EESTI NSV TEADUSTE AKADEEMIA TOIMETISED. 19. KÖIDE
BIOLOOGIA. 1970. Nr. 4

ИЗВЕСТИЯ АКАДЕМИИ НАУК ЭСТОНСКОЙ ССР. ТОМ 19
БИОЛОГИЯ, 1970, № 4

https://doi.org/10.3176/biol.1970.4.08

V. JAASKA, VILVE JAASKA

BIOCHEMICAL DATA ON THE ORIGIN OF TRANSCAUCASIAN ENDEMIC WHEATS

Transcaucasia, comprising the Georgian, Armenian and Azerbaijan Soviet Republics together with the northern parts of Iran and north-eastern Turkey, is known as an area of great diversity of wild-growing and cultivated wheats (for references see Жуковский, 1964). Up to eight wheat taxa which were raised to the species rank by several distinguished wheat taxonomists were found to be endemic to this area. These include: the diploid *T. urartu* Tum., the tetraploids *T. georgicum* Dek., *T. persicum* Vav., *T. timopheevi* Zhuk, *T. araraticum* Jakubz., and the hexaploids *T. macha* Dek. et Men., *T. vavilovii* Zhuk., and *T. zhukovskyi* Eriz. et Men.

The origin of Transcaucasian endemics and their relationships with the wheats from other geographic areas have been the subject of many special investigations. Despite of this, it has remained a matter of dispute up to date (see Jakubziner, 1959; Dekaprelevich, 1961; Menabde, 1961; Wagenaar, 1966; Канделаки, 1967; Gorgidze, 1968; Dorofeyev, 1969, etc.).

In our previous paper (Jaaska, 1969) we applied polyacrylamide gel electrophoretic patterns of seedling enzymes to establish the phylogenetic relationships among the wheat taxa. The results of that work presented biochemical evidence in support of the view about the allopolyploid origin of the tetraploid and hexaploid wheats, with *T. monococcum* L., *Aegilops speltoides* Tausch and *A. squarrosa* L. as the parental precursor diploids. The data also showed that acid phosphatase isoenzymes were especially suitable as biochemical markers of the composite genomes in the polyploid wheats, showing clear-cut genome-specific differences in their electrophoretic mobilities.

The present report is an attempt to use the electrophoretic patterns of seedling acid phosphatases to study the phylogenetic relationships and the origin of the Transcaucasian endemic wheats.

Materials and methods

Plant material. The seed collections were received from the World Collection of the Vavilov All-Union Institute of Plant Industry in Leningrad through the courtesy of Drs. M. Jakubziner and E. Migushova, and from the Institute of Genetics of the Georgian Academy of Sciences through the courtesy of Prof. L. Dekaprelevich. The wheat taxa studied are given in those botanical names under which they were obtained and listed in the Table.

The seeds were germinated in Koch dishes on two sheets of filter paper with 5 ml 2×10^{-4} M $CaSO_4$ solution in the dark at 25 °C for 4 to 5 days.

List of taxa, collection numbers and places of origin

Botanical name and collection number	Place of origin
I. Diploid wheats	
T. boeoticum Boiss., K-25807	Armenia
T. urartu Tum. var. *nigrum*, K-33870	Armenia
T. monococcum L. var. *flavescens*, K-35915	Georgia
T. monococcum L. var. *hornemanni**	Georgia
II. Tetraploid wheats	
T. georgicum Dek.*	Georgia
T. persicum Vav. var. *stramineum*, K-18013	Armenia
T. dicoccoides (Körn.) Aarons, var. *arabicum*, K-20403	Israel
T. timopheevi Zhuk.*	Georgia
T. araraticum Jakubz. var. *nachitschevanicum*, K-31123	Azerbaijan
T. araraticum Jakubz. var. *thumaniani*, K-31121	Azerbaijan
T. araraticum Jakubz., K-30212	Azerbaijan
III. Hexaploid wheats	
T. vavilovii Jakubz. var. *vaneum*, K-28168	Armenia
T. *macha* Dek. et Men. var. *letschumicum* (=*T. tubalicum* Dek.), K-28165	Georgia
T. macha Dek. et Men. var. *colchicum* (=*T. tubalicum* Dek.), K-38547	Georgia
T. macha Dek. et Men. var. *palaeo-imereticum* (=*T. imereticum* Dek.), K-28191	Georgia
T. macha Dek. et Men. ssp. *imereticum* Dek.*	Georgia
T. macha Dek. et Men. ssp. *tubalicum* Dek.*	Georgia
T. zhukovskyi Men. et Eriz.*	Georgia
IV. *Aegilops* L. and *Secale* L.	
A. speltoides Tausch, K-2, K-21	Asia Minor
A. squarrosa L., K-160	Azerbaijan
S. segetale Roshev., K-7984	Georgia
V. *Triticale*	
T. durum Desf. × *S. kuprianovii* Grossh., K-43632, 2n=42	Azerbaijan

* The samples noted with an asterisk were received from the Institute of Genetics of the Georgian Academy of Sciences, while the remaining samples were obtained from the Vavilov All-Union Institute of Plant Industry.

Tissue extracts and electrophoresis. A 400—500 mg sample of excised coleoptiles together with the first leaves was homogenized by grinding in a pre-chilled mortar with an addition of 2.0 ml of cold buffer mixture at a pH of about 7.1 consisting of 0.1 M tris-hydroxymethylaminomethane, 0.08 M ascorbic acid and 0.005 M EDTA. The resulting homogenate was centrifuged at 18,000 g for 30 minutes. Sucrose was added to the supernatants in small vials to a final concentration of about 20—30 per cent, together with about 10—15 mg/ml Sephadex G-200 as an inert protein carrier. The protein extracts were stored frozen at —10 °C.

A modified method of vertical polyacrylamide gel electrophoresis in glass tubes, using only a photopolymerized, small-pore gel layer without large-pore layer, has been employed as described in detail by V. Jaaska and V. Jaaska (1968). All the electrophoretic runs were made in duplicate, with two parallel gels for every sample simultaneously in each run. Acid phosphatase activity on gels was localized by means of an azo-dye coupling method with 1-naphthyl phosphate as a substrate and

hexaazotized pararosanilin as a coupler (Jaaska, Jaaska, 1968). After staining the gels were photographed in a transmitting light for a permanent record.

The maintaining of the extraction and electrophoresis conditions constant proved to be essential for obtaining reproducible enzyme patterns.

Results and discussion

A photograph of polyacrylamide gel electrophoretic patterns of acid phosphohydrolases from etiolated seedlings of various Transcaucasian wheats and of related species is presented in the Figure. The isoenzyme bands are designated by the distances of migration from the origin to the anode, given in arbitrary units.

The diploid wheats. Enzymograms *a, b, c,* and *d* present acid phosphatase patterns of four taxa of Transcaucasian diploid wheats. Two of them specified as *T. boeoticum* Boiss. and *T. urartu* Tum. are wild-growing, whereas the other two collections represent varieties of cultivated einkorn. It can be seen from the enzymograms that the patterns of all the four diploid forms studied here are essentially similar, revealing one band near the origin and two closely spaced bands. The major bands showed similar migration distances at about 4.6 and 5.1 respectively, except for *T. urartu* which revealed a slight shift towards the higher electrophoretic mobility.

Upon prolonged reaction times, one or two bands of weaker staining intensity and phosphatase activity appeared in the region from 3.2 to 4.1, in addition to the major fractions. These phosphatase fractions are scarcely distinguishable in the Figure, but when they became intense enough for photography, the major phosphatase bands became already fused and formed a large and intense staining area. However, these minor phosphatase fractions are interesting in this respect that they show some variation among the taxa studied. *T. urartu*, in addition, showed a weak and diffuse staining area before the major fractions. These results may presumably indicate some intra-genomal differentiation among the diploid wheats in the genetic system controlling the presence and electrophoretic mobility of these minor phosphatases.

The data obtained here indicate that the seedlings of wild-growing as well as cultivated diploids contain essentially similar major phosphatases. It means that their genomes must contain similar structural genes for these phosphatases as well. This is in good line with the view that all forms of wild-growing and cultivated diploid wheats, even if morphologically distinct and easily distinguishable, are phylogenetically closely related and of common origin. On the basis of the evidence that most of the einkorn strains, cultivated as well as wild-growing, can be readily crossed, resulting in fully fertile hybrids with regular chromosome pairing in meiosis (Smith, 1936), several investigators (Harlan, Zohary, 1966; Mac Key, 1966) have even proposed to lump all the diploid wheats in one species under the name *T. monococcum* L.

The tetraploid wheats. On the basis of the sterility barriers, the tetraploid wheats have been divided (Lilienfeld, Kihara, 1934; Mac Key, 1966; Wagenaar, 1966) in two groups: the Emmer group and the Timopheevi group. The F_1 hybrids between the wheats of the two groups proved to be almost completely sterile and showed significant meiotic irregularities (Хинчук, 1929; Декапрелевич, Менабде, 1932; Lilienfeld, Kihara, 1934; Kostoff, 1937; Svetozarova, 1939, etc.). The Emmer group includes several cultivated forms and *T. dicoccoides* Körn. as a wild member. The

Transcaucasian endemics, *T. persicum* Vav. (=*T. carthlicum* Nevski) and *T. georgicum* Dek. (=*T. palaeo-colchicum* Men.) belong to the Emmer group together with other cultivated forms, such as *T. durum* Desf., *T. dicoccum* Schrank, *T. polonicum* L. and *T. turgidum* L.

The Timopheevi group consists of a cultivated form *T. timopheevi* Zhuk. which is restricted to a limited area in West Georgia and of a wild member *T. araraticum* Jakubz. which occurs in some mountainous regions of Armenia and Azerbaijan (Якубцинер, 1932; Менабде, Ерицян, 1942; Mac Key, 1966; Wagenaar, 1966).

The comparison of enzymograms *f* through *j* in the Figure clearly shows that acid phosphatase patterns of the tetraploids fall into the same two groups. The patterns for the cultivated Transcaucasian tetraploids *T. persicum* (enzymogram *f*) and *T. georgicum* (enzymogram *g*) as well as for a wild-growing *T. dicoccoides* (enzymogram *h*) from Israel proved to be essentially similar, but distinctly different from the patterns for *T. timopheevi* (enzymogram *i*) and *T. araraticum* (enzymogram *j*). These data support the separation of the tetraploid wheats into the Emmer and Timopheevi groups and demonstrate the occurrence of biochemical differences between them in the isoenzyme systems of acid phosphatases. Since *T. araraticum* and several forms of *T. dicoccoides* are morphologically quite similar (Harlan, Zohary, 1966; Wagenaar, 1966) and are hardly distinguishable on purely morphological grounds, acid phosphatase electrophoretic patterns can be suggested as a useful taxonomic marker to distinguish between the two groups of wild-growing tetraploids.

As it was shown in our previous paper (Jaaska, 1969), a phosphatase pattern involving four successive bands of intermediate electrophoretic mobility is characteristic of the tetraploid wheats of the Emmer group. It was shown in that report and it appears again from the Figure presented here that a doublet of phosphatase bands at about 4.6 and 5.1 in the pattern of the Emmer wheats is derived from the genetic information encoded in the genome *A* of the diploid wheats (see enzymograms *a* through *d*), and that another doublet of phosphatases with mobilities at about 5.6 and 6.0 is characteristic of the genome *B* derived from the diploid species *Aegilops speltoides* Tausch (see enzymogram *e*). A band at about 6.0 was much weaker than the remaining three and is hardly discernible in the Figure. It appeared clearly only after prolonged reaction times when the other three successive bands tended to fuse.

Thus, the acid phosphatase electrophoretic pattern of the Emmer wheats is composed of the fractions found in the diploid wheats and of those characteristic of *A. speltoides*. The data support the view that all the tetraploids of the Emmer group, including Transcaucasian endemics *T. persicum* and *T. georgicum*, a wild-growing *T. dicoccoides* from the Middle East and the cultivated forms *T. dicoccum*, *T. polonicum*, *T. durum*, and *T. turgidum* studied in our previous report (Jaaska, 1969) are all of common allopolyploid origin involving an einkorn and *A. speltoides* as the parental species. Based on the data that members of the Emmer group can be readily crossed and yield highly fertile hybrids showing regular chromosome pairing J. Mac Key (1966) proposed to include all the members of the Emmer group under the name *T. turgidum* L.

Enzymograms *i* and *j* in the Figure present acid phosphatase patterns for *T. timopheevi* and *T. araraticum*, respectively. The comparison of the two patterns shows that they are of the same type. This result is consistent with the view that the two taxa, *timopheevi* and *araraticum*, are phylogenetically closely related and form a separate group biochemically distinct from the Emmer wheats. It has been shown by several investigators

(Svetozarova, 1939; Менабде, Ерицян, 1942, etc.) that hybrids between *T. timopheevi* and *T. araraticum* have regular meiotic chromosome pairing, indicating close chromosome homology and genetic relatedness. On these grounds, J. Mac Key (1966) suggested to consider the two taxa as one species under the name of *T. timopheevi* Zhuk. However, M. Tanaka and S. Ichikawa (1968) recently reported a hybrid between *timopheevi* and *araraticum* which was sterile and formed no seeds, despite fully regular meiosis. At the same time, the F_1 hybrid of *timopheevi* with an another strain of *araraticum* from the same population showed both regular meiosis and seed formation. These data seem to suggest a sympatric speciation to occur within the *araraticum*-complex.

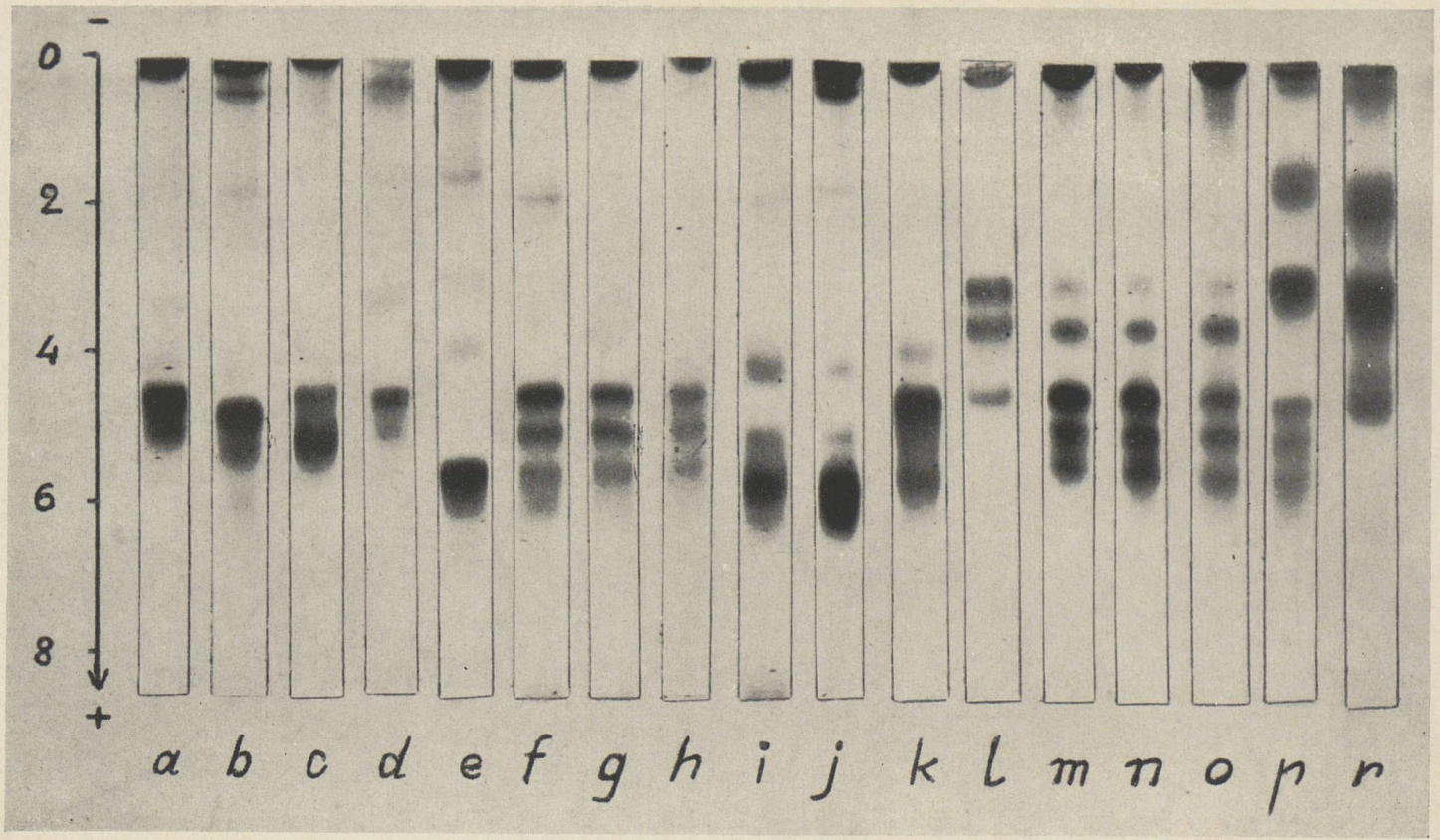
In our biochemical experiments, two accessions of *timopheevi* and three accessions of *araraticum* which we studied all showed similar, in major features, phosphatase patterns. This means that the difference between phosphatase patterns of the Emmer and the Timopheevi wheats is not an occasional variation but is the result of the historical development which has accompanied the phylogenetic differentiation of the two groups. We found no further differentiation in the acid phosphatase isoenzyme composition within the two groups, although some variations in the electrophoretic mobilities could be suspected.

It can be seen in the Figure that the acid phosphatase pattern for the Timopheevi wheats is characterized by the presence of four bands with the migration distances at about 4.1, 5.0, 5.6 and 6.0. The bands at 5.6 and 6.0 tended to fuse upon prolonged incubation times. The comparison of enzymograms *i* and *j* with those for the diploid wheats (*a* through *d*) clearly shows the absence, in the Timopheevi pattern, of an isoenzyme band at the migration distance of 4.6 which is characteristic of the genome *A* of the diploids. Instead of this band, a new fraction appeared in the Timopheevi pattern at about 4.2. The second isoenzyme characteristic of the genome *A* and located at about 5.0 becomes discernible in the Timopheevi pattern upon prolonged reaction time only.

From the comparison of the Timopheevi pattern with that of *A. speltoides* (enzymogram *e*) it follows that a doublet of phosphatase isoenzymes characteristic of the genome *B* of *A. speltoides* is clearly present in the Timopheevi wheats. It can be even said that the bands determined by the *B*-genome are comparatively more intensive in the Timopheevi wheats than in the Emmers.

Thus, it follows from our data that the evolutionary differentiation of the Emmer and Timopheevi wheats has been accompanied by changes in the genetic system of the genome *A* controlling an acid phosphatase isoenzyme, and leaving the structural genes for the phosphatase isoenzymes in the genome *B* unchanged, if judged by the identity of the electrophoretic mobilities.

On the basis of their studies of meiotic chromosome conjugation in the F_1 hybrids between the einkorn and *timopheevi* and between the Emmer wheats and *timopheevi*, F. Lilienfeld and H. Kihara (1934) concluded that the einkorn, the Emmers and *timopheevi* all share a common genome designated as $A_{\text{Eink.}}$, $A_{\text{Em.}}$ and $A_{\text{Tim.}}$, respectively. The second genome in the Emmers and *timopheevi* showed only partial homology, judged by the presence of unpaired univalents at the meiosis of the F_1 hybrids. For this reason, the second genome of timopheevi has been designated by the symbol *G* to distinguish it from the genome *B*. Several other investigators (Kostoff, 1937; Sachs, 1953, etc.), however, inclined to think that the differences between the second genome of *timopheevi* and of the Emmers are not so significant as to justify separate symbols. More recently, E. B. Wage-



Polyacrylamide gel electrophoretic patterns of seedling acid phosphatases for the Transcaucasian endemic wheats and related taxa. Enzymograms:

a — *T. boeoticum* Boiss., *b* — *T. urartu* Tum. v. *nigrum*, *c* — *T. monococcum* L. v. *hornemanni*, *d* — *T. monococcum* L. v. *flavescens*, *e* — *A. speltoides* Tausch, *f* — *T. persicum* Vav., *g* — *T. georgicum* Dek., *h* — *T. dicoccoides* (Körn.) Aarons v. *arabicum*, *i* — *T. timopheevi* Zhuk., *j* — *T. araraticum* Jakubz., *k* — *T. zhukovskyi* Men. et Eriz., *l* — *A. squarrosa* L., *m* — *T. vavilovii* Jakubz., *n* — *T. imereticum* Dek., *o* — *T. tubalicum* Dek., *p* — *T. durum* Desf. × *S. kuprianovii* Grossh., *r* — *S. segetale* Roshev.

naar (1961) showed that meiotic irregularities and chromosome unpairing in the F_1 hybrids between *timopheevi* and the Emmers were not so much a result of differences in the chromosome structure as due to the presence in the *timopheevi*-genome of mutant genes preventing meiotic conjugation between several pairs of homologous chromosomes.

Our biochemical data are consistent with the view about the common allopolyploid origin of the Emmer and Timopheevi wheats involving the einkorn and *A. speltoides* as the parental species. Both the Emmer and Timopheevi wheats contain electrophoretically similar acid phosphatase isoenzymes controlled by the genome *B* derived from *A. speltoides*. At the same time, our data also suggest the occurrence of differences between the Emmer and Timopheevi wheats in the genic structure of the *A*-genome. In this connection, it is of interest to note that B. L. Johnson (1967) and B. L. Johnson *et al.* (1967) also revealed differences between the Emmer and Timopheevi wheats in the composition of seed proteins controlled by the genome *A*. Presumably, both genomes of the tetraploid wheats have accumulated a number of genic mutations which become fixed in the course of the phylogenetic development of the two groups. Biochemical experiments enabled us to reveal differences in the *A*-genomes which were undetectable in cytogenetic investigations.

When taking into consideration the evidence (Zohary, 1966) that one of the parental species for the tetraploid wheats, *A. speltoides*, is not distributed in Soviet Transcaucasia, it appears likely that this area had not been the primary centre of origin of the Emmer and Timopheevi wheats. The contemporary area of distribution of *A. speltoides* extends from northern Israel, Syria and Turkey to northern Iraq and western Iran (Harlan, Zohary, 1966; Zohary, 1966). Wild einkorn and *A. speltoides* are reported (Harlan, Zohary, 1966) to form sympatric populations in south-east Turkey, northern Iraq and western Iran. V. Menabde and A. Eritzian (Менабде, Ерицян, 1942) suggested that *T. timopheevi* has been brought to Transcaucasia by ancient Georgian tribes on their immigration from the territory of Urarthu. Recent studies of J. H. Harlan and D. Zohary (1966), L. Sachs (1953) and E. B. Wagenaar (1966) indicate that the Timopheevi group is not restricted to the Transcaucasian Soviet Republics, but extends to eastern Turkey, Iran and Iraq. All these data support the suggestion put forward by E. B. Wagenaar (1966) that the Timopheevi group originated in northern Iraq where the distribution areas of *araraticum* and *dicoccoides* overlap. This hypothesis is also supported by the fact that earliest archeological finds of tetraploid wheats are known from Iraqi-Kurdistan (Helbaek, 1959).

On the origin of the Zanduri population. The Georgian endemic population Zanduri consists mainly of a diploid *T. monococcum* var. *hornemanni* and of a tetraploid *T. timopheevi* (Декапрелевич, Менабде, 1932). More recently (Менабде, Ерицян, 1960) a hexaploid form named as *T. zhukovskyi* Men. et Eriz. has been found among the plants of this population.

The origin of this population and the phylogenetic interrelationships between its member-species have been the subject of diverse opinions. M. Tumanian (Туманян, 1939) put forward a hypothesis about the autopolyploid origin of *T. timopheevi* from the diploid component of the Zanduri population — *T. monococcum* var. *hornemanni*. This suggestion has been questioned by other investigators (Lilienfeld, Kihara, 1934; Менабде, 1962, etc.), who suspected the allopolyploid origin of *T. timopheevi*. Recently, A. Gorgidze (1968) found, among the progeny from the seeds of *T. monococcum* var. *hornemanni* exposed to radiation, tetraploid plants

morphologically resembling *T. timopheevi*. On the basis of this experimental evidence, A. Gorgidze (1968) considers *T. timopheevi* as an autotetraploid containing a duplicated genome *A* of *T. monococcum* var. *hornemanni*.

The results of our study present biochemical evidence in support of the origin of *T. timopheevi* through allopolyploidy involving einkorn and *A. speltoides* as the genome donors. The comparison of the acid phosphatase patterns for *T. timopheevi* (enzymogram *i*) and for *T. monococcum* var. *hornemanni* (enzymogram *c*) clearly shows that *T. timopheevi* is not a simple autopolyploid, since it contains acid phosphatase isoenzymes characteristic of *A. speltoides* which are not found in the diploid wheats, and it lacks an isoenzyme present in *T. monococcum* var. *hornemanni*.

The hexaploid wheats. Our study involved four different taxa of hexaploid Transcaucasian endemics: *T. zhukovskyi* Men. et Eriz., *V. vavilovii* Jakubz. and two forms of *T. macha* Dek. et Men., *T. imereticum* Dek. and *T. tubalicum* Dek.

T. zhukovskyi is a hexaploid derivative of the Zanduri population (Менабде, Ерицян, 1960). On the basis of cytogenetic and morphological studies of artificially produced hybrids, V. Menabde (Менабде, 1962), E. Tavrin (Таврин, 1964), and M. D. Upadhya and M. S. Swaminathan (1963, 1965) reached the conclusion that *T. zhukovskyi* represents an allopolyploid derived from the diploid and tetraploid member of the Zanduri population, *T. monococcum* var. *hornemanni* and *T. timopheevi*, through spontaneous hybridization and the following chromosome duplication.

This conclusion is supported by the biochemical evidence of the present study. It can be seen in enzymogram *k* in the Figure that the acid phosphatase pattern of *T. zhukovskyi*, in addition to the bands characteristic of *T. timopheevi* (enzymogram *i*), shows the presence of an intense band with the migration distance at about 4.6 which was absent in the *timopheevi*-pattern and is characteristic of the genome *A* of the diploid wheats involving *T. monococcum* var. *hornemanni*.

T. vavilovii represents a morphological form of the hexaploid wheat endemic of the Armenian mountains (Якубцинер, 1933). *T. macha* has been considered by Dekaprelevich and Menabde (1932) as a polymorphous collective species which can be divided into two morphologically distinct groups. The loose-eared form of *macha* was specified as *T. tubalicum* Dek. and the compact-eared form of *macha* was named as *T. imereticum* Dek. (Декапрелевич, 1942).

Acid phosphatase patterns for *T. vavilovii*, *T. imereticum* and *T. tubalicum* (two accessions) (see enzymograms *m*, *n* and *o* in the Figure) proved to be, in major features, identical and distinctly different from the pattern of *T. zhukovskyi*. As it was already shown in our previous report (Jaaska, 1969), a phosphatase pattern involving three doublets of phosphatase bands is characteristic of the Dinkel wheats. The sixth isoenzyme band at about 6.0 is very faint in the hexaploid pattern and is not seen in the enzymograms presented in the Figure. The comparison of enzymograms shows that acid phosphatase pattern of the hexaploids *T. vavilovii*, *T. imereticum* and *T. tubalicum* (enzymograms *m*, *n* and *o*) is composed of fractions (localized at about 4.5, 5.0, and 5.5) characteristic of the Emmer wheats (enzymograms *f*, *g* and *h*) and of fractions (at about 3.0 and 3.6) found to be present in the pattern of *A. squarrosa* (enzymogram *l*). *T. zhukovskyi* clearly lacks a doublet of phosphatase isoenzymes characteristic of the genome *D* of *A. squarrosa* and of other hexaploid wheats.

Since acid phosphatase electrophoretic patterns are essentially similar in all forms of the hexaploid wheats, except for *T. zhukovskyi*, they yield

no information on the relative antiquity or on the phylogenetic relations of the members within this group. The data only indicate that the hexaploids *T. spelta* L., *T. spherococcum* Perc. and *T. aestivum* L. studied previously (Jaaska, 1969) as well as the Transcaucasian endemics *T. vavilovii* Jakubz., *T. imereticum* Dek. and *T. tubalicum* Dek. are all of common allopolyploid origin involving an Emmer wheat and *A. squarrosa* as precursor species.

Recently, G. V. Kandelaki (Канделаки, 1967) found high quantities of trifructosane, a carbohydrate characteristic of rye, to be present in *T. tubalicum*. On the basis of this evidence she suggested that *T. tubalicum* has originated as an amphidiploid between *T. georgicum* and rye, and must therefore contain the genome of rye. Our enzymological data, however, reject this hypothesis by showing the presence in both *T. tubalicum* and *T. imereticum* of the phosphatase isoenzymes characteristic of the genome of *A. squarrosa*. Moreover, the data presented in the Figure clearly show that an artificial amphidiploid *T. durum* Desf. × *S. kuprianovii* Grossh. with 2n=42 contains two acid phosphatase bands located at about 1.6 and 3.0 (enzymogram *p*) which were also found in a weedy rye, *S. segetale* Roshev. (enzymogram *r*), and thus are characteristic of the rye-genome. These two isoenzyme bands are clearly absent in the pattern of *T. tubalicum*. From our data, thus, it follows that *T. tubalicum* contains the *D*-genome of *A. squarrosa* and does not contain a full genome of rye. However, the above results do not rule out the possibility that *T. tubalicum* may be a substitution line containing some chromosome fragments of rye in the composition of its genome.

Summary

Based on acid phosphatase electrophoretic patterns, the wheats can be divided into the following five phylogenetic groups: the diploid wheats, the Emmer tetraploids, the Timopheevi tetraploids, the *aestivum* hexaploids and *T. zhukovskyi* Men. et Eriz.

The enzymograms of the diploid wheats *T. boeoticum* Boiss., *T. urartu* Tum. and *T. monococcum* L. showed the presence of two major phosphatases, but differed in some minor fractions.

Acid phosphatase patterns of the Transcaucasian Emmers, *T. persicum* Vav. and *T. georgicum* Dek., were similar, consisting of a doublet of isoenzymes characteristic of the genome *A* of the diploid wheats and of another doublet of isoenzymes, electrophoretically similar to that found in *A. speltoides* Tausch. The patterns of *T. timopheevi* Zhuk. and *T. araraticum* Jakubz. proved to be qualitatively similar, showing the presence of isoenzymes characteristic of *A. speltoides* Tausch, but differing from those of the Emmer wheats by the absence of an isoenzyme controlled by the genome *A*.

The hexaploids *T. vavilovii* Jakubz., *T. imereticum* Dek. and *T. tubalicum* Dek. showed electrophoretically identical enzymograms consisting of isoenzymes characteristic of the Emmer wheats and of *A. squarrosa* L. Acid phosphatase isoenzymes characteristic of rye were absent in *T. tubalicum* Dek.

Acid phosphatase pattern of *T. zhukovskyi* Men. et Eriz. lacked isoenzymes characteristic of the genome *D* of *A. squarrosa* and of other hexaploids and proved to be the sum of isoenzymes found in *T. timopheevi* Zhuk. and *T. monococcum* L.

REFERENCES

Dekaprelevich L. L., 1961. Die Art *Triticum macha* Dek. et Men. im Lichte neuester Untersuchungen über die Herkunft der hexaploiden Weizen. Z. Pflanzenzücht. **45** : 17—30.

Dorofeyev W. E., 1969. Die Weizen Transkaukasiens und ihre Bedeutung in der Evolution der Gattung *Triticum* L. I. Die Formenmannigfaltigkeit der Weizen Transkaukasiens. Z. Pflanzenzücht. **61** : 1—29.

Gorgidze A. D., 1968. Mutagenic effect of ionizing radiations. Bull. Acad. Sci. Georgian S.S.R. **52** : 739—798 (in Georgian, summary in Russian).

Harlan J. H., Zohary D., 1966. The distribution of wild wheats and barley. Science **153** : 1074—1080.

Helbaek H., 1959. Domestication of food plants in the Old World. Science **130** : 365—372.

Jaaska V., 1969. Electrophoretic studies of seedling phosphatases, esterases and peroxidases in the genus *Triticum* L. Eesti NSV TA Toimet., Biol. **18** (2) : 170—183.

Jaaska Vilve, Jaaska Vello, 1968. Soluble phosphohydrolases and esterases in maize seedlings. ENSV TA Toimet., Biol. **17** : (3) 274—283.

Jakubziner M. M., 1959. New wheat species. Proc. First Internat. Wheat Genetics Symp. 1958, Public Press Ltd. : 207—220.

Johnson B. L., 1967. Tetraploid wheats: seed protein electrophoretic patterns of the Emmer and Timopheevi groups. Science **158** : 131—132.

Johnson B. L., Barnhart D., Hall O., 1967. Analysis of genome and species relationships in the polyploid wheats by protein electrophoresis. Amer. J. Bot. **54** : 1089—1098.

Kostoff D., 1937. Chromosome behaviour in *Triticum* hybrids and allied genera, I. Interspecific hybrids with *Triticum timopheevi*. Proc. Indian Acad. Sci. **5** : 231—236.

Lilienfeld F., Kihara H., 1934. Genomanalyse bei *Triticum* und *Aegilops*. V. *Triticum timopheevi* Zhuk. Cytologia (Tokyo) **6** : 87—122.

Mac Key J., 1966. Species relationship in *Triticum*. Hereditas. Suppl. **2** : 237—275.

Menabde V. L., 1961. Wheats of Georgia and their part in general evolution of the genus *Triticum* L. Trans. Bot. Inst. Tbilisi (21) : 229—259 (in Georgian, English summary).

Sachs L., 1953. Chromosome behaviour in species hybrids with *Triticum timopheevi*. Heredity **7** : 49—58.

Smith L., 1936. Cytogenetic studies in *Triticum monococcum* L. and *T. aegilopoides* Bal. Univ. Missouri, Agric. Exp. St., Coll. Agric. (248) : 1—38.

Svetozarova V. V., 1939. Second genome of *Triticum timopheevi* Zhuk. C. r. acad. Sci. U.S.S.R. **23** : 473—477.

Tanaka M., Ichikawa S., 1968. Cytogenetical examinations of *Triticum araraticum* Jakubz., a wild-type tetraploid wheat species. Genetics **60** : 229.

Upadhya M. D., Swaminanathan M. S., 1963. Genome analysis in *Triticum zhukovskyi* Men. et Eriz., a new hexaploid wheat. Chromosoma **14** : 589—600.

Upadhya M. D., Swaminanathan M. S., 1965. Studies on the origin of *Triticum zhukovskyi* and on the mechanisms regulating chromosome pairing in *Triticum*. Indian J. Genet. and Plant Breed. **25** : 1—13.

Wagenaar E. B., 1961. Studies on the genome constitution of *Triticum timopheevi* Zhuk. I. Evidence for genetic control of meiotic irregularities in tetraploid hybrids. Canad. J. Genet. and Cytol. **3** : 47—60.

Wagenaar E. B., 1966. Studies on the genome constitution of *Triticum timopheevi* Zhuk. II. The *T. timopheevi* complex and its origin. Evolution **20** : 150—164.

Zohary D., 1966. The evolution of genomes in *Aegilops* and *Triticum*. Hereditas, Suppl. **2** : 207—217.

Декапрелевич Л. Л., 1942. Роль Грузии в происхождении пшениц. III. Сообщ. АН Груз. ССР **3** : 445—450.

Декапрелевич Л. Л., Менабде В. Л., 1932. Пленчатые пшеницы Западной Грузии. Тр. по прикл. ботан., генет. и селекции, Сер. 5 : 3—46.

Жуковский П. М., 1964. Культурные растения и их сородичи. Л.

Канделаки Г. В., 1967. К происхождению *Triticum macha* Dek. et Men. Генетика : 34—46.

Менабде В. Л., 1962. Полиплоидный ряд в популяции грузинской пшеницы Зандури. Тр. МОИП **5** : 134—141.

Менабде В. Л., Ерицян А. А., 1942. К филогенезу *Triticum timopheevi* Zhuk. Сообщ. АН Груз. ССР **3** : 823—830.

Менабде В. Л., Ерицян А. А., 1960. К изучению грузинской пшеницы Зандури. Сообщ. АН Груз. ССР **25** : 731—736.
Таврин Э. В., 1964. К происхождению вида *Tr. zhukovskyi* Men. et Er. Тр. по прикл. ботан., генет. и селекции **36** : 89—96.
Туманян М. Г., 1939. О происхождении пшеницы *Tr. timopheevi* Zhuk. Тр. биол. ин-та, Ереван : 139—151.
Хинчук А. Г., 1929. К генетике *Triticum timopheevi* Zhuk. Тр. по прикл. ботан., генет. и селекции **20** : 625—654.
Якубцинер М. М., 1932. К познанию дикой пшеницы Закавказья. Тр. по прикл. ботан., генет. и селекции, Сер. 5 : 147—198.
Якубцинер М. М., 1933. Новый вид пшеницы *Triticum vavilovii* (Tum.). Тр. по прикл. ботан., генет. и селекции **A7** : 222.

Academy of Sciences of the Estonian SSR,
Institute of Zoology and Botany

Received
Oct. 21, 1969

V. JAASKA, VILVE JAASKA

BIOKEEMILISED ANDMED TAGA-KAUKAASIA ENDEEMSETE NISUDE PÄRITOLU KOHTA

Resümee

Happelise fosfataasi isoensüümide elektroforeetilise koostise alusel jaotuvad nisud viide fülogeneetilisse rühma: diploidsed nisud, Emmeri rühma tetraploidid, Timofeevi rühma tetraploidid, *aestivum*-rühma heksaploidid ja *T. zhukovskyi* Men. et Eriz.

Diploidsete nisude *T. boeoticum* Boiss., *T. urartu* Tum. ja *T. monococcum* L. ensümogrammidel täheldati kõigil kaht domineerivat fosfataasi isoensüümi, kuid nad erinesid mõnede vähemaktiivsete fraktsioonide poolest.

Taga-Kaukaasia Emmerite *T. persicum* Vav. ja *T. georgicum* Dek. ensümogrammidel ilmnes kaks diploidsele nisule iseloomulikku fosfataasi isoensüümi ja veel kaks isoensüümi, mis olid elektroforeetiliselt samasugused kui torupeal *A. speltoides* Tausch.

T. timopheevi Zhuk. ja *T. araraticum* Jakubz. ensümogrammidel esinesid samuti kaks torupeale *A. speltoides* Tausch iseloomulikku fosfataasi isoensüümi, kuid puudus üks genoom *A* poolt kontrollitavatest isoensüümidest.

Ühesugusteks osutusid heksaploidide *T. vavilovii* Jakubz., *T. imereticum* Dek. ja *T. tubalicum* Dek. ensümogrammid, kus esinesid Emmeri rühma nisudele ja torupeale *A. squarrosa* L. iseloomulikud fosfataasi isoensüümid. Rukki genoomile spetsiifilisi isoensüüme nisul *T. tubalicum* Dek. ei leitud.

T. zhukovskyi Men. et Eriz. ensümogrammil puudusid teistele heksaploididele ja torupeale *A. squarrosa*'le omased fosfataasi isoensüümid ning see koosnes *T. timopheevi* Zhuk. ja *T. monococcum* L. tõusmetes esinevate isoensüümide summast.

Eesti NSV Teaduste Akadeemia
Zooloogia ja Botaanika Instituut

Saabus toimetusse
21. X 1969

В. ЯСКА, ВИЛЬВЕ ЯСКА

БИОХИМИЧЕСКИЕ ДАННЫЕ О ПРОИСХОЖДЕНИИ ЗАКАВКАЗСКИХ ЭНДЕМИЧНЫХ ПШЕНИЦ

Резюме

По электрофореграммам кислых фосфатаз таксоны пшениц подразделяются на пять филогенетических групп: 1) диплоидные пшеницы, 2) тетраплоиды группы Emmer, 3) тетраплоиды группы Timopheevi, 4) гексаплоиды группы *aestivum* и 5) гексаплоид *T. zhukovskyi* Men. et Eriz.

Энзимограммы кислых фосфатаз диплоидов *T. boeoticum* Boiss., *T. urartu* Tum. и *T. monococcum* L. состоят из двух основных изоферментов и различаются по некоторым второстепенным фракциям.

Энзимограммы закавказских пшениц группы Emmer — *T. persicum* Vav. и *T. georgicum* Dek. сходны и состоят из двух дублетов, из которых один по электрофоретической подвижности соответствует изоферментам диплоидных пшениц (геном *A*), а другой —

A. speltoides Tausch. Качественно одинаковы энзимограммы *T. timopheevi* Zhuk. и *T. araraticum* Jakubz., также включающие изоферменты, характерные для *A. speltoides* Tausch., но отличающиеся от группы Emmer отсутствием изофермента, контролируемого геномом *A*.

Энзимограммы гексаплоидов *T. vavilovii* Jakubz., *T. imereticum* Dek. и *T. tubalicum* Dek. качественно идентичны и состоят из суммы изоферментов, характерных для группы Emmer и *A. squarrosa* L. На энзимограмме *T. tubalicum* Dek. не обнаружены изоферменты фосфатаз, свойственные ржи. Изоферменты, характерные для генома *D* гексаплоидов и *A. squarrosa*, отсутствуют на энзимограмме кислых фосфатаз *T. zhukovskyi* Men. et Eriz. Показано, что она состоит из суммы изоферментов, обнаруженных у *T. timopheevi* Zhuk. и *T. monococcum* L.

Институт зоологии и ботаники
Академии наук Эстонской ССР

Поступила в редакцию
21/X 1969