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

1. Intraspecific variability

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Summary. Intraspecific variability of A, S and D genome diploid species and AAGG and AABB allotetraploid species of the genus *Triticum* was examined in a comparative study using isoenzymatic characters (peroxidases of embryo plus scutellum, and endosperm; and alkaline phosphatases) of dry mature seeds. The methodology followed was based on the definition of variables from characters and three functions related with total intraspecific, intrapopulational and interpopulational variabilities. The diploid species with the greatest intraspecific variability were *speltoides* and *longissimum,* and among the allotetraploid species, *timopheevii.* Concerning all variables, interpopulational variability was found to be greater than intrapopulational in *urartu, monococcum, timopheevii, dicoccoides* and *sharonensis.* Intraspecific variability differences found among species are discussed with reference to Nevo (1978) and a hypothesis concerning intraspecific variability differences between allotetraploids is suggested. The final objective of the present paper is to provide information on intraspecific variability differences among species for future use in discussing the interspecific relationships.

Key words: *Triticum* – Isozymes – Allopolyploids – Interpopulational variability – Intrapopulational variability

Introduction

The classification of Morris and Sears (1967) recognizes ten diploid *Triticum* species, three allopolyploid wheats, and some ten other allopolyploid *Triticum* species (see also Sears 1975). The relationships among the genomes of *Triticum* species are sufficiently known so that a capital Roman letter has been assigned to each genome of each species. *Triticum aestivum* (2n = 6x = 42) contains genomes A, B and D. The D genome was contributed by *T. tauschii* and the A and B genomes by *T. turgidum.* The A genome came from *T. monococcum.* The source of the B genome of *T. turgidum* as well as that of the G genome of *T. timopheevii* (2n = 4x = 28), are as yet a matter of controversy.

In spite of the great importance of intraspecific genetic variability studies in the interpretation or discussion of phylogenetic relationships (Lewontin 1967; Templeton et al. 1981), very few authors have studied, intraspecific variability in the genus *Triticum.*

Zohary (1966) observed a sharp contrast in variation patterns between diploid and polyploid species in the wheat group. Diploid genomic groups "are apparently completely isolated from one another in nature. Ecologically too, diploids display a clear-cut evolutionary divergence and each genomic group has its rather specific adaptative specialization". On the other hand, "the majority of the tetraploid and hexaploid species are extraordinarily variable. They occupy wide eco-geographical amplitudes – but mainly man-made habitats" "... in addition to the lack of discontinuity, polyploids are also not entirely reproductively isolated from one another".

Jaaska (1974) found intraspecific and intrapopulational polymorphism for esterases and acid phosphatases in the outbreeding species *T. espeltoides,* while *T. bicornis* and wheats, characterized by extensive inbreeding, are largely monomorphic with respect to those isozyme characters, though differences between local populations of autogamous species exist. More

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recently, Nevo et al. (1982) have found electrophoretically discernable protein variation in 12 representative populations of *T. dicoccoides* in Israel, revealing considerable regional and local differentiation.

Lastly, there also exist differences among diploid groups which can be correlated to their reproductive isolation degrees. *T. monococcum* 'boeoticum' and *T. monococcum* 'urartu' are reproductively isolated (Jaaska 1974; Johnson and Dhaliwal 1976) while interspecific hybrids between the taxa of S genome diploid species show full or almost full chromosome pairing in meiosis and are fertile or semi-fertile (Zohary 1983).

Therefore, a comparative intraspecific study in *Triticum* is needed before attempting to discuss any phylogenetic relationship. This comparative intraspecific study in those *Triticum* species related with the origins of *T. turgidum, T. timopheevii* and *T. aestivum* is the objective of the present paper (part 1); the phylogenetic relationships will appear in a subsequent paper (part 2).

Material and methods

Biological material and methodology

The material studied is shown in Table 1. The species were classified following Morris and Sears (1967). The populations were kindly 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).

Five kernels per population were prepared for analysis and assayed by horizontal polyacrylamide gel slab electrophoresis following methods described in Benito and Pérez de la Vega (1979) and Salinas et al. (1981). The enzymatic systems examined were the cathodal peroxidases of the dry kernel (CPX) – embryo plus scutellum (CPX_{E+S}) and endosperm (CPX_{Ed}) – and the alkaline phosphatases of dry endosperm (Aph).

Durum wheat cultivar 'D' was always used as control in the electrophoresis. For CPX, the isozymatic patterns were studied and the bands were denoted by their relative mobility (Rm) in the gels with respect to isozyme a_2 (the fastest in cultivar 'D').

Statistical methodology: definition of variables and measurements of variability

Every populational or evolutionary study has two limitations: the size of the sample (number of observations per population, number of populations , number of characters, etc.) and its representativeness.

Since our study intends to be comparative among species, which are mostly autogamous, limitations related to sample size per species could be considered as unimportant unless some species were characterized by a fewer, and therefore not representative, number of populations than others.

We assume the sample of populations to be representative for each species, but the representativeness of characters is very difficult, if not impossible, in any study because they should be a random sample from the whole genome loci (structural and regulatory loci; loci responsible of isoenzymatic, morphological and metric characters). However, when studies are comparative among species with regard to a group of characters, and among results from different sets of characters, limitations can be discussed if data from these characters are available.

Genetic data from enzymatic characters provide information on a species' inherent variability and make the definition of variables much easier. The way these variables are defined (genotypes or phenotypes at a locus or at a group of loci) is very important because the comparisons should be objective and the analysis of data must be performed by means of an adequate measurement.

Concerning the enzymatic systems for which *T. turgidum* L. is not monomorphic, genetic data are available on dry kernel peroxidases (Benito and Pérez de la Vega 1979; Asins et al. 1981; Benito et al. 1980; Asins and Pérez de la Vega 1985a; Asins 1985) and on dry kernel endosperm alkaline phosphatases (Salinas et al. 1981; Asins and Perez de la Vega

Table 1. Species and subspecies studied

Species[a]	Genomes[b]	Varietal group	Symbol	No. of populations
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] According to Morris and Sears (1967), and Brody and Mendlinger (1980)
[b] According to Sears and Feldman (1981)

1985 b) for both *T. aestivum* L. and *T. turgidum* L. According to findings reported by these authors, variables (columns of the contingency table) are then defined as follows.

For CPX, all isoenzymes characterized by a distinctive Rm (faintly stained bands were disregarded as they were possibly artifacts from earlier maturation stages). Thus, given that these isozymes are monomers and, usually, monogenically controlled, each isozyme (variable) could be considered as a different locus. Differences at a certain number of variables would then correspond to the same number of loci.

For Aph, some of the isoenzymes might be dimers so variables were defined by the whole isoenzymatic pattern: there were as many Aph variables as patterns. Therefore, it is not possible to assume that differences at a certain number of variables correspond to the same number and type of loci.

By the way we have defined these variables, CPX variables are statistically independent (though not genetically independent for all of them) while Aph are statistically dependent.

The study on intraspecific variability has been carried out by comparing among species the relative importance of interpopulational (V_i) versus intrapopulational (V_w) variabilities contributing to the total variability of the species (V_t).

A measure of V_w is given by the percentage of non-uniform populations. A population is considered non-uniform when in at least one of the five kernels, the variable being considered (Rm or isozymatic pattern) does not agree with results seen in the others. Given that the sample size per population is always the same (five kernels), the same genetic system is assumed for all populations within a species and, according to the assumptions above mentioned, then the V_w values here defined are such that the comparison among species regarding the relative importance of V_i versus V_w is established in an objective way.

As a measure of V_i, the mean interpopulation quadratic distance per species (d^2) was used. This approach to V_i has been previously followed by Nevo et al. (1982).

The chi-square distance as defined by Benzecri (1970) was used to obtain the distance between each pair of populations (rows of the contingency table). This distance is defined as:

$$d^2(i, i') = \sum_{j=1}^{k} \frac{1}{f_{.j}} \left(\frac{f_{ij}}{f_{i.}} - \frac{f_{i'j}}{f_{i'.}} \right)^2$$

where j symbolizes each of k variables; i and i', two observations at any level (here two populations); f_{ij}, the number of kernels of population i that showed variable j; $f_{.j}$ is the sum of f_{ij} over populations for variable j; and $f_{i.}$, the sum over variables for population i.

The chi-square distance is preferred to other widely used distances based on frequencies (Cavalli-Sforza and Edwards 1967; Nei 1972, 1974) because using the former a variable does not need to be a gene (due to the existence of nulls and the lack of the Hardy-Weinberg equilibrium) nor a genotype, but a band (CPX) or a isozymatic pattern (Aph): i.e., one of the two possible phenotypes at a single locus (CPX) or the phenotype resulting from all the Aph loci involved. In addition, the chi-square distance has a clear meaning: each absolute frequency at a variable is relativized within each population in such a way that results in the relative importance of the variable in the population. The quadratic difference between these relative frequencies concerning two populations at a variable is further relativized by the importance of the variable in the species. Moreover, as Jacquard (1974) indicates, the classical Euclidean distance does not satisfy the condition that if in all populations, two variables (genes, genotypes, bands, patterns, etc) occur in frequencies that are proportional to one another, one should be able to condense the information from them, without altering the distance between the populations. When all variables cannot be assumed to be independent from one another, it is possible, for instance due to linkage, that the two variables are redundant in their information about population differentiation. It should then be desirable that the methodology would treat them as only one variable. It can be easily shown that this property is satisfied by the chi-square distance.

Total variability (V_t) is expressed in terms of the number of not fixed variables per species considering all five kernels of all its populations. A variable is considered to be fixed when all kernels of all populations of a species show that variable. Again, if the assumptions given for V_w are true, for comparison purposes among species the V_t values are useful in order to get objectivity.

Values for V_w, V_i and V_t were calculated for CPX_{E+S} variables, CPX_{Ed} variables, Aph variables and all variables simultaneously (CPX-Aph).

Results

Results on intraspecific variability are summarized in Table 2. For clarity and to avoid involving any quantitative meaning, graphical representation of these results is given in Fig. 1 for CPX_{E+S}, Fig. 2 for CPX_{Ed}, Fig. 3 for Aph and Fig. 4 for all characters simultaneously. The values of V_w are represented by a dot and those for V_i (where the correspondence of the maximum value of V_i to that of V_w was previously performed in order to allow relative comparisons of the same order of magnitude) by an x. Thus, a continuous line indicates $V_i - V_w$ when $V_i > V_w$ and a broken line when $V_w > V_i$.

From existing data on the characters here studied, the way variables have been defined and the allotetraploid nature of some species under the present study, the following points have to be taken into account before analyzing the results concerning V_i, V_w and V_t.

1. This study deals with three independent sets of variables corresponding separately to CPX_{E+S}, CPX_{Ed} and Aph.
2. Results obtained from Aph variables are very limited therefore data and our interpretations of it are not comparable to these from CPX though they can be used as additional information among species.
3. The gene synteny relationships that existed in the ancestral wheat genome have in large part been conserved in each of the three genomes of *Triticum aestivum* cv. 'Chinese Spring' (AABBDD), (Hart 1979). Therefore, on studying diploid species for a set of variables, the number of linkage groups involved might be supposed to be approximately the same. But on screening allotetraploids for the same set of variables, the number of linkage groups involved should be at least twice that found upon screening diploids. Then, intraspecific variability comparisons between diploids and allotetraploids could be misleading.

Table 2. Results on intraspecific variability. V_t represents the number of variables not fixed; other components are explained in the text

2n	Genome	Species	V_t			% unif. pop. (100-V_w)				d^2 (V_i)			
			CPX_{E+S}	CPX_{Ed}	Aph	CPX_{E+S}	CPX_{Ed}	Aph	CPX-Aph	CPX_{E+S}	CPX_{Ed}	Aph	CPX-Aph
14	A	*monococcum*	3	0	5	89	100	89	78	0.045	0	0.113	0.022
		urartu	1	0	4	100	100	92	92	0.042	0	0.214	0.034
		boeoticum	4	3	3	82	88	100	71	0.014	0.015	0.059	0.008
	S	*sharonensis*	7	4	12	64	27	73	18	0.022	0.018	1.034	0.072
		bicorne	7	3	10	53	89	63	37	0.021	0.018	0.248	0.029
		speltoides	9	7	28	21	63	37	5	0.028	0.049	0.544	0.071
		longissimum	10	5	24	33	71	42	21	0.035	0.034	0.379	0.048
		searsii	2	0	0	60	100	100	60	0.011	0	0	0.033
28	D	*tauschii*	2	0	0	92	100	100	92	0.017	0	0	0.002
	AG	*araraticum*	5	4	3	33	83	75	33	0.009	0.123	0.185	0.017
		timopheevii	5	5	9	71	86	57	43	0.021	0.174	0.348	0.048
	AB	*dicoccoides*	3	2	8	100	95	79	79	0.025	0.004	0.313	0.022
		carthlicum	1	2	2	80	100	80	60	0.003	0.001	0.074	0.004

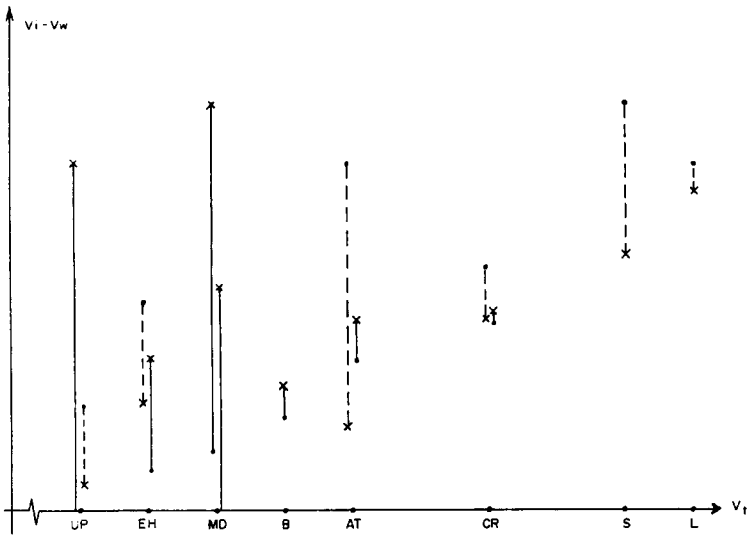

Fig. 1. Distribution of species by comparing intraspecific variability for the CPX_{E+S} variables

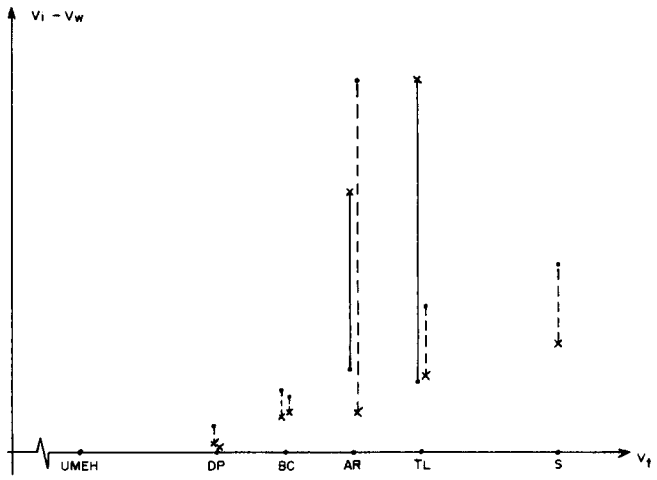

Fig 2. Distribution of species by comparing intraspecific variability for the CPX_{Ed} variables

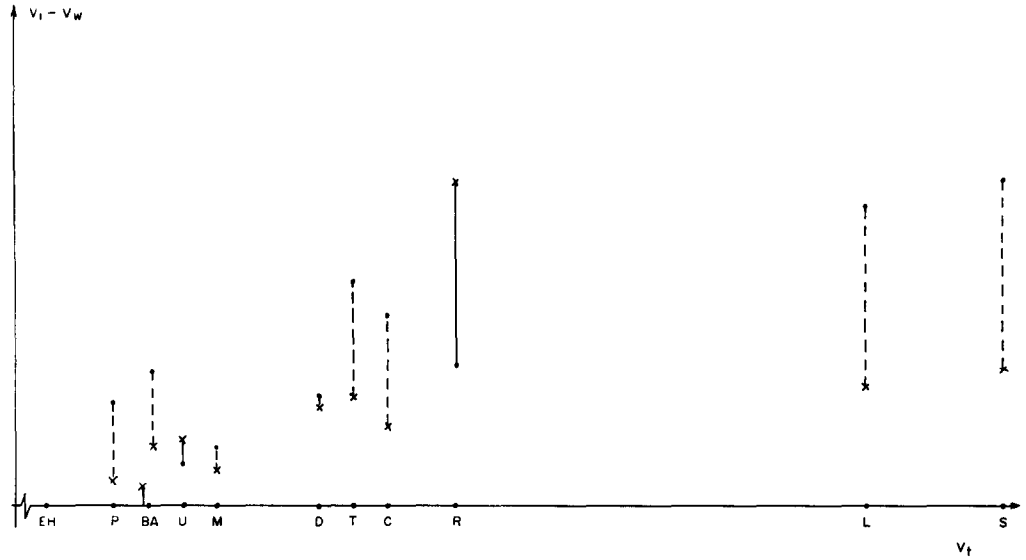

Fig. 3. Distribution of species by comparing intraspecific variability for the Aph variables

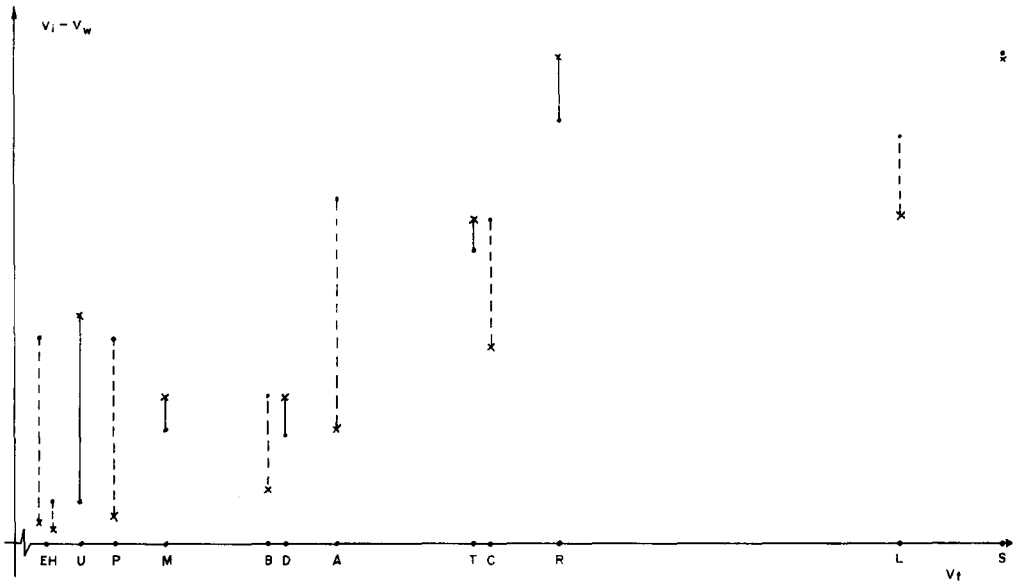

Fig 4. Distribution of species by comparing intraspecific variability for *all* variables

Diploid species

S genome species. From Figs. 1, 2, 3 and 4, it is clear that, *longissimum* and *speltoides* behaved in a similar fashion whereas *sharonensis* differed in the nature of its variability and *searsii* in its degree of variability.

The low value of V_t for *searsii* as compared with the rest of the S genome species might be due the low number of populations under study for this species, but it should also be taken into account that the nature of its variability seemed mainly to be due to the V_w component and not to V_i; therefore, this species just may be amply characterized with the number of populations here used.

D genome species. Tauschii always showed very low variability and was located very near to *searsii.* Only for CPX_{E+S} was an important V_i-V_w relation found and, in contrast to *searsii,* the main component was V_i.

A genome species

Concerning V_t, all three species (subspecies) were located to the left of *timopheevii* and most of the S genome species. As far as V_i–V_w is concerned, there are clear differences between 'boeoticum' (wild) and *monococcum* (cultivated) or 'urartu' (wild).

Allotetraploid species (AG and AB)

Timopheevii (cultivated) showed a higher V_t than 'araraticum' (wild). Both species were located at an intermediate position and for CPX_{Ed} they had higher V_t than *bicorne*. 'Carthlicum' (cultivated) showed a lower V_t than 'dicoccoides' (wild) which was always found to the left of *timopheevii*. Hence, regarding the V_t values, important differences among allotetraploids were found. As far as their nature is concerned, there were analogies between 'dicoccoides' and *timopheevii* (V_i slightly higher than V_w) and between 'carthlicum' and 'araraticum' (V_w much higher than V_i).

It should be pointed out the high value of V_w for 'araraticum' was even higher than that for *bicorne* (see Fig. 4). Only 'dicoccoides' (AB, wild), *timopheevii* (AG, cultivated), *monococcum* (A, cultivated), *sharonensis* (S) and, mainly, 'urartu' (A, wild) presented a positve sign for V_i–V_w (see Fig. 4).

Discussion

In addition to the kind of characters and the way variables have been defined (phenotypes at individual loci or the whole enzymatic pattern), genetic variation is also affected by the breeding system. Thus, for outbreeding species, the V_w component is expected to be more important than V_i though the latter might be also important due to, for instance, the action of natural selection.

Outbreeding annual species are expected to be more heterozygous and polymorphic per population than their inbreeding counterparts (Levin 1975). Our data support this statement because *T. speltoides,* known to be a crosspollinated species, had the highest value of intrapopulation variability (V_w). Other species, such as *longissimum, bicorne, sharonensis, timopheevii* and *araraticum* also showed high V_w values, while *tauschii,* 'urartu', *monococcum,* 'boeticum' and 'dicoccoides' had lower V_w values. If the diploid species mentioned above, excepting *speltoides,* are all autogamous and come from the same ancestral species, and if only two different phenotypes per CPX locus exist, how can such differences arise? There are several plausible hypothesis. Different gene flow indexes could affect genetic heterozygosity. High heterozygosity, in spite of self-fertilization, can be maintained in structural heterozygote species (Levin 1975). It is also possible that either overdominance, epistatic interactions among loci, or frequency dependent selection (see Nevo 1978) could be responsible for the same situation.

Differences in the gene flow index do not seem to be the causal factor in genetic heterozygosity in allotetraploids because *T. timopheevii* is more autogamously estric than *T. turgidum* within the same location (Sanchez-Monge, personal communication). Given that an important difference between these two species is the number of polymorphic variables (V_t), the following hypothesis about a different origin could explain such differences. If both species share a common A genome the origin of the second genome could involve two different diploids. However, it is widely admitted that if these diploid species are not the same, they must be very similar or closely related; therefore, great differences in the number of CPX loci between both B and G genome donors would not be expected.

Differences in the regulatory processes of gene expression could arise through two types of new interactions in the allotetraploids: intergenomic and nucleus-cytoplasm interactions. For instance, if an electrophoretic discernible band for the diploid donors B and G had the same Rm on the gels and if a simple additive model took place in the allotetraploids (AABB and AAGG), they would show an unique band represented by two isozymes with the same Rm. On the contrary, if this additive model is not applicable, i.e., if interaction affected gene expression at any regulatory level in the AAGG but not in the AABB allotetraploid, new isozymatic mobilities not observed in diploids could appear in the AAGG species and also fewer double isozymatic bands than in the AABB species. The existence of double isozymatic bands for CPX has been suggested in *T. aestivum* (Benito and Pérez de la Vega 1979) and *T. turgidum* (Asins and Pérez de la Vega 1985 b), on the other hand, it is noteworthy the existence of several CPX mobilities in *T. timopheevii* (AAGG) that were not observed in the diploids under study (Asins and Carbonell 1986, Table 2).

According to Nevo (1978) ecological amplitude is also associated with genic variation: the levels he found differed more within than between life zones. Powell (1975) concluded that, in general, there are no differences in genic variation among life zones. Our data did not provide information on this matter because the comparative populational study was only among species and not among species and life zones.

According to Nevo (1978), when neither taxonomy, life zone patterns nor breeding systems alone can explain the genetic patterns of populations, there remains the ecological background structure and the relationship between species and their habitats. He concluded that populations or species largely generalists

are relatively more polymorphic and heterozygous though no correlations occur in inbreeders – polytypic species with local adaptation. Here, genetic variation is stored in the species as a whole rather than in the heterozygosity of individual populations. Heterozygosity data are not available from our study but different V_i–V_w associations might be comparatively studied within and among both types of species.

Using data on the geographical and ecological characterization of *Aegilops* and wild *Triticum* species (*T. speltoides* excepted because of its different breeding system) (Zohary 1966), polyploids, *T. tauschii*, and *T. monococcum* 'boeoticum' could be called habitat generalists with respect to *bicorne* (restricted to xeric sandy soils), *sharonensis* (endemic of the sandy soils of the Israeli Mediterranean coastal plain) and *longissimum* (sandy loams in the Mediterranean coastal plain and a variety of steppic habitats though its distribution is also relatively limited).

Among *bicorne, longissimum* and *sharonensis,* the latter is the most distributionally limited species; its V_i–V_w depends on its enzymatic system but considering all its variables on a whole, it was the only species of the S genome group whose V_i component predominated. Therefore, it does not follow the correlation between distributional amplitude and degree of polymorphism but rather it is an inbreeding species with local (over short distances) adaptations which are reflected in the Aph system. These three species showed, in general, higher V_i and V_t values than the habitat generalist diploids, *T. tauschii* and *T. monococcum* 'boeoticum'. The latter showed very low V_i values and the predominant component, when one appeared, seemed to be V_w (Fig. 4). The low variability found in 'boeoticum' and *tauschii* agreed with findings by Stebbins (1957) in the sense that "the combination of an aggressive, widely adapted and self-pollinating genotype would be advantageous for colonizing species". This fact has been also reported for some well-known plant colonizers, such as the wild barley *H. spontaneum* in Israel (Nevo et al. 1979).

Both wild allotetraploids occupy wide-spread eco-geographical areas (Zohary 1966) and showed important differences related to intraspecific variability. The most important component of 'dicoccoides' variability was V_i, for 'araraticum' it was V_w (see Fig. 4). The inverse relation between the associations of its variability components for CPX_{E+S} and CPX_{Ed} is noteworthy although for both systems, the V_w component of the latter species was much greater than that of 'dicoccoides'. This fact means that V_i values do not only depend on the species and the enzymatic system separately but can also depend on enzymatic systems-species associations. Thus, while the V_i component regarding CPX_{E+S} variables was usually greater than the corresponding one for CPX_{Ed} variables; 'timopheevii' and often 'araraticum' showed the inverse relation. Perhaps, this fact might have an evolutionary meaning.

The present data from 'dicoccoides' are in close agreement with those previously reported by Nevo et al. (1982). They found a mean of 0.10 over genetic distances and a range of 0.02–0.25 while the squared root of the mean chi-squared distance for all variables we have studied in 'dicoccoides' was 0.15 and its range 0.00–0.30. This intraspecific variability data from other species is, to our knowledge, the first to be reported to date. Doubtlessly, more studies are needed to explain the quantitative and qualitative differences in intraspecific variability among *Triticum* species.

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