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PHYLOGENETIC DIFFERENTIATION OF TETRAPLOID WHEATS

On the basis of existing genetic barriers, the tetraploid wheats have been divided in two groups: the Emmer group involving most of the cultivated tetraploids and the wild *T. dicoccoides* (Körn.) Thell., and the Timopheevi group involving the cultivated Transcaucasian endemic *T. timopheevi* Zhuk. and the wild *T. araraticum* Jakubz. Recently, Mac Key (1966) has suggested to consider the two groups as genetically isolated biological species under the names *T. turgidum* (L.) Thell. and *T. timopheevi* Zhuk., and to reduce the previously known "species" to subspecies and convariety ranks.

Our recent electrophoretic studies (Jaaska, 1969; Jaaska, Jaaska, 1970) of acid phosphatase isoenzyme composition strongly support the above grouping of the tetraploid wheat taxa. It has been shown that, on the basis of distinct acid phosphatase isoenzyme patterns, the tetraploid wheat taxa fall in the same two groups. The data confirmed that the two groups of tetraploid wheats are genetically unique, being enzymologically differentiated from each other.

This short communication presents additional enzymological evidence on the evolutionary differentiation of the wild-growing tetraploid wheats in the two genetically distinct groups. Polyacrylamide gel electrophoretic patterns of acid phosphatases and esterases were studied for 19 strains of the wild tetraploid wheat from Israel (collections K-20403, K-23664, K-5198, K-5199, K-5201, K-17256, K-26117, K-26118, K-41965, K-41966, U-238294 and U-236696), Iraq (collections K-40120, K-40121, K-40122 and K-40123, K-41907 and K-42632) and Syria (K-17157), for 12 strains of *T. araraticum* from Nakhitshevan ASSR (K-28239, K-28244, K-28280, K-30210, K-30216, K-30234 and K-30240), Armenian SSR (K-30258, K-31828) and Azerbaijan SSR (K-39098, K-31121 and K-31123), and for a strain of *T. timopheevi* var. *typicum* (K-29548) from West Georgia. In addition, 18 strains of wild diploid wheat from Turkey, Iraq, Armenia and Azerbaijan were studied. All the seed samples were received from the World Collection of the Vavilov Institute of Plant Industry (Leningrad) through the kindness of Dr. E. Migushova. The experimental procedures were the same as reported previously (Jaaska, 1969), except for performing the electrophoresis in gel slabs instead of glass tubes.

Results and Discussion

Acid phosphatase electrophoretic pattern of *T. araraticum* and *T. timopheevi*, as seen in Fig. 1A, is mainly characterized by a broad fast-moving major zone of activity actually consisting of two closely spaced isoenzyme bands. In addition, 3—4 weak, scarcely distinguishable bands of intermediate electrophoretic mobility and a staining near the origin can be seen. All the 12 accessions of the wild tetraploid *T. araraticum* originating from Nakhitshevan and Azerbaijan and an accession of the cultivated *T. timopheevi* var. *typicum* from Western Georgia revealed an essentially similar phosphatase pattern, except for a variation in the enzyme activity remaining near the origin.

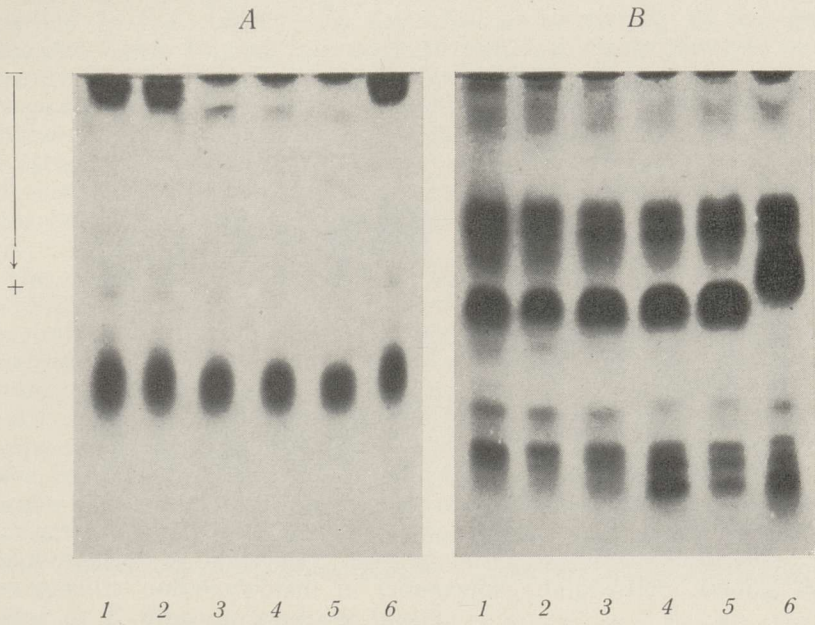


Fig. 1. Acid phosphatase (A) and esterase (B) enzymograms for the strains K-39098 (1), K-31123 (2), K-31628 (3), K-31121 (4), K-30212 (5) of *T. araraticum* and for the strain K-29548 (6) of *T. timopheevi*.

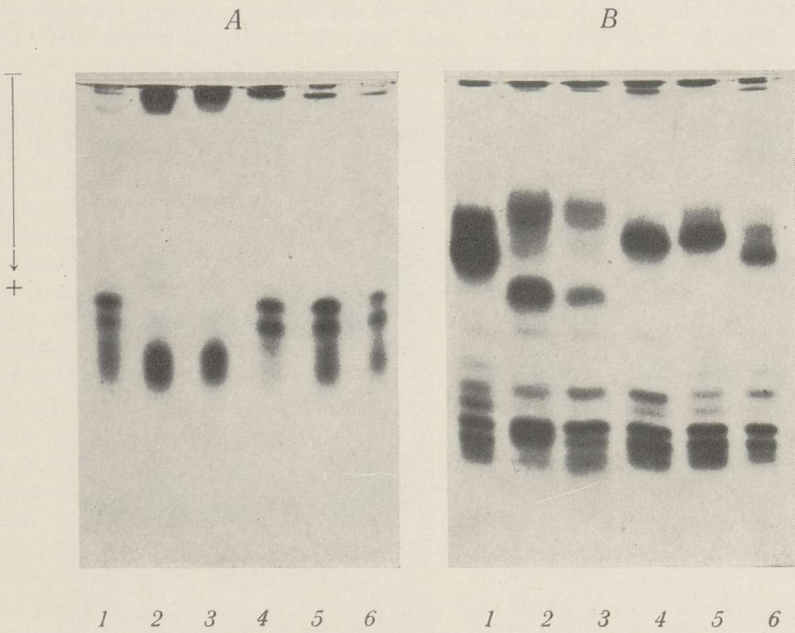


Fig. 2. Acid phosphatase (A) and esterase (B) enzymograms of wild tetraploid wheat: K-42 632 (1), K-40120 (2) and K-40122 (3) from Iraq; K-5198 (4), K-20403 (5) and K-23664 (6) from Israel.

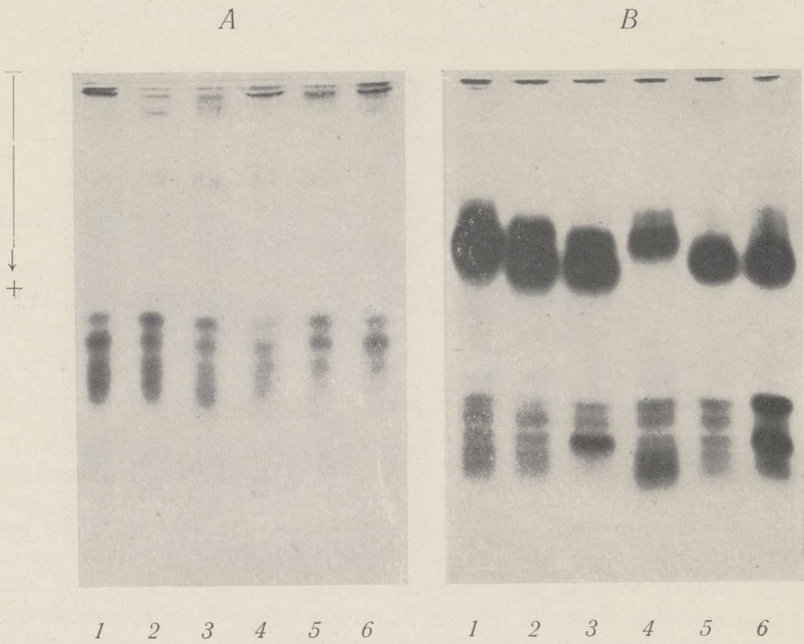


Fig. 3. Acid phosphatase (A) and esterase (B) enzymograms of *T. dicoccoides* from Israel: K-17256E (1), K-26117 (2), K-41965 (3), K-26118 (4), K-5199 (5), K-5201 (6).

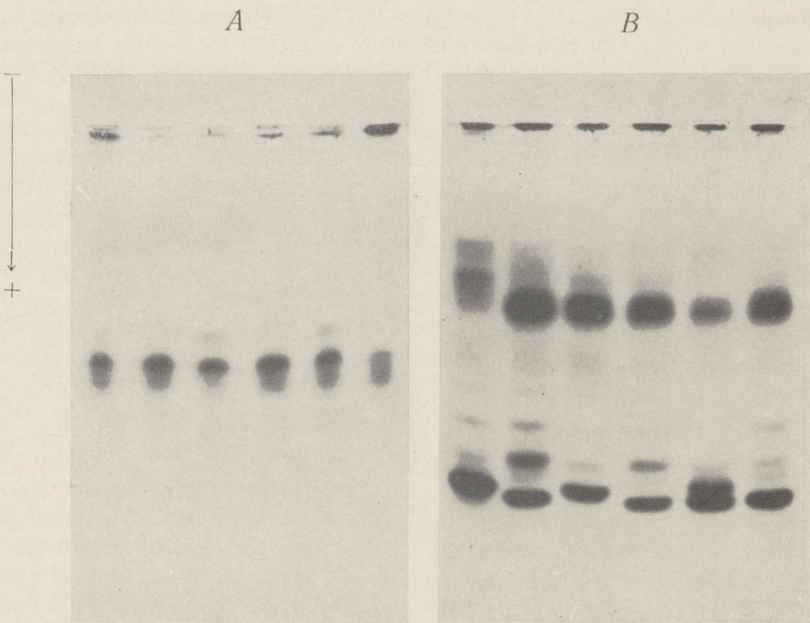


Fig. 4. Acid phosphatase (A) and esterase (B) enzymograms for different strains of wild diploid wheat.

Esterase electrophoretic pattern of *T. araraticum* and *T. timopheevi*, presented in Fig. 1B, can be described as consisting of two groups of isoenzyme bands having intermediate and fast electrophoretic mobilities, respectively. The pattern was essentially similar for all the 12 strains of *T. araraticum* studied, showing mainly quantitative variation in comparative staining intensity of the fastest-moving triplet of isoenzyme bands. The esterase pattern of *T. timopheevi* showed distinct difference from that of *T. araraticum* by having a shift in the electrophoretic mobility of the major esterase zone, although the remaining bands were common to both taxa.

The accessions of wild tetraploids received under the name of *T. dicoccoides* fell in two groups, according to the appearance of their acid phosphatase and esterase electrophoretic patterns. One group of the *dicoccoides* strains showed phosphatase and esterase electrophoretic patterns qualitatively similar to those previously (Jaaska, 1969; Jaaska, Jaaska, 1970) found for the cultivated tetraploids of the Emmer group (enzymograms 1, 4, 5 and 6 in Fig. 2A and B). All the strains of *T. dicoccoides* from Israel showed qualitatively non-variant phosphatase electrophoretic patterns of the Emmer type characterized by the presence of four successive isoenzyme bands, as demonstrated in Fig. 3A. In contrast to phosphatases, the esterases, as shown in Fig. 3B, revealed a clear-cut intra-specific polymorphism in isoenzyme composition among the same strains of *T. dicoccoides* from Israel.

The second group of strains, also received under the name *T. dicoccoides*, proved to be enzymologically qualitatively similar to *T. araraticum* (enzymograms 2 and 3 in Fig. 2A and B).

Among the 6 strains of the wild tetraploid wheat from Iraq only one (K-42632) showed phosphatase and esterase patterns characteristic of the Emmer group, as well as the sole strain of the wild tetraploid from Syria. The remaining five strains from Iraq revealed phosphatase and esterase isoenzyme patterns characteristic of *T. araraticum* from Soviet Transcaucasia.

The above data conclusively support earlier cytogenetic data of E. B. Wagenaar (1966) suggesting that the distribution area of *T. araraticum* is not restricted to Soviet Transcaucasia but extends southwards to Iraq. Recent hybridization studies by E. Migushova (1970, personal communication) carried out with the same strains which were used in the present investigation have demonstrated the differentiation of the wild Iraqi tetraploids in two groups, depending on the formation of fertile or sterile hybrids with *T. timopheevi*. The available evidence thus supports the view (Wagenaar, 1966) that the populations of wild tetraploid wheat in Iraq (and probably in Syria) actually consist of the biotypes of two genetically isolated biological species, *T. dicoccoides* and *T. araraticum*, which can be distinguished on the basis of their distinct acid phosphatase and esterase electrophoretic patterns. The enzymological differences between the two species involve the absence in *T. araraticum* of one major phosphatase isoenzyme controlled by the genome A and differences in the esterase isoenzymes of intermediate electrophoretic mobility (see Fig. 2A and B).

In our previous paper (Jaaska, Jaaska, 1970) we presented enzymological evidence in support of the allopolyploid origin of both the Emmer and Timopheevi wheats from the diploids *T. boeoticum* Boiss. and *A. speltoides* Tausch. Theoretically, there is a possibility that *T. araraticum* and *T. dicoccoides* are of independent amphidiploid origin, involving initially different biotypes of the diploid precursors. In this case, the genome A of *T. arara-*

ticum must have come from a biotype of *T. boeoticum* lacking at least one major phosphatase isoenzyme. However, our preliminary survey of 18 strains of the wild diploid wheat available from the Vavilov-Collection failed to find such a biotype and showed a uniform presence of the characteristic doublet of major isoenzymes in all the accessions studied, although it was shifted in *T. urartu*. Fig. 4A and B illustrate the constancy of major phosphatase isoenzymes and the kind of variation in the esterase pattern among the strains of *T. boeoticum*. The esterase pattern of *T. urartu* (unpublished) was distinctly different from those of *T. boeoticum*, *T. araraticum* and *T. dicoccoides*.

The second alternative is that both *T. araraticum* and *T. dicoccoides* had a common tetraploid progenitor and the divergence of these two species has occurred on the tetraploid level as the result of mutational changes of involved genomes. Moreover, the loss of one acid phosphatase isoenzyme as well as the decrease in the activity of the second isoenzyme controlled by the genome A could preferentially occur on the tetraploid level when the phosphatase isoenzymes controlled by the second genome B compensate this loss and secure the survival despite the enzyme deficiency. Comparison of enzymograms in Fig. 2 shows that in the *araraticum*-type pattern the fastest-moving phosphatases controlled by the genome B are intensely stained, while in the Emmer-type enzymograms they appear comparatively less intense.

From the above considerations, the origin of *T. araraticum* and *T. dicoccoides* from a common initial allotetraploid through the accumulation of genic mutations seems to be acceptable. However, available data still do not exclude their possible independent polytopic origin, through the separate amphidiploidization events, from previously divergent biotypes of the same parental species.

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TETRAPLOIDSETE NISUDE FÜLOGENEETILINE DIFERENTSEERUMINE

Resüme

Metsikult kasvavad tetraploidsed nisud on diferentseerunud kaheks geneetiliselt isoleeritud liigiks *T. dicoccoides* (Körn.) Aarons ja *T. araraticum* Jakubz., mis on selgesti eristatavad polüakrüülamiidgeelelektroforeetilisel määratud happelise fosfaataasi ja esterasaasi isofermentide koostise järgi. Kõik 12 Armeenist, Nahhitševanist ja Azerbaidžaanist pärinevat metsiku tetraploidi proovi, viis kuuest Iraagi päritoluga proovist ning Gruusia kultuurendem *T. timopheevi* Zhuk. kuuluvad isoensüümide koostise alusel liiki *T. arara-*

ticum Jakubz. Kõigil 12 Israeli päritoluga metsiku tetraploidi proovil, ühel Süüria ja ühel Iraagi proovil oli Emmeri rühma kultuuritetraploididega ühine happelise fosfataasi ensüümogramm, kuid nende esteraasi isofermentses koostises täheldati liigisest polü-morfismi.

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ВЕЛЛО ЯАСКА

ФИЛОГЕНЕТИЧЕСКАЯ ДИФФЕРЕНЦИАЦИЯ ТЕТРАПЛОИДНЫХ ПШЕНИЦ

Резюме

Дикорастущие тетраплоидные пшеницы дифференцированы на два генетически изолированных вида — *T. dicoccoides* (Кörn.) Aarons и *T. araraticum* Jakubz., которые отчетливо различаются по изоферментным составам кислой фосфатазы и эстеразы, выявленным методом электрофореза в полиакриламидном геле. Все 12 изученных образцов дикой тетраплоидной пшеницы из Армении, Нахичевана и Азербайджана, пять из шести иракских образцов, а также культурный *T. timopheevi* Zhuk. из Грузии относятся к *T. araraticum* Jakubz. Все 12 изученных образцов дикой тетраплоидной пшеницы из Израиля, один из Сирии и один образец из Ирака имеют одинаковые с культурными тетраплоидами группы Эммера энзимогаммы кислой фосфатазы, но выявляют внутривидовой полиморфизм в изоферментном составе эстеразы.

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