M. Feldman

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The Evolution of Genomes in Aegilops and Triticum

By **DANIEL ZOHARY**[*)]

Dept. of Botany, The Hebrew University, Jerusalem,
Israel

The purpose of the present paper is to review the evidence indicating that polyploids in *Aegilops* and *Triticum* are not simple amphidiploids but rather products of amphiploidy coupled with extensive interconnections between polyploids. It aims at a representation, and discussion, of an evolutionary model (Zohary and Feldman, 1962) according to which polyploids in the wheat group - and the modified genomes which most of them contain - are products of characteristic type of hybridization: between initial amphidiploids sharing a common genome (see diagramme 1). Effort will be made to summarize pertinant information on variation, distribution, population structure and cytogenetic aspects of *Aegilops* and *Triticum* so as to show that a system of amphidiploidy coupled with past and present reticulate connections between polyploids fits well the situation found in the wheat group.

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Variation and species delimitation

There is a sharp contrast in variation patterns between diploid species and polyploid species in the wheat group:

(a) Diploids: On the diploid level one is confronted with easily definable or "good" species. In other words diploids have each a relatively limited range of morphological variation and show sharp specific boundaries. These obvious morphological discontinuities between species, are coupled by genomic distinctiveness and by the presence of effective reproductive isolation. Most conspicuous are barriers of hybrid sterility (for details see Kihara 1954, Sears 1941). The 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 adaptive specialization.

(b) Polyploids: On the polyploid level one faces an entirely different situation. The majority of the tetraploid and hexaploid species are extraordinarily variable. They occupy wide eco-geographical amplitudes - but mainly man-made habitats. Species boundaries between polyploids are many times blurred and species delimitation is made difficult by presence of interconnecting types. Significantly such blurred specific boundaries are most conspicuous between polyploids sharing a common genome. It will be shown later that in addition to the lack of discontinuity, polyploids are also not entirely reproductively isolated from one another.

Polyploid species clusters

The polyploid species of *Aegilops* and *Triticum* readily fall into three natural species clusters - both on cytogenetic

and morphological grounds (table 1). Cytogenetically each species cluster is characterized by the presence of a common or pivotal genome. Species grouped in a given cluster differ from one another by virtue of their additional or differential genome (or sometimes two genomes in hexaploids). Kihara and his group (1954, 1959) established, by means of genome analysis, that the pivotal genome in each polyploid cluster is identical with a chromosome set of a given diploid analyzer. In contrast the differential genome in each species was found to be usually modified i.e. only partially homologous with the chromosomes of any known diploid. Thus most polyploid Aegilops and Triticum species show the peculiar situation: of the presence modified genome side by side with an unaltered one. Moreover the unchanged genome is a common one - to a whole species group.

Morphologically too, polyploids sharing a common genome tend to cluster around the diploid pivotal species. The variation range exhibited by the cluster of polyploids is much wider than the range found in the single pivotal diploid species. But in Aegilops and Triticum, polyploids within a cluster are morphologically unmistakably "variations on the theme" set by the diploid donor of the pivotal genome. This is particularly obvious in the shape of the fruiting spike. All polyploids of the C^u cluster (see table 1) display "variations on the theme" of Ae. umbellulata trend of dispersal apparatus; the members of the D genome cluster have Ae. squarrosa-like barrel units, while the tetraploid (wild) wheats have an arrow-like seed dispersal device similar in function to T. boeoticum.

Distribution and ecology

The general difference, in geographical distribution and ecological preferences, between diploids and polyploids in Aegilops has already been pointed out (see Kihara 1954,

Stebbins 1959). Diploids, as a rule, are rather restricted in their distribution, and many times show distinct ecological specificity. Polyploids are much more widely spread. But one should also stress the fact that the diploids themselves vary considerably as to the size of their range. Table 2 summarizes the information on the ecology and distribution of the diploids. Some species have indeed very narrow ranges. But there are three exceptions: Ae. squarrosa, Ae. umbellulata and T. boeoticum. They show wide amplitude of ecological adaptation and massive colonization of wide geographical areas. Significantly these three evolutionary successful diploids are also the contributors of the pivotal genomes to the polyploid level.

Population structure

The following features have been found to be characteristic of native Aegilops and wild Triticum populations in Israel, Turkey and Greece:

(a) Polytypic populations: As a rule any given species is not represented, at any given station, by a single line only. Populations are usually composed of a whole collection of morphologically recognizable types.

(b) Mixed stands: Colonization of a given site is usually the concern of several species. This is particularly true in habitats heavily affected by man's activity: opened-up and degraded forests, maquis and steppes, edges of cultivation, etc. Such habitats - in the geographical centre of the group - frequently harbour 3-5 or even a larger number of species side by side. Such mixed occupation is very conspicuous in the case of the members of the C^u species cluster. The following examples might serve as illustrations:

In Israel three species: Ae. variabilis, Ae. ovata and Ae. biuncialis are widely spread in Judea and in the Galilee. They often occur together in mixed colonies of two or all three species. In the northern Galilee Ae. triuncialis is a fourth component of such mixed stands.

In Turkey the number of species involved is even bigger. On the central Anatolian plateaux (e.g. Eskishehir, Ankara, Kayseri) we have repeatedly encountered mixed stands of 3, 4 or even all 5 of the following tetraploids: Ae. triuncialis, Ae. biuncialis, Ae. triaristata, Ae. columnaris and Ae. cylindrica - and frequently also together with the diploids Ae. umbellulata, Ae. caudata and T. boeoticum. In western Turkey (Izmir) species involved are Ae. triuncialis, Ae. biuncialis, Ae. ovata, Ae. triaristata, Ae. umbellulata, Ae. comosa and Ae. caudata. In south Turkey (Malatya-Gaziantep) Ae. triuncialis, Ae. biuncialis, Ae. columnaris, Ae. triaristata, Ae. ovata, Ae. umbellulata, Ae. speltoides, T. dicoccoides and T. boeoticum.

These examples serve to illustrate what is apparently a general rule. Mixed colonization is common throughout the Middle Eastern countries.

Natural inter-specific hybridization

Loose genetic connections between polyploid species sharing a common genome are apparently a general feature of mixed populations. In examination of mixed stands in Israel, Turkey and Greece, we repeatedly encountered natural inter-specific hybridization between the various tetraploids of the C^u cluster as well as between Ae. triuncialis and Ae. cylindrica (for combinations detected see table 3). It is the present author's impression that whenever well developed

mixed stands are carefully screened - intermediates and recombinants are detected. Hybridization products are indeed very rare in stable habitats; they are much more frequent in sites recently disturbed by man. Here occassionally one comes across whole series of intermediates and recombinants bridging two (and sometimes even larger number) parental types. In some favourable stations the frequency of pronounced intermediate and introgressed individuals can reach 1-5%.

Natural F_1 interspecific hybrids

In Israel, F_1 interspecific hybrids Ae. variabilis x Ae. ovata and Ae. variabilis x Ae. biuncialis were detected in mixed stands. Such hybrids are rare - in the order of one to thousands or ten thousands; but they are readily screened on basis of their intermediate morphology and male sterility. Their F_1 generation can be assessed by examination of the old spike from which the plant germinated (determination of the female parent). Such F_1 hybrids are totally male sterile; their anthers do not dehisce. But, they do set a small amount of seed. This is apparently the result of pollination of these hybrids by pollen of parental types. Progeny raised from such F_1 hybrids (Feldman 1963, B. Pazi - unpublished data) indicate the operation of two-way introgression.

Intra-specific chromosomal variation

As already pointed out (Zohary and Feldman 1962) hybridization between amphidiploids should be expected to produce intra-specific chromosomal variation - parallel to morphological variation. Moreover, since species involved share a common pivotal genome such variation should be concentrated in the modified genome of each polyploid species.

There are several reports on wide inter-varietal chromosomal

variation in the polyploid Aegilops and Triticum species. As examples one may cite Ae. triuncialis (Senjaninova-Korczagina, 1932; Matsumura and Kondo 1942; Kihara and Kondo, 1943) and T. dicoccoides (Sachs 1953; Davidson, 1958). But one cannot find out, conclusively from these data, whether one genome is mainly effected or not.

Feldman (1963) has recently found intra-varietal chromosomal differences between different lines of Ae. variabilis. He examined several F_1 combinations between six Israeli collections. The F_1 intraspecific hybrids revealed the presence of several translocations (up to 2 in a given F_1 combination). // Moreover they all exhibited reduction in chiasma formation. Feldman further crossed the variabilis lines to a standard Ae. ovata line and standard Ae. longissima. Hybrids with ovata showed similar chromosomal association while hybrids with Ae. longissima differed one from another - indicating the concentration of the differences in genome S^v.

Conclusions

The data presented indicate that polyploids in the Aegilops and Triticum can not be considered as simple independent units. They are interconnected to form species clusters and build a loosely connected polyploid superstructure.

The origin of polyploids is envisaged as follows: tetraploids within each cluster are considered to be the derivatives of only a restricted number of initial amphidiploid combinations, most likely between the same diploids which exist today. But initial amphidiploids which shared a common genome hybridized with one another, their common genome serving as a buffer in the process of hybridization. As a result numerous recombinations were possible - but only between the unshared chromosome sets - resulting in their differential modification

and the establishment of a modified genome side by side with an unaltered set. The existing polyploid forms within each cluster represent the new combinations which have been favoured by natural selection. Their modified genomes do not necessarily contain chromosomes or chromosome segments linearly derived from an original diploid parent. Instead, such modified genomes represent new chromosomal recombinations derived from two or even larger number of original diploid genomes.

The apparent and recent evolutionary success of the weedy polyploid Aegilops is not attributed to polyploidy as such but to the fact that polyploidy made possible the establishment of a large, common gene pool. While diploids are isolated from one another - several initial amphidiploids could establish genetic connections. Thus on the polyploid level the genetic material of the various diploid groups was brought together and could be recombined and remoulded.

The genetic system established is admirably suited for rapid colonization. Polyploids in each cluster have a rich potential of genetic variation. Flexability is assured by formation of mixed stands and by occasional hybridization. On the other hand plants are predominately self-pollinated. Successful combinations are thus rapidly fixed.

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Another feature that emerges from the present data is that species build-up on the polyploid level was far from random; instead it followed the most successful trends previously established on the diploid level by Ae. squarrosa, Ae. umbellulata and T. boeoticum. These evolutionary most successful three diploids contributed the pivotal genomes or the main "themes" for the polyploid clusters. The other diploid groups provided only material for chromosomal recombination: i.e. the material for "variations on these three themes".

One should also point out that by virtue of their genetic

system, polyploids in the wheat group are generally better adapted for hybridization and for interspecific introgression. In other words polyploids, in contrast to diploids, are balanced to withstand drastic incorporation of alien genetic material (as well as mutations with drastic effects). Comparable genetic changes will be deleterious in diploids. This fact is well illustrated by the numerous - and different - cases of successful experimental substitution of chromosomes or chromosome segments in polyploid (and only in polyploid) wheats. One should therefore bear in mind that similar processes could have occurred in nature as well and contributed their share to the variation and evolution of polyploid species in the wheat group. Thus the frequent and recurrent type of hybridization between amphidiploids sharing a common genome need not necessarily be the only hybridization process by which polyploids in the __Aegilops-Triticum__ group were able to enrich their pool of genetic variation. Additional types of interspecific connections could have operated as well. The evolutionary role of the following types of introgression needs yet careful assessment.

There are some indications that genetic connections and gene-flow are occasionally achieved also between polyploid species which do not share a fully common genome. The overlapping variation between __Ae. crassa__ and __Ae. kotschyi__ in places where these two species grow together might well be due to mutual introgression. Another case is presented by the hybrids between hard and soft wheats and various tetraploid __Aegilops__ species. Such hybrids have been occasionally encountered by botanists in nature. Significantly they are not always entirely sterile and occasionally set some seed.

clusters

Another possible contribution to the genetic variation of the polyploids is a diploid to tetraploid gene-flow, via triploid hybrids. Spontaneous triploids are sporadically produced in mixed populations of tetraploids and diploids. Again they are

not completely sterile and occasionally produce some seed as result of their pollination with parental pollen. In Israel we found several times natural hybrids between Ae. variabilis and Ae. longissima and between Ae. kotschyi and Ae. longissima, and there are indications for present day connections between them.

Similar connections could be expected to occur also between tetraploid and hexaploid entities - when they share in common one or two genomes. Indeed the fertility of pentaploid hybrids between hard wheats and soft wheats is rather high. Such pentaploids - when grown under field conditions together with their parental lines - are many times semifertile. Thus the hexaploid and tetraploid wheats cannot be considered as completely isolated from one another - as far as the A and B genomes are concerned. Parallel situation might exist also between 4 x and 6 x forms of Ae. triaristata and of Ae. crassa.

Finally one should consider also the possibility of distant introgression - i.e. the incorporation of alien chromosome segments from distant species or even from different genera (e.g. Agropyrum). Such incorporated segments should be expected to have little homology with the recipient genome and would therefore behave as gene blocks or "supergenes". Obviously such a process should be expected to be more feasible in the hexaploid level. Some of the "macromutations" characteristic of the cultivated hexaploid wheats could have originated in this way - particularly those with null-allelic behaviour.

Summary

It is suggested that polyploid species in the wheat group have evolved through amphidiploidy coupled with extensive hybridization between the initial polyploid units - and particularly those sharing a common genome. The evidence supporting this hypothesis is reviewed.

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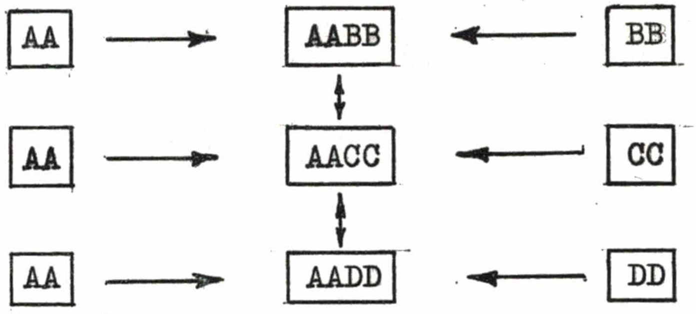

Diagramme 1: Schematic representation of the mode of formation of a polyploid species cluster. Diploid AA is the donor of the common genome; it forms initial amphidploids with diploids BB, CC and DD. Hybridization between the initial amphidiploids results in recombination and modification of B, C and D genomes while the common A genome remains constant and buffers the hybridization process.

Table 1: Species and species groups in *Aegilops* and *Triticum*
(Genomic formulation after Kihara 1954, 1959).

Natural units	Species	Genome type
A. Diploid genomic groups		
1. Genome B (= S) group:	*Ae. bicornis* (Forsk.) Jaub. et Sp.	S^b
	Ae. sharonensis Eig.	S^l
	Ae. longissima Schweinf. et Musch.	S^l
	Ae. speltoides Tausch.	S
2. Genome D group:	*Ae. squarrosa* L.	D
3. Genome C group:	*Ae. caudata* L.	C
4. Genome M group:	*Ae. comosa* Sibth. et Sm.	M
	Ae. uniristata Vis.	M^u
5. Genome C^u group:	*Ae. umbellulata* Zhuk.	C^u
6. Genome A group:	*T. boeoticum* Boiss.	A
	T. monococcum L.	A
B. Polyploid complexes		
1. Genome D species cluster	*Ae. crassa* Boiss. 4x	DM^{cr}
	Ae. crassa Boiss. 6x	DD^2M^{cr}
	Ae. juvenalis (Thell). Eig.	DC^uM^j
	Ae. ventricosa Tausch	DM^v
	Ae. cylindrica Host.	DC
2. Genome C^u species cluster	*Ae. triuncialis* L.	C^uC
	Ae. columnaris Zhuk.	C^uM^c
	Ae. biuncialis Vis.	C^uM^b
	Ae. triaristata Willd. 4x	C^uM^t
	Ae. triaristata Willd. 6x	$C^uM^tM^{t2}$
	Ae. ovata L.	C^uM^o
	Ae. variabilis Eig.	C^uS^v
	Ae. kotschyi Boiss.	C^uS^v
3. Genome A species cluster	*T. dicoccoides* Koern.	AB
	T. timopheevi Zhuk.	AB (= AG)
	T. dicoccum Schübl.	AB
	T. durum Desf.	AB
	T. aestivum L. em Thell.	ABD

Table 2: Geographical and ecological characterization of diploid species of Aegilops and (wild) Triticum.

Species and genome type	Distribution and habitats
Ae. bicornis (S^b)	Relatively limited distribution: S. Israel, Lower Egypt, Cyrenaica. Restricted to xeric sandy soils.
Ae. sharonensis (S^l)	Very limited distribution: endemic to the sandy soils of the Israeli mediterranean coastal plain.
Ae. longissima (S^l)	Relatively limited distribution: Israel, Jordan, S. Syria. Occupies sandy loams in the mediterranean coastal plain and, in addition, a variety of steppic habitats, mainly in the sage-brush formation.
Ae. speltoides (S)	Medium size range: Common in the 'fertile crescent' belt (N. Israel, Syria, S. Turkey, N. Iraq, W. Iran), more sporadically spread over the Anatolian plateau. Occupies open steppe-like herbaceous formations and cleared-up maquis, also common in alluvial plains and edges of cultivation.
Ae. squarrosa (D)	Widely spread over Central Asia from N. Iraq to Iran, Transcaucasia, Transcaspia, Afghanistan and Pakistan. Occupies a wide array of habitats from xeric sage-brush steppes to opened up temperate forests. Common also as weed in cultivation.
Ae. caudata (C)	Medium sized range: spread over Greece, Turkey, N. Syria and N. Iraq. Occupies steppe and steppe-like herbaceous formations as well as opened maquis. Also at edges of cultivation.
Ae. comosa (M)	Relatively limited distribution: Restricted to mediterranean formations in Greece, the Aegean Islands and W. Turkey. Inhabits mainly dwarf shrub and maquis formations, as well as cleared-up areas and edges of cultivation.

Table 2 (continued)

Species and genome type	Distribution and habitats
Ae. uniaristata (M^u)	Very limited distribution: scattered mediterranean maquis and dwarf shrub formations in Greece and the Marmara Sea area, and apparently more common in the Adriatic zone of Yugoslavia.
Ae. umbellulata (C^u)	Widely spread over N. Iraq, Western Asia: Most of Turkey, N. Syria, N. and W. Iran, Transcaucasia. Occupies a wide range of habitats: e.g. Irano-Anatolian inner steppes, herbaceous steppe-like formations in the 'fertile crescent', mediterranean open up maquis in W. Turkey, also common at edges of cultivation and road sides.
Tr. boeoticum (A)	Widely spread over Western Asia and the Southern Balkan: from Greece to Turkey, Syria, N. Iraq, N. and W. Iran, Transcaucasia. A component of the open, herbaceous park forest and steppe-like formations in the 'fertile crescent' belt, inhabits opened-up areas and edges of cultivation throughout the area.

Table 3: Natural hybridization between tetraploid species of the Aegilops - Triticum group: representative stations of mixed populations containing series of intermediate and recombinant plants sampled in Israel, Turkey and Greece.

Species involved and their genomic constitution		Localities and habitats
Ae. variabilis $C^uC^uS^vS^v$	Ae. ovata $C^uC^uM^oM^o$	Israel: Jerusalem, Safad (Galilee); particularly at roadsides, abandoned cultivation and sites disturbed by recent earth moving.
Ae. variabilis $C^uC^uS^vS^v$	Ae. biuncialis $C^uC^uM^bM^b$	Israel: Jerusalem, Safad (Galilee); in sites similar to former combination.
Ae. variabilis $C^uC^uS^vS^v$	Ae. triuncialis $C^uC^uC\ C$	Israel: Manara (North Galilee); roadsides.
Ae. ovata $C^uC^uM^oM^o$	Ae. biuncialis $C^uC^uM^bM^b$	Israel: Jerusalem, Upper Galilee, particularly at roadsides and placed disturbed by recent earth moving. Turkey (Western): Izmir, Denizli; roadsides.
Ae. ovata $C^uC^uM^oM^o$	Ae. triaristata $C^uC^uM^tM^t$	Turkey (Western): Izmir, roadsides; Greece: (Macedonia) 40 km East of Tessalonica, between Kozani and Larisa; roadsides and edges of maquis.
Ae. triuncialis $C^uC^uC\ C$	Ae. biuncialis $C^uC^uM^bM^b$	Turkey: Malatya, Balikesir, Denizli; roadsides and edges of cultivation. Greece (Macedonia): Kozani; edges of vineyards.
Ae. triuncialis $C^uC^uC\ C$	Ae. triaristata $C^uC^uM^tM^t$	Turkey (Western): Balikesir, Izmir, Ushak; roadsides, edges of cultivation and edges of cleared-up maquis.
Ae. triuncialis $C^uC^uC\ C$	Ae. columnaris $C^uC^uM^cM^c$	Turkey (central): Ankara, Malatya, Gaziantep; roadsides and edges of cultivation.
Ae. triaristata $C^uC^uM^tM^t$	Ae. columnaris $C^uC^uM^cM^c$	Turkey (central): Malatya; edges of cultivation.
Ae. triaristata $C^uC^uM^tM^t$	Ae. biuncialis $C^uC^uM^bM^b$	Turkey (Western): Ushak, Izmir, edges of cultivation and roadsides. Greece (Thessaly): between Larisa and Kozani; roadsides.

Table 3 (continued)

Species involved and their genomic constitution		Localities and habitats
Ae. triuncialis $C^uC^uC\ C$	Ae. cylindrica D D C C	Turkey (Western): Eskishehir, roadsides and recently ploughed fire zone protecting afforestation.
Ae. variabilis $C^uC^uS^vS^v$	Ae kotschyi $C^uC^uS^vS^v$	Israel: Lahav, southern coastal plain; roadside and heavily overgrazed sites.
T. dicoccoides A A B B	T. durum A A B B	Israel: Eastern Galilee; places of contact at edges of cultivation.

Compiled from Zohary and Feldman (1962), Feldman (1963), Zohary and Brick (1961) and field notes of trips to Turkey and Greece 1959, 1962.