species, *longissimum,* from which both independently originated. The close relationship between *sharonensis* and *longissimum* and the great variability of *sharonensis* as compared with *bicorne,* might be due to the absence (or very weak) of isolating barriers between those two species. This fact can be supported by the high degree of fertility found in their hybrid by Tanaka (1955) and Roy (1959) and by the fact that although all three are sympatric, no hybrid swarm, except between *sharonensis* and *longissimum* (Ankory and Zohary 1962), has been reported.

Other authors have reported the on association between *searsii* and *bicorne* (Tsumewaki and Ogihara 1983) thus, we think that the similarities between *searsii* and *longissimum* came from a hypothetical origin of *bicorne* from *longissimum.*

Brody and Mendlinger (1980) have found *T. tauschii* almost equidistant from all other diploid groups while from our data and samples it appeared to be more related to the S genome group (because of its greater relationship with *searsii* than with the A genome group.

The supposed original species for both the A and S genome groups, *boeoticum* and *speltoides,* respectively, were quite closely related for the CPX_{Ed} system and the A genome marker d (Rm = 0.75). Due to this fact, and since *T. speltoides* showed many more polymorphic CPX loci, an ancestral origin of *boeoticum* from *speltoides* or a closely related species might be hypothesized.

Brody and Mendlinger (1980) have also reported a relatively close genetic similarity between the A and S genome groups.

The AABB allotetraploids. In spite of morphological differences, data from the enzymatic systems studied here provided the closest relationship between two species (see Fig. 8). 'Carthlicum' showed no new enzymatic pattern for CPX_{Ed} and Aph that had not been observed in 'dicoccoides', as it could be expected by its origin from this species (one cultivated subspecies and the wild subspecies of *T. turgidum* L., respectively) (Feldman 1976).

The AAGG allotetraploids. Both species showed a high intraspecific variability in both CPX_{E+S} and CPX_{Ed} systems but it is surprising that higher intraspecific variability has been found in *timopheevii* than in *araraticum* (see part 1) as the former was originated from the latter (Feldman 1976). A plausible explanation is that *timopheevii* was promptly refused by farmers choosing other domesticated polyploid wheats.

Both subspecies appear to be related by the same pattern of intraspecific variability for CPX, the high frequency of CPX_{E+S} isoenzyme e (Rm = 0.54), and the presence of the CPX_{Ed} band of Rm = 0.54 that was not found in any other species of this study. The differences have been mainly of a frequental nature but much stronger than those found in the S genome group, suggesting the existence of isolating barriers between both subspecies.

Relationships and origin of T. turgidum L. and T. timopheevii Zhuk

Relationships between both species were found but were limited to the high and characteristic presence of CPX_{E+S} isoenzyme e (Rm = 0.54) and just the number of common CPX_{Ed} variables that constituted the basis of a closer relationship of *T. timopheevii* with *T. turgidum* than with any other species. Therefore, such relationships do not need to be explained by a common tetraploid progenitor (monophyletic origin) but through similarities among the diploids involved in a diphyletic origin (Kihara 1963; Tsunewaki 1980). Both species share the A genome likely donated by *T. monococcum* 'boeoticum' (the wild and broadly distributed species of the A genome group). Hence, differences must be due to the second genome donor.

Since for the CPX loci under study no species-specific marker has been found among any S genome species, there can be no conclusion as to what specific diploid S genome species contributed to the second genomes of allotetraploids. However, the simultaneous presence of band Rm = 0.96 from CPX_{Ed}, characteristic of S genome species in both allotetraploids, agrees with the fact that both genome donors should belong to the same group, namely the S genome group. So great was the intraspecific variability found in S genome species, mainly, *sharonensis, longissimum* and *speltoides,* and so closely related are these species, that the assignation of G or B genome donors to specific species is just a probability feature, at least from our data. On the contrary, if species-specific genes or DNA sequences lacking intraspecific variability within each S genome species were available (as seems to be the case of the paper reported by Tsumewaki and Ogihara 1983), the assignation would suppose a proof.

Concerning our data, we only dare suggest that the least likely species involved in the origin of either *T. turgidum* or *T. timopheevii,* would be *T. bicorne* because of its high frequency of CPX_{Ed} band Rm = 1.04 (a) absent in *T. turgidum* 'dicoccoides', 'carthlicum', durum (Asins et al. 1981) and *T. timopheevii* ssp.

An important question may arise from data here reported. If S genome species seem to be so closely and, perhaps, phylogenetically related, at least considering the enzymatic systems here studied, why do such important differences between both allotetraploids exist? Not only the existence of two different diploids involved in their nuclear constitution but also the nucleus-cytoplasm interaction must be an important cause of differences through their effects on gene expression regulation.

Hence, our data provides the following suggestions for further phylogenetic studies where allopolyploid species are involved:

1. The more knowledge that is available on the characters being used, the deeper the discussion of results and the conclusions to be drawn.
2. The expression of characters in allotetraploids might be modified by nucleus-cytoplasm interactions through their effects on the gene expression regulation process. Therefore, large deviations from a simple additive model describing the expression of characters in allotetraploids should be taken into consideration.
3. Other intraspecific variability studies or data, using the same characters, in species involved in phylogenetic relationships are a must in order to understand and weigh the limitations to any phylogenetic study.

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