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Species Formation in Aegilops and Triticum

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We will discuss four aspects of species formation in *Aegilops* and *Triticum*: (1) the mode of evolution of the diploid species and especially the origin of *Aegilops sharonensis*; (2) the possible existence of genes or systems which, when combined, promote the formation of unreduced gametes in otherwise sterile interspecific hybrids and result in the formation of polyploid embryos; (3) the seed protein patterns of *Ae. searsii*, a newly recognized diploid species from Israel, Jordan, Lebanon, and Syria, and the relevance of those protein patterns to the evolution of the wild tetraploid wheats *Triticum turgidum* var. *dicoccoides* and *T. timopheevii* var. *araraticum*; and (4) the leaf flavonoid patterns of diploid species of *Aegilops* and *Triticum* and their relevance to the evolution of the wild tetraploid wheats.

We recognize *Aegilops* as a genus separate from and larger than *Triticum*. In *Aegilops* there are at present eleven diploid species ($2n = 2x = 14$), ten allotetraploid species ($2n = 4x = 28$), and four allohexaploid species ($2n = 6x = 42$), all of which are wild (Table 1). In *Triticum* ($x = 7$) there are at present two wild diploid species and a domesticated form, two wild allotetraploid species with domesticated forms of both species, and two domesticated allohexaploid species, each of which involves a different tetraploid wheat species and appears to have arisen after the tetraploids were domesticated (Table 1). There are many papers that outline the various hypotheses for the origin of the tetraploid and hexaploid

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TABLE 1. The species of *Aegilops* and *Triticum* and their genomic formulae. The genomic formulae are taken for the most part from Kihara (1954); however, as pointed out by Waines (1969), the formulae of some of the *Aegilops* tetraploids and hexaploids appear to have been determined on evidence other than chromosome-pairing studies. The relevance of the formulae to evolutionary studies today is questionable because of genes in the wheat group that are known to affect chromosome pairing and/or chiasma formation (Driscoll, Bielig, and Darvey, 1979).

Species	Formula
1. Diploids	
Ae. speltoides Tausch [(*Ae. aucheri* Boiss. and *Ae. ligustica* (Savign.) Cosson]	S
Ae. bicornis (Forsk.) Jaub. & Spach.	S^b
Ae. longissima Scheinf. & Muschl.	S^l
Ae sharonensis Eig	S^{sh}
Ae. searsii Feldman & Kislev	S^{se}
Ae. mutica Boiss.	M^t
Ae. squarrosa L.	D
Ae. uniaristata Vis.	M^u
Ae. comosa Sibth. & Sm. [*Ae. heldreichii* Holzm.]	M
Ae. caudata L.	C
Ae. umbellulata Zhuk.	C^u
2. Allotetraploids	
Ae. cylindrica Host	DC
Ae. ventricosa Tausch	DM^u
Ae. crassa Boiss.	DM
Ae. kotschyi Boiss.	C^uS^k
Ae. variabilis Eig.	C^uS^v
Ae. ovata L.	C^uM^o
Ae. triaristata Willd.	C^uM^t
Ae. biuncialis Vis.	C^uM^b
Ae. columnaris Zhuk.	C^uM^c
Ae. triuncialis L.	C^uC

3. Allohexaploids	
Ae. crassa Boiss.	$\mathbf{D^1D^2M^c}$
Ae. vavilovi (Zhuk.) Chenn.	$\mathbf{DMS^r}$
Ae. juvenalis (Thell.) Eig	$\mathbf{DMC^u}$
Ae. recta (Zhuk.) Chenn.	$\mathbf{C^uM^{t1}M^{t2}}$
4. Diploids	
Wild	
T. monococcum L. var. *boeoticum* Boiss.	$\mathbf{A^b}$
T. urartu Tum.	$\mathbf{A^u}$
Domesticated	
T. monococcum L. var. *monococcum*	$\mathbf{A^m}$
5. Allotetraploids	
Wild	
T. turgidum L. var. *dicoccoides* (Körn. *in* Schweinf.) Bowden	**AB**
T. timopheevii Zhuk. var. *araraticum* Jakubzn.	**AG**
Domesticated	
T. turgidum var. *dicoccon* Schrank	
var. *durum* Desf.	**AB**
var. *turgidum*	
var. polonicum L.	
var. *carthlicum* Nevski	
T. timopheevii Zhuk. var. *timopheevii*	**AG**
6. Allohexaploids	
Domesticated	
T. aestivum L. *em*. Thell. var. *spelta* L.	
var. *macha* Dek. & Men.	
var. *vavilovi* Jakubzn.	**ABD**
var. *aestivum*	
var. *compactum* Host	
var. *sphaerococcum* Per.	
T. zhukovskyi Men. & Er.	**AAG**

wheats. At present there is little controversy over the origin of the two hexaploid wheats, *T. aestivum* and *T. zhukovskyi*. The former is thought to have a domesticated form of *T. turgidum* and wild *Ae. squarrosa* as its ancestors (Kihara, 1944; McFadden and Sears, 1944, 1946), while the latter is thought to have arisen from a cross between domesticated *T. timopheevii* and *T. monococcum* (Upadhya and Swaminathan, 1963; Johnson, 1968). The controversy in wheat evolution centers around the origin of the two wild tetraploid species and, in particular, around the source of the **B** and **G** genomes. Briefly, there are two hypotheses: one hypothesis maintains that the **B** or **G** genome of tetraploid wheat was donated by a diploid species of *Aegilops*, of which at least five might qualify (Jenkins, 1929; Pathak, 1940; Riley *et al.*, 1958; Sears, 1956; Feldman, 1976, 1978); the other hypothesis maintains that the **B** or **G** genomes were donated by a diploid species of *Triticum*, of which only two possibilities are known (Tumanian, 1937; Johnson, 1975).

THE EVOLUTION OF THE DIPLOID SPECIES AND THE ORIGIN OF *AEGILOPS SHARONENSIS*

Of the eleven diploid species of *Aegilops* and the two diploid species of *Triticum*, all are thought to have evolved independently from common ancestors. Although there is little evidence for speciation through hybridization, a hybrid origin for two taxa has been hypothesized. The most publicized of these is a hybrid origin for *Ae. sharonensis* (Waines, 1969). The other is an origin involving introgression for domesticated *T. monococcum* (Dhaliwal, 1977).

Eig (1928) first considered *Ae. sharonensis* as a climatically gigas race of *Ae. bicornis*, which grows along the coast of the Mediterranean from Libya to the Negev Desert area of Israel (Figure 1). Eig thought that the increased rainfall in the Sharon Plain of Israel resulted in the increase in size. Later Eig (1929) recognized the race as a separate species, *Ae. sharonensis*, because he found no hybrid populations or intermediate forms in the Negev where the two taxa are sympatric. Kihara (1954) and Tanaka (1955) looked at meiotic chromosome pairing in pollen mother cells in hybrids of *Ae. sharonensis* and *Ae. longissima*, which also extends into the Negev. They observed five bivalents and a quadrivalent, which indicated that those two taxa differed by a reciprocal translocation. The F_1 hybrids were highly fertile, which led Kihara (1954) to assign the two species the same genome formula S^l. The next year Tanaka (1955) reported that the F_1 hybrid of *Ae. sharonensis* and *Ae. bicornis* showed six or seven bivalents and sometimes a few univalents. Pollen and seed fertility in the hybrid was high, even though the plants were weak and dwarflike.

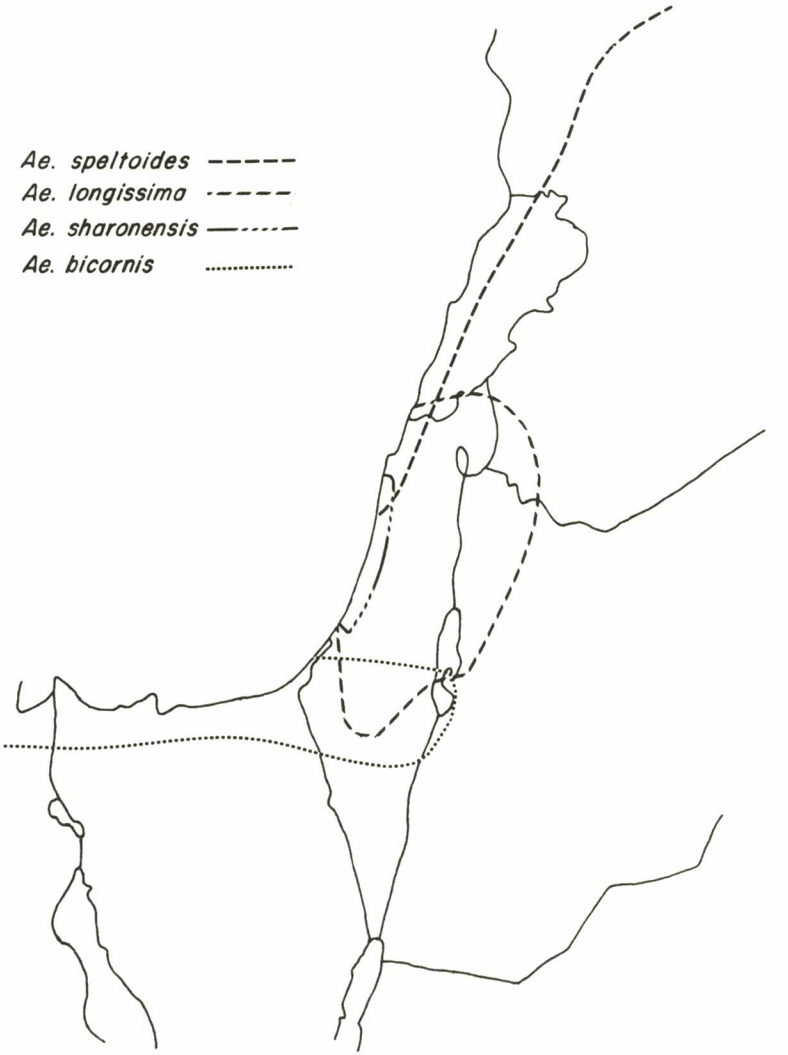

FIGURE 1. Distributions of *Aegilops* species in Southwest Asia. *Aegilops sharonensis* is occasionally sympatric with *Ae. bicornis* and also grows in the sandy coastal areas of Cyprus.

Kimber (1961) also studied meiosis of the F_1 hybrid of *Ae. longissima* and *Ae. bicornis* and observed five bivalents and a quadrivalent, evidence that these species also differ by a single reciprocal translocation. This hybrid was reported to be self-sterile at Cambridge, England. In spite of this cytogenetic evidence and the close morphological similarity of *Ae. bicornis* and *Ae. sharonensis*, most taxonomists and cytogeneticists have maintained *sharonensis* as a variety of *Ae. longissima* and not *Ae. bicornis* (Kihara, 1954; Bowden, 1959; Morris and Sears, 1967; MacKey, 1968). Perhaps this is because Kihara assigned *Ae. sharonensis* the same genome formula as *Ae. longissima*.

Ethanol-extracted seed-protein electrophoretic patterns of *Ae. sharonensis* were observed to be intermediate between those of *Ae. longissima* and *Ae. bicornis*, which prompted Waines (1969) and Waines and Johnson (1969, 1972) to suggest that *Ae. sharonensis* might be a species formed from a segregant of a hybrid between *Ae. longissima* and *bicornis* that has colonized the sandy Sharon Plain of Israel and a sandy coastal area of southeast Cyprus (Figure 1). Williams (1971), who performed cluster analysis of correlation coefficients of the albumin proteins of diploid *Aegilops* species, also suggested that *Ae. sharonensis* might be a stabilized product of hybridization between *Ae. longissima* and *Ae. bicornis*. Morphologically *Ae. sharonensis* lies between *Ae. longissima* and *Ae. bicornis* (Table 2, Figure 2).

We tested this hypothetical origin of *Ae. sharonensis* experimentally. Many hybrids were made between different accessions of *Ae. longissima* and *Ae. bicornis* in both directions. At Riverside these F_1 hybrids are fully fertile, in contrast to the hybrid made in England (Kimber, 1961). The hybrids show the presence of a reciprocal translocation in pollen-mother-cell meiosis, but this appears to have little effect on seed set. The F_1 hybrid is morphologically intermediate between the two parents, and the spike shatters, indicating that this *Ae. bicornis* character is dominant over the intact rachis of *Ae. longissima*. The F_2 generation was grown in the field, and a 3:1 segregation for spike shattering was observed, which indicates that this character is controlled by a simple Mendelian, diallelic gene (Waines, 1978a). The F_2 population contained some segregants that looked like the parents, but most were intermediate like the F_1 hybrid. Seed was collected from those plants which were morphologically closest to *Ae. sharonensis*, and a F_3 generation was grown in the greenhouse in the spring of 1979.

Two of the F_3 populations had some seedlings that were albino (19% and 11%), which soon died. These results are interpreted to indicate that there are incomplete physiological barriers to hybridization between these two species, which may be lethal for plants in the F_3 generation.

TABLE 2. Morphological characters of *Aegilops* species.

	Ae. longissima	*Ae. sharonensis*	*Ae. bicornis*
Height, cm	50–80	50–70	20–35
Spike length, cm	10–20	7–13	5–8
Spikelet, number	8–15	8–20	8–20
Spikelet width, mm	12–14	8–13	5–9
Floret, number	3–5	3–5	3
Sterile florets, number	1–2	1–2	1
Glume length, mm	7–8	6–7	3–5
Glume width, mm	2–2.5	2–2.5	1–2
Glume teeth	2–3	2–3	2
Lemma awns	–	+	+

Albino seedlings were not noticed in the F_2 population, but as it was grown in the field, and as we were not specifically looking for albino seedlings, these may have been missed. The F_3 plants were more or less uniform, none had awns on the lateral spikelets like *Ae. sharonensis*, and all were more similar morphologically to the F_1 hybrid than to *Ae. sharonensis* (Figure 2). These results indicate that the hybrid between *Ae. longissima* and *Ae. bicornis* is fertile and that it is possible for a segregant from this hybrid to produce fertile offspring in the F_3 generation. The original hypothesis (Waines, 1969) is certainly a possibility, but it is not the only one.

Aegilops speltoides also grows today within the range of *Ae. longissima* and *Ae. sharonensis* (Figure 1). *Aegilops speltoides* is a dimorphic species: in one form, *speltoides*, the spike remains intact, and there are no lateral awns; in the other form, *ligustica*, there are lateral awns, and the spike disarticulates. This dimorphism appears to be controlled by a group of closely linked genes (Sears, 1941; Zohary and Imber, 1963): the character combination of *ligustica* is dominant over the characters of *speltoides* in the F_1, and *ligustica* segregates 3:1 in the F_2. Even though Kihara (1954) found that the hybrids of *Ae. speltoides* and *Ae. longissima* or *Ae. speltoides* and *Ae. bicornis* were sterile in Japan, these hybrids should be remade and grown to test their fertility. Hybrids between *Ae. speltoides* f. *ligustica* and *Ae. longissima*, or *Ae. speltoides* f. *speltoides* and *Ae. bicornis*, might approach the morphology of *Ae. sharonensis*.

A hybrid origin for *Ae. sharonensis* is not the simplest explanation (C. E. Taylor, unpubl.). If we are to follow Occam's Razor, as we believe we should, then we must entertain the possibility of the independent evo-

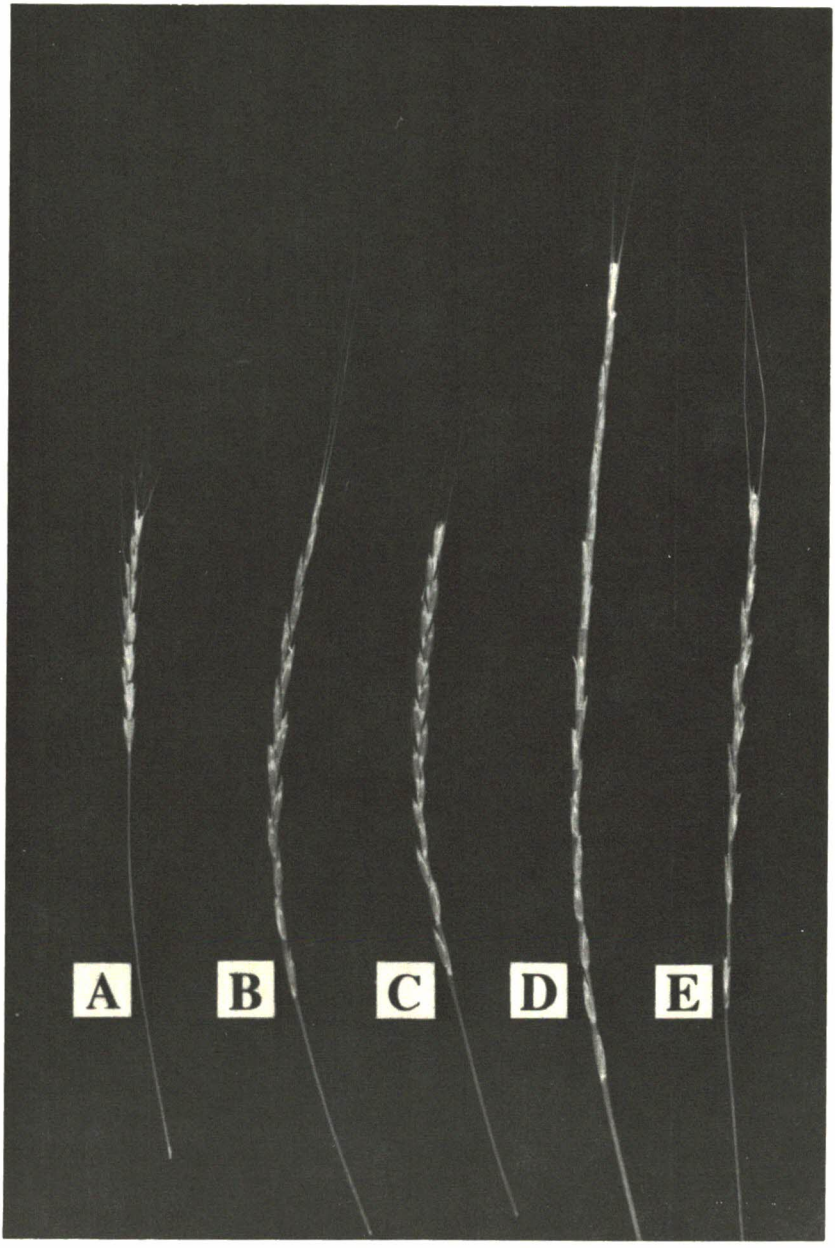

FIGURE 2. Spikes of *Aegilops* species and hybrids. A—*Ae. bicornis*. B—F_1 *Ae. longissima* × *Ae. bicornis*. C—*Ae. sharonensis*. D—*Ae. longissima*. E—F_3 *Ae. longissima* × *Ae. bicornis*.

lution of *Ae. sharonensis* from the ancestral *Aegilops* stock, or from *bicornis* or *longissima*, as one of the simplest and most probable explanations of its evolutionary history.

We hope that taxonomists will not use these crossing results to merge *Ae. longissima* and *Ae. bicornis*, as they earlier used chromosome pairing and fertility studies to merge *Ae. sharonensis* and *Ae. longissima*. All three species have differing morphologies and differing ecological requirements (Ankori and Zohary, 1962). Certainly, meiotic analysis reveals that the genome formula of *Ae. sharonensis* should be separated from that of *Ae. longissima* and *Ae. bicornis*; we suggest S^{sh} (Table 1).

GENES PRODUCING POLYPLOID EMBRYOS IN HYBRID COMBINATION

During the last 15 years at Riverside many hybrids have been made between various diploid species of *Aegilops* and *Triticum*. Apart from F_1 hybrids between *Ae. bicornis*, *Ae. longissima*, and *Ae. sharonensis*, all hybrids were sterile. When seeds were obtained through artificial manipulation, none was tetraploid.

We have recently made hybrids between tetraploid and diploid species. Most of the resulting triploid plants were also sterile. A few plants, however, produced some seed on selfing, and one or two produced a considerable number. A cross was made between *T. turgidum* var. *durum* 'Produra' and *Ae. squarrosa* G3489 from Afghanistan, which is unusual in that it is the only accession of *Ae. squarrosa* known to have a rachis that does not disarticulate at maturity (Metzger and Silbaugh, 1968–69). The embryos from three developing seeds were dissected and cultured, and the plantlets were transferred to soil in pots. To be certain that the plants were true hybrids, we allowed them to flower before subjecting tillers to colchicine treatment to produce allohexaploids. To our surprise all three plants set some seed (Table 3), and the plants' morphology indicated that they were indeed hybrids. This was later confirmed by root-tip mitotic counts. We did not apply colchicine. Of the 49 seeds produced by these three triploid plants, we have germinated seven. They are all hexaploid ($2n = 42$), and presumably the genome formula is **ABD**. These hexaploid plants are fully fertile. Other crosses among other durum wheats and other *Ae. squarrosa* accessions produced triploid hybrids that were completely sterile.

Of crosses between two accessions of *T. monococcum* and one accession of *T. turgidum* var. *carthlicum* only four plants bore seeds (Tables 4 and 5). All 22 of the seeds produced proved to be hexaploid.

These results suggest to us that there are genes or gene-systems which,

TABLE 3. Seed set of triploid hybrids of *Triticum turgidum* var. *durum* 'Produra' (4*x*) × *Aegilops squarrosa* G3489 (2*x*).

No. of plants	Total no. of spikes	No. of spikes with at least 1 seed	Total no. of seeds
1	13	9	16
2	17	10	23
3	22	7	10

TABLE 4. Fertility of triploid hybrids between *Triticum turgidum* var. *carthlicum* (4*x*) and *Triticum monococcum* (2*x*). Accession suffix indicates taxon: b = var. *boeoticum*, c = *carthlicum*, m = *monococcum*.

Triploid	No. of plants	No. of plants with seeds
G3315m × G378c	17	4
G2576b × G378c	13	0

TABLE 5. Seed set of triploid hybrids of *Triticum turgidum* var. *carthlicum* G378 × *T. monococcum* G3315.

No. of plants	No. of spikes	No. of spikes with at least 1 seed	Total no. of seeds
1	13	4	5
2	20	2	7
3	10	2	2
4	18	4	8

in hybrid combination, promote the formation of unreduced gametes in both anthers and ovules and that these gametes are able to combine to form hexaploid zygotes and finally plants with the genome constitution **AAB**. Wagenaar (1968) also found an influence of genotype on polyploid seed set in pentaploid *Aegilops crassa* × *T. turgidum* hybrids.

The phenomenon reported here is not new in hybrids in the Triticinae. Love and Craig (1919) reported a fertile F_1 hybrid of the cross *T. aestivum* 'Dawson's Golden Chaff' and *Secale cereale* (rye), and a review of the subject was recently published by Maan and Sasakuma (1977). It is of interest

that our hypothesized genes have been found only in triploid hybrids involving *T. turgidum* **AABB** and two different diploid species. So far we have not found such genes in diploid interspecific hybrids in the wheat group, but Kihara (1937) reported a more or less sterile diploid hybrid of *Ae. speltoides* × *Ae. umbellulata*, which produced a few spontaneous amphidiploid seed. In the fall of 1979 we shall cross two obvious diploids *T. monococcum* G3315 and *Ae. squarrosa* G3489 to investigate this phenomenon further. Maan and Sasakuma (1977), working with triploid hybrids of *T. durum* and *Ae. comosa*, demonstrated that unreduced gametes were formed in these plants in considerable numbers. Harlan and deWet (1975) have indicated that in some grasses unreduced gametes are produced by the diploid parents and that polyploids arise spontaneously without going through the F_1 hybrid generation. They call these class I polyploids. This is certainly the most parsimonious explanation for the origin of polyploidy. Although in the wheat group we have little evidence that the simplest explanation applies we do have evidence that a more complicated pathway results in the formation of some polyploid taxa; this pathway may have been that followed in the formation of bread wheat *T. aestivum* (**ABD**) and *T. zhukovskyi* (**AAG**) and possibly the other polyploids in the *Aegilops-Triticum* group. Such polyploids would be termed class II polyploids in Harlan and deWet's scheme.

AEGILOPS SEARSII IN THE EVOLUTION OF THE TETRAPLOID WHEATS

In 1959 the Botanical Mission of the University of Kyoto collected a new variety of *Ae. longissima* from Jordan and Syria (Yamashita and Tanaka, 1967). The seed protein electrophoretic patterns of this new variety were determined by Williams (1971) at Riverside. Unfortunately, Williams incorrectly reported the length of the pattern of the new variety, although his cluster analysis of correlation coefficients indicated that accessions of this variety were only distantly related to the remaining accessions of *Ae. longissima*. Plants similar to this new variety of *longissima* were found growing in Israel and Jordan by Ladizinsky and Feldman, and they were assigned specific rank as *Ae. searsii* by Feldman and Kislev (1977). *Aegilops searsii* was put forward as the donor of the **B** genome of tetraploid wheat by Feldman (1978). This stimulated us to examine the electrophoretic patterns of *Ae. searsii* and the varieties of *Ae. longissima*. The protein patterns and morphology for *Ae. searsii* and the new variety are identical, from which we conclude that the new variety and *Ae. searsii* are the same (Waines, 1978b). The protein pattern of *Ae. searsii* is distinct from that of typical *Ae. longissima* (Fig. 3).

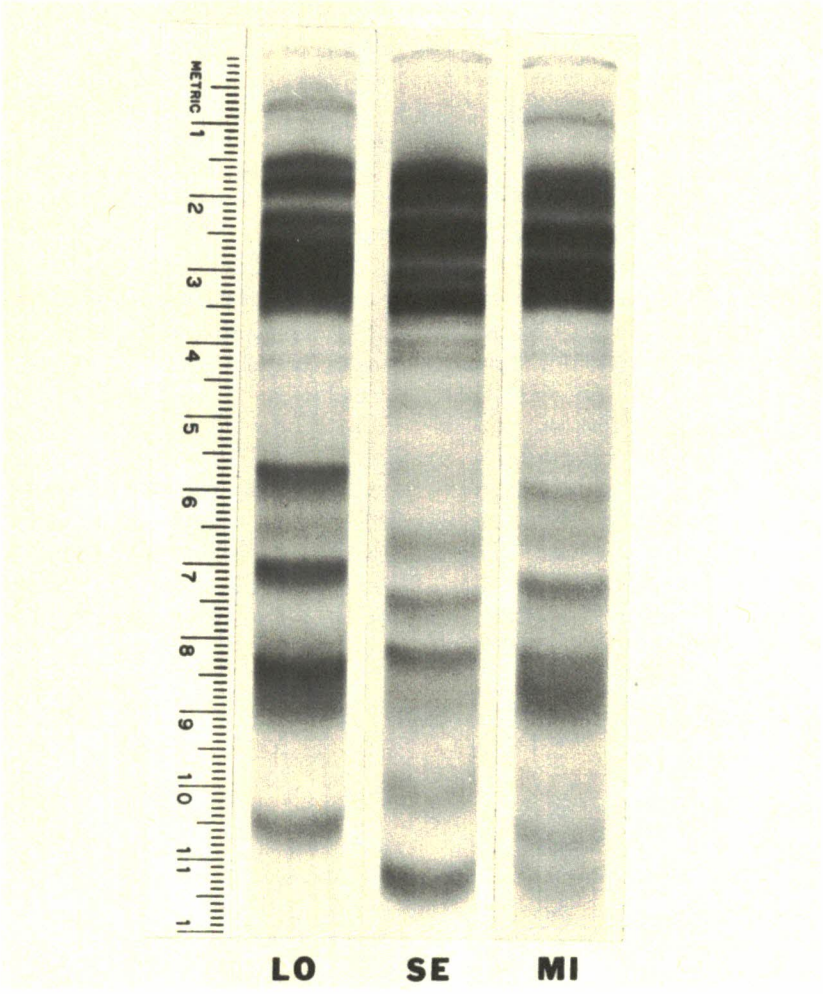

FIGURE 3. Seed-protein electrophoretic patterns of *Aegilops longissima* (LO), *Ae. searsii* (SE), and their mixture 1:1 (MI).

Aegilops searsii has a unique complement of seed proteins. In particular, there is a single protein band (11.3 cm from the origin) which is not found in any other diploid or polyploid *Aegilops*, and which is the fastest running band in the genus. To test Feldman's hypothesis, we mixed seed proteins of *Ae. searsii* with those of *T. monococcum* var. *boeoticum* and *T. urartu*. The two resulting patterns were compared with that of *T. turgidum* var. *dicoccoides* (Figs. 4 and 5). As can be seen, the patterns differ signifi-

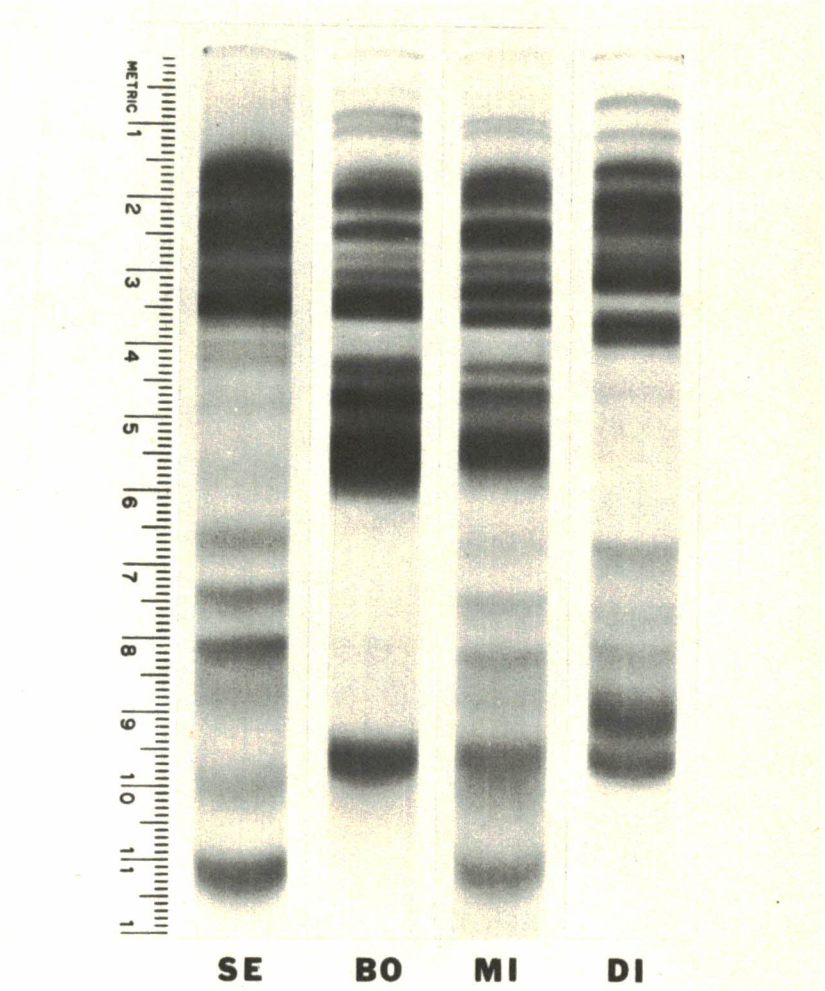

FIGURE 4. Seed-protein electrophoretic patterns of *Aegilops searsii* (SE), *Triticum monococcum* var. *boeoticum* (BO), their mixture 1:1 (MI), and tetraploid *T. turgidum* var. *dicoccoides* (DI).

cantly. Therefore, if *Ae. searsii* is indeed the donor of the **B** genome, then the derived tetraploid doesn't show simple addition of the parental diploid proteins.

Last year we crossed several accessions of *Ae. searsii* with accessions of *T. monococcum* var. *boeoticum* and *T. urartu*, and no viable seed developed. This year we have repeated the crosses, and only with the help of

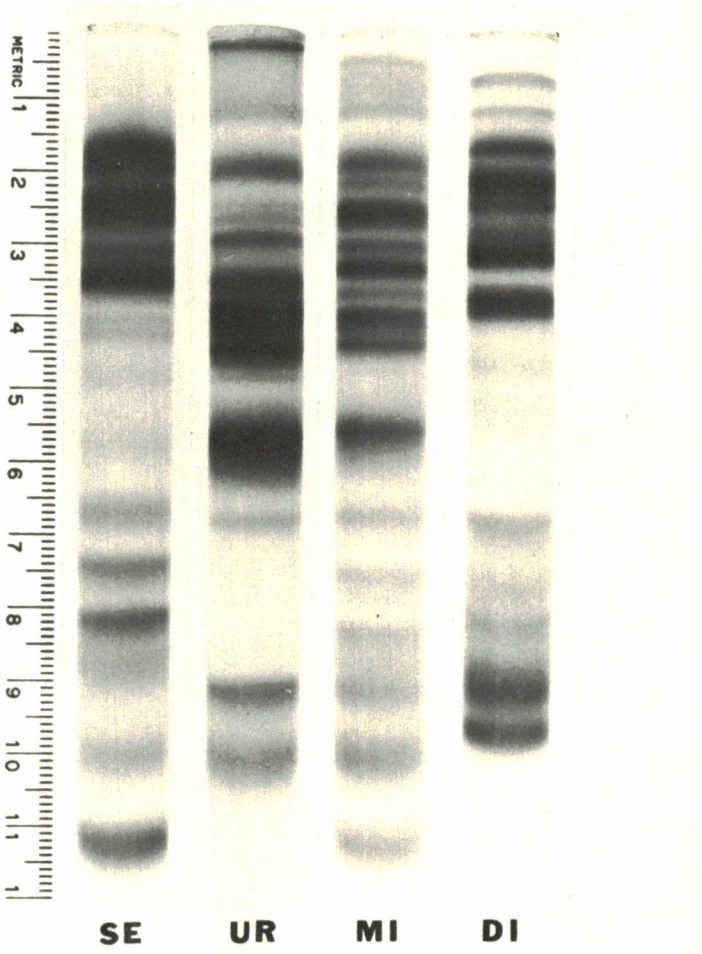

FIGURE 5. Seed-protein electrophoretic patterns of *Aegilops searsii* (SE), *Triticum urartu* (UR), their mixture 1:1 (MI), and tetraploid *T. turgidum* var. *dicoccoides* (DI).

embryo culture have we produced hybrid plants. In contrast, *Ae. longissima*, which Feldman (1976) has also suggested as a potential donor of the **B** genome of wheat, readily sets fertile seed when pollinated with *T. monococcum* var. *boeoticum* or *T. urartu*. However, the derived amphidiploids do not closely resemble *T. turgidum* var. *dicoccoides* or *T. timopheevii* var. *araraticum* (Johnson and Dhaliwal, 1978).

To conclude, *Ae. searsii* remains a possible donor of the **B** genome of

the tetraploid wheats, but there are several other *Aegilops* and *Triticum* species which are, in our view, stronger contenders.

LEAF FLAVONOIDS OF DIPLOID *AEGILOPS* AND *TRITICUM* SPECIES AND THE TETRAPLOID WHEATS

Our preliminary study of the leaf flavonoids of the S genome species of *Aegilops* and the four wild species of *Triticum* revealed 27 compounds (Table 6). In addition, the two taxa appear to be fairly similar in their flavonoid constituents. The various species examined are with one exception easily distinguished on the basis of their flavonoid patterns. Intraspecific variation in flavonoids was observed to different degrees in the relatively small number of accessions examined. This variation, however, did not affect the discreteness of the various species patterns.

The two wild diploid species, *T. monococcum* var. *boeoticum* and *T. urartu*, differ with respect to the presence or absence of seven compounds, of which compounds 10, 11, and 14 are the most pronounced and least variable. The pattern of *Ae. speltoides* is distinct from that of *Ae. searsii* and both are distinct from *Ae. longissima*, *Ae. bicornis*, and *Ae. sharonensis*. The pattern of *Ae. sharonensis* is the same as that of *Ae. bicornis*, and both are distinct from that of *Ae. longissima*. All S-genome diploids of *Aegilops* contain compound 21, which has not yet been found in accessions of the diploid wheats.

The two diploid wheats *T. turgidum* var. *dicoccoides* and *T. timopheevii* var. *araraticum* have very similar flavonoid patterns. The latter taxon does not have compounds 10 and 11, which we have so far found only in *T. urartu* and *T. turgidum* var. *dicoccoides*. The two tetraploid species do have compound 21, which is characteristic of the *Aegilops* species and has not yet been found in diploid *Triticum* species. The pattern of *T. monococcum* var. *boeoticum* × *T. urartu* synthetic amphiploid is very similar to the pattern of the tetraploid *T. turgidum* var. *dicoccoides* and to a lesser extent to that of *T. timopheevii* var. *araraticum*. Compound 21, found in diploid species of *Aegilops* and tetraploid species of *Triticum*, was not observed in these amphiploids. Compounds 6, 7, 8, 14, and 20 are overlapping and require further separation for better comparison.

We do not yet have a synthetic amphiploid of *Ae. speltoides* and *T. monococcum* var. *boeoticum*. The flavonoid pattern of the synthetic amphiploid of *Ae. speltoides* and domesticated *T. monococcum* lacks compounds 10, 11, 12, and probably 20, which are found in the tetraploid species of wheat. The other *Aegilops* × *Triticum* amphiploid patterns do not exactly match those of the wild tetraploid wheats.

Definite conclusions should not be drawn from this study for the fol-

TABLE 6. Flavonoid compounds found in wild species and amphiploids of *Triticum* and *Aegilops*.

Compounds	R_f(%)		Color[a]		Taxa													
	BAW	5% HOAc	UV	NH_3	*urartu*	*boeoticum*	*speltoides*	*bicornis*	*longissima*	*searsii*	*sharonensis*	*araraticum*	*dicoccoides*	*boeoticum* × *urartu*	*speltoides* × *monococcum*	*boeoticum* × *bicornis*	*sharonensis* × *monococcum*	*boeoticum* × *longissima*
1	35	6	flB	flY	+	+	+	+	+	−	+	+	+	+	+	+	+	+
2	42	8	Gr	BrY	+	+	+	+	+	+	+	+	+	+	−	+	+	+
3	40	13	Gr	Og	+	+	−	+	+	+	+	+	+	+	+	+	+	+
4	20	13	Pk	Pk	+	+	−	+	−	+	+	+	+	+	−	+	+	+
5	52	21	P	G	+	+	+	+	+	+	+	+	+	+	+	−	+	+
6	33	33	P	Y	+	+	+	+	+	−	+	+	−	+	−	−	+	+
7	40	42	P	GY	+	+	+	+	+	+	+	−	+	+	+	+	+	+
8	42	49	P	Br	+	+	+	+	+	+	+	+	+	+	+	+	+	+
9	40	46	P	Br	−	+	−	−	−	−	−	−	−	−	−	−	+	−
10	55	72	P	GrBr	+	−	−	−	−	−	−	−	+	+	−	−	−	−
11	56	69	P	P	+	−	−	−	−	−	−	−	+	+	−	−	−	−
12	53	66	P	YG	+	−	−	−	−	−	−	+	+	+	−	−	−	−
13	45	59	P	Br	+	−	+	−	−	−	−	−	−	−	+	−	−	+
14	51	48	P	Br	−	+	+	+	+	+	+	+	+	+	+	+	+	+
15	71	31	P	GY	−	+	−	−	−	+	−	+	+	+	−	−	−	−
16	60	8	iv	Y	+	+	−	+	+	+	+	+	+	+	+	+	−	+

17	93	4	Pk	Pk	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
18	86	9	B	GB	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
19	75	5	iv	Y	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
20	33	45	P	Br	−	−	−	+	−	+	+	+	+	+	−	−	−	−	−
21	18	6	B	btB	−	−	+	+	+	+	+	+	+	−	+	+	−	+	−
22	28	7	iv	Y	−	−	+	−	−	−	−	−	−	−	+	−	−	−	−
23	30	9	iv	ltG	−	−	+	−	−	−	−	−	−	−	+	−	−	−	−
24	26	58	P	P	−	−	−	+	−	−	+	+	−	−	−	+	−	+	−
25	60	16	B	Y	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
26	68	26	P	YG	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−
27	43	52	P	YG	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−

[a]B = Blue, Y = Yellow, G = Green, Gr = Gray, Og = Orange, Pk = Pink, P = Purple, Br = Brown, iv = invisible, fl = fluorescent, bt = bright, lt = light. Combinations of colors indicate intermediate status.

lowing reasons: (1) the compounds have not been totally isolated, (2) the compounds have not been identified, (3) a larger sample of the wild species needs to be examined to determine the extent of intraspecific variation, and (4) more amphiploids need to be synthesized using different biotypes. Nonetheless, the following tentative conclusions can be drawn: (1) The pattern for *Ae. sharonensis* appears to be the same as that for *Ae. bicornis*, but it is different from that of *Ae. longissima*; (2) unidentified compounds common to *T. urartu* and *T. turgidum* var. *dicoccoides* may be interpreted to indicate that *T. urartu* is one ancestor of *T. turgidum* var. *dicoccoides*; whether it is the donor of the **A** genome or the **B** genome is not yet clear.

CONCLUSIONS

Most diploid species of *Aegilops* and *Triticum* appear to have evolved monophyletically from a common ancestor. A hybrid origin for *Ae. sharonensis* is a viable hypothesis, but it is not the simplest explanation. The two hexaploid wheat species *T. aestivum* and *T. zhukovskyi* may have arisen as the result of genes which, when combined, promote the formation of unreduced gametes in triploid interspecific hybrids. The evidence for *Ae. searsii* as the donor of the **B** genome of tetraploid wheat is not as convincing as that for other diploid species of *Aegilops* or *Triticum*. The leaf flavonoid compounds of *Aegilops* and *Triticum* appear to be useful biosystematic characters for the study of evolution.

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