INTROGRESSION FROM TETRAPLOID DURUM WHEAT TO DIPLOID AEGILOPS LONGISSIMA AND AEGILOPS SPELTOIDES

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SUMMARY

Tetraploid to diploid introgression by means of interspecific triploid hybrids was followed in two species combinations:

- (i) *T. durum* × *Ae. longissima* ABS¹ combination.
- (ii) *T. durum* × *Ae. speltoides* ABS combination.

Triploids set rare seeds when exposed to massive back pollination by their diploid parents.

Third-hybrid generation progenies of both combinations were diploid $2n = 14$ or almost diploid $2n = 15$ or 16 , with high fertility, and bore a close morphological resemblance to their respective diploid parent.

1. INTRODUCTION

In previous papers (Vardi and Zohary, 1967; Vardi, 1970) evidence was presented to indicate that, in wheats, genetic variation can be enriched through introgression from diploid to polyploid species. Furthermore, it was demonstrated that interspecific triploid hybrids serve as an effective bridge in such gene transfer.

The present study assesses the reverse possibility, namely, gene flow from tetraploid to diploid entities. An indication that such a process can actually take place has been shown in the work of Kihara (1954), who backcrossed the triploid hybrid *Aegilops caudata* × *Aegilops cylindrica* to its diploid parent and obtained several seeds. Our aim was to examine the possibility of this type of transfer on a larger scale by using two related diploid species, *Aegilops longissima* and *Aegilops speltoides*. These two species differ in their effect on meiotic pairing when crossed with tetraploid or hexaploid wheat (Riley, 1960).

2. METHODS

Meiosis in P.M.C.s served both for the determination of chromosome numbers and for the study of chromosome pairing. Anthers were fixed in 3:1 alcohol-acetic acid for 24 hours, stored in 70 per cent alcohol and stained in acetocarmine.

Since chromosome numbers varied from plant to plant, pairing was expressed not only in values of "chiasmata per cell". The values of "association per chromosome" were also used, *i.e.* twice the number of chiasmata per cell divided by the number of chromosomes in the examined plant. In the parental lines, the F_1 triploid, the F_2 , and the majority of F_3 plants, this value was based on examination of 30 randomly picked metaphases.

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Pollen fertility was determined by dissecting mature anthers soaked in 4 per cent acetocarmine and scoring about 500 pollen grains per plant. Grains were considered normal when they were rounded and well stained.

Seed fertility was determined by examination of two lower florets in the spikelet. A floret was considered fertile if a well-developed kernel was found in it. In the more fertile plants a sample of 100 florets (*i.e.* 50 spikelets) was employed. In semi-sterile plants, and particularly in the triploids themselves, seed set was determined by examination of all available spikes.

3. EXPERIMENTAL PROCEDURES AND RESULTS

The following two interspecific triploid combinations were produced and utilised:

(i) *ABS*^l combination:

Triticum durum (*AABB*) × *Aegilops longissima* (*S*^l*S*^l)

(ii) *ABS* combination:

Triticum durum (*AABB*) × *Aegilops speltoides* (*SS*).

As shown by Sarkar and Stebbins (1956) and Riley *et al.* (1958), genome *S* is closely related to genome *B*.

These two combinations are identical to *ABS*^l (low pairing) and *ABS* (high pairing) triploids employed previously (Vardi and Zohary, 1967; Vardi, 1970) in the study of introgression from diploid to tetraploid wheat. Each *F*₁ triploid hybrid combination was planted intermixed with its diploid parental lines and isolated from other *Triticum* or *Aegilops* species. The functional male-sterile *F*₁ hybrids were thus exposed to backcross pollination by their diploid parent. This open-pollination was supplemented by some artificial back-pollination. Only a few backcross seeds were obtained from the highly sterile triploids. Second-generation hybrid derivatives raised from these seeds were interplanted with their parents in order to promote seed production. *Ae. longissima* was used as pollen donor for *durum* × *longissima* derivatives, and both *T. durum* and *Ae. speltoides* were used to provide pollen for *durum* × *speltoides* derivatives. Because some second-generation plants were semi-fertile, the seeds produced may possibly have been a mixture of selfing and second backcross products. Selected families of third-generation hybrid derivatives were also grown. Fig. 1 illustrates the experimental design employed.

FIG. 1.—The breeding programme.

The results obtained can be summarised as follows:

(i) *Introgression from T. durum to Ae. longissima*(a) *F₁ triploid ABS^t hybrids*

Four *ABS^t* triploid plants were used. The present triploids were vegetatively vigorous and meiosis was characterised by an almost total lack of pairing (table 1), the number of chiasmata, 1.20 per cell, being very low. This behaviour has been previously described in plants representing a similar genome combination (Vardi and Zohary, 1967). Anthers in all four plants failed to dehisce and contained about 1 per cent of stainable pollen. However, back-pollination to the diploid *Ae. longissima* resulted in an occasional set of well-developed seeds.

(b) *Second-generation hybrid derivatives*

Fifteen backcross products were examined. Morphologically, most plants were intermediate between the *F₁* triploid hybrid and typical *Ae. longissima*. However, some *F₂* plants bore a close resemblance to their *longissima* parental line.

Chromosome numbers in the second hybrid generation varied from $2n = 22$ to $2n = 28$ (table 1). Eleven plants were tetraploid or almost tetraploid and contained 26-28 chromosomes. Twelve plants displayed five or six bivalents in meiosis (table 1). Furthermore, some *F₂* individuals had an occasional trivalent or quadrivalent. Pollen and seed fertility in the second generation was low and several plants failed to set seed (table 1). It is, however, of interest to note the relatively high seed fertility of plant no. 6859-57 ($2n = 23$). Although no pollen counts were made in this plant, the dehiscence of its anthers indicated low pollen abortion. This plant was used as seed parent to most of the *F₃* progeny analysed.

The cytological data thus corroborate our previous findings (Vardi and Zohary, 1967) that unreduced or almost unreduced female gametes are, in the main, the functional gametes produced by *ABS^t* triploids. In other words, the data on chromosome number and meiotic pairing indicate that the majority of *F₂* plants obtained from *ABS^t × S^tS^t* backcrosses were roughly of an *ABS^tS^t* constitution. The occasional formation of trivalents and quadrivalents in the *F₂* plants is also noteworthy. This indicates the occurrence of chromosomal exchange during meiosis in the triploid, presumably between homoeologous chromosomes.

(c) *Third-generation hybrid derivatives*

A sample of 29 plants, derived from plant 6859-57 ($2n = 23$) and an additional single plant obtained from plant 6859-51 ($2n = 28$), were examined. All *F₃* plants resembled *Ae. longissima* very closely.

As seen from table 3, all third-generation derivatives had lower chromosome numbers than plants of the second generation. Twenty-seven plants were diploid ($2n = 14$) and three were almost diploid ($2n = 15$). Chromosome pairing in the $2n = 14$ plants was normal, i.e. there were seven bivalents with 1.86-1.98 chiasmata per chromosome. Plants with a $2n = 15$ number, that produced a single trivalent, may have been trisomic for the additional chromosome. However, $2n = 15$ plants that displayed seven bivalents plus a single univalent, probably contained an additional chromosome of the *A* or *B* genome. In contrast to the second generation, high restoration of pollen fertility (table 5) and marked recovery in seed set (table 6) were achieved.

TABLE 1

Backcross of durum $\times$ longissima ABS¹ triploid to its diploid parent: cytology and fertility of F_1 hybrid and second-generation derivatives

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Accession No.	Chromosome No. (2n)	No. of cells examined	Chromosome association in metaphase I				Associations per chromosome	Fertility		
			Univalents	Bivalents	Trivalents	Quadrivalents		Per cent normal pollen	Per cent seed-set	
F₁ Triploid hybrid										
<i>T. durum</i> × <i>Ae. longissima</i> (genomes <i>ABS</i> ¹)										
21	46	18-63 (11-21)	1-15 (0-5)	0-02 (0-1)	—	0-11	1-40	4-10		
F₂ Second hybrid generation										
6859-1	30	16-00 (12-21)	5-60 (2-8)	2-26 (0-2)	—	0-54 ± 0-12	2-40	0		
6859-3	30	13-93 (11-18)	5-80 (3-8)	0-73 (0-3)	0-06 (0-1)	0-66 ± 0-12	7-60	0-35		
6859-17	30	10-16 (5-14)	6-50 (3-10)	6-83 (0-1)	0-13 (0-1)	0-93 ± 0-14	0	0		
6859-26	30	13-00 (7-17)	5-66 (2-10)	0-80 (0-2)	0-06 (0-1)	0-74 ± 0-18	4-18	0		
6859-28	20	17-75 (14-24)	5-00 (2-8)	0-05 (0-1)	—	0-59 ± 0-33	8-38	0		
6859-29	30	11-00 (5-16)	6-46 (2-9)	0-60 (0-3)	0-06 (0-1)	0-87 ± 0-02	3-00	0		
6859-35	23	17-30 (14-20)	2-34 (1-4)	—	—	0-25 ± 0-09	—	—		
6859-40	—	—	—	—	—	—	—	—		
6859-42	30	10-80 (6-14)	6-90 (4-10)	1-13 (0-3)	—	0-89 ± 0-12	0	0-23		
6859-43	30	20-16 (17-23)	2-16 (0-5)	0-16 (0-1)	—	0-23 ± 0-10	0	1-25		
6859-51	30	13-13 (9-18)	6-73 (5-9)	0-46 (0-1)	—	0-81 ± 0-15	3-00	0-54		
6859-52	30	12-70 (8-16)	6-26 (4-9)	0-50 (0-2)	0-06 (0-1)	0-73 ± 0-14	0-80	0-38		
6859-53	30	12-86 (9-16)	5-90 (3-8)	0-40 (0-2)	0-03 (0-1)	0-78 ± 0-13	3-60	0-22		
6859-55	30	12-10 (8-17)	6-63 (4-10)	0-83 (0-2)	0-03 (0-1)	0-84 ± 0-16	3-00	0		
6859-57	11	10-09 (5-13)	6-45 (5-7)	—	—	1-08 ± 0-17	—*	16-70		

* Relatively high pollen fertility was indicated by anther dehiscence in this plant.

TABLE 2
Backcross of durum × speltoïdes ABS triploid to its diploid parent: cytology and fertility of F₁ Hybrid and second-generation derivatives

Accession No.	Chromosome No. (2n)	No. of cells examined	Chromosome association in metaphase I				Associations per chromosome	Fertility		
			Univalents	Bivalents	Trivalents	Quadrivalents		Per cent normal pollen	Per cent seed-set	
F ₁ Triploid hybrid										
<i>T. durum</i> × <i>Ae. speltoïdes</i> (genomes <i>ABS</i>)	21	44	5.07 (1.9)	4.62 (0.5)	2.50 (0.5)	—	1.03	2.20	0.31	
F ₂ Second hybrid generation										
6860-2	21	30	4.76 (2.9)	4.56 (2.7)	2.33 (0.4)	0.03 (0.1)	1.22 ± 0.13	5.40	0.11	
6860-6	21	30	5.06 (2.8)	4.43 (2.7)	2.13 (0.2)	0.16 (0.2)	1.12 ± 0.12	25.05	0.74	
6860-7	21	30	9.40 (6.13)	5.00 (3.7)	0.53 (0.2)	—	0.75 ± 0.13	0.60	0	
6860-8	21	30	5.53 (3.8)	5.43 (3.7)	1.50 (0.4)	—	1.18 ± 0.11	26.20	21.42	
6860-9	21	30	6.13 (3.10)	5.83 (4.8)	1.66 (0.3)	—	1.13 ± 0.14	19.00	0.53	
6860-10	21	11	4.50 (2.7)	5.66 (3.8)	1.50 (0.3)	0.16 (0.1)	1.22 ± 0.18	24.10	0.70	
6860-12	22	30	6.71 (4.12)	5.90 (4.8)	0.93 (0.3)	0.13 (0.1)	1.02 ± 0.16	23.40	0.44	

In summary, the third generation of hybrid derivatives of the *ABS*⁴ combination showed an almost complete stabilisation at the diploid level. This rapid establishment of the diploid chromosome number appears to be due to a striking elimination of redundant chromosomes during meiosis of *F*₂ plants. Presumably the 14 chromosomes in third-generation derivatives represent more or less the complete genome of *Ae. longissima*.

(ii) *Introgression from T. durum to Ae. speltoides*

(a) *F*₁ triploid *ABS* hybrid

Three *ABS* triploid plants were employed. As in previously studied *ABS* triploids (Vardi, 1970), meiosis was characterised by four to seven

TABLE 3
Frequency distribution of chromosome numbers in third hybrid generation

Triploid combination and accession numbers	Chromosome No. in F ₂ parent	No. of F ₃ plants examined	Chromosome numbers													
			14	15	16	...	21	22	23	24	25	26	27	28	29	
(i) <i>T. durum</i> × <i>Ae. longissima</i>																
6859-51	28	1	1	—	—		—	—	—	—	—	—	—	—	—	—
6859-57	23	29	27	2	—		—	—	—	—	—	—	—	—	—	—
(ii) <i>T. durum</i> × <i>Ae. speltoides</i>																
6860-6	21	12	1	2	—		4	2	—	1	1	—	—	—	—	1
6860-8	21	53	39	13	1		—	—	—	—	—	—	—	—	—	—

bivalents and the frequent occurrence of trivalents (as many as five trivalents in some microsporocytes). The relatively high frequency of trivalents is probably due to a suppression of the 5*B* diploidisation effect by *Ae. speltoides* chromosomes (Riley and Chapman, 1964).

Also in the present experiment, *durum* × *speltoides* triploids were functionally completely male-sterile and their anthers did not dehisce. Yet, massive exposure to *Ae. speltoides* pollen resulted in the formation of seven well-developed backcross seeds.

(b) *Second-generation hybrid derivatives*

All seven second-generation plants resembled their *F*₁ triploid parents in general morphology, although some variation between plants was obtained. Six of the seven plants had a triploid chromosome number ($2n = 21$), while one had a number of $2n = 22$ (table 2). Pairing of chromosome in the *F*₂ plants was very similar to that observed in the original *durum* × *speltoides* *F*₁ triploids. But, significantly, in four of the seven *F*₂ plants, one to two quadrivalents were also detected (table 2). Another conspicuous difference between the *F*₁ and second-generation hybrid derivatives was the partial restoration of pollen fertility (table 2). In some *F*₂ plants anthers dehisced partially. One of these male-fertile plants, 6860-8, also showed a remarkable recovery of seed fertility (table 2).

Although the triploid chromosome number was maintained in the individuals of the second generation, the cytological data for *F*₁ triploids

TABLE 4
Chromosome pairing in third hybrid generation: frequency distribution of "association per chromosome" values

Triplod combination and accession numbers	Chromosome No. in F ₂ parent	No. of F ₃ plants examined	Association per chromosome															
			0.51- 0.60	0.61- 0.70	0.71- 0.80	0.81- 0.90	0.91- 1.00	1.01- 1.10	1.11- 1.20	1.21- 1.30	1.31- 1.40	1.41- 1.50	1.51- 1.60	1.61- 1.70	1.71- 1.80	1.81- 1.90	1.91- 2.00	
(i) <i>T. durum</i> × <i>Ae. longissima</i>																		
6859-51	28	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	
6859-57	23	28	—	—	—	—	—	—	—	—	—	—	—	—	1	7	20	
(ii) <i>T. durum</i> × <i>Ae. speltoides</i>																		
6860-6	21	10	—	3	2	1	—	1	1	—	—	1	—	—	—	1	—	
6860-8	21	45	—	—	—	—	—	—	—	—	1	—	7	9	14	14	—	

suggest that the genomic constitution of the F_2 derivatives of these triploids is the outcome of some chromosome reshuffling between the original parental genomes. This means that second-generation progenies are already the products of homoeologous recombination which occurred during meiosis of the original F_1 triploids. Furthermore, the present results are in full agreement with previous data on *ABS* triploids (Vardi, 1970). Here, as in the

TABLE 5
Frequency distribution of pollen-fertility values scored in third hybrid generation

Triploid combination and accession numbers	Chromosome No. in F ₂ parent	No. of F ₃ plants examined	Pollen-fertility classes (in per cent)							
			0-5	6-15	16-30	31-45	46-60	61-75	76-90	91-100
(i) <i>T. durum</i> × <i>Ae. longissima</i>										
6859-51	28	1	—	—	—	—	—	—	1	—
6859-57	23	28	—	—	—	—	—	—	5	23
(ii) <i>T. durum</i> × <i>Ae. speltooides</i>										
6860-6	21	8	2	5	1	—	—	—	—	—
6860-8	21	37	—	—	—	1	1	6	14	15

TABLE 6
Frequency distribution of seed-set values scored in third hybrid generation

Triploid combination and accession numbers	Chromosome No. in F ₂ parent	No. of F ₃ plants examined	Seed-set classes (in per cent)							
			0-5	6-15	16-30	31-45	46-60	61-75	76-90	91-100
(i) <i>T. durum</i> × <i>Ae. longissima</i>										
6859-57	23	27	—	3	1	3	7	6	5	2
(ii) <i>T. durum</i> × <i>Ae. speltooides</i>										
6860-6	21	10	9	1	—	—	—	—	—	—
6860-8	21	47	—	2	2	4	10	14	14	1

previously examined triploids, it is obvious that the main type of functional gamete produced by *durum* $\times$ *speltooides* triploids has roughly an *AB* constitution.

(c) *Third-generation hybrid derivatives*

Two families of the third generation were grown and analysed. Twelve plants were derived from seed parent 6860-6 and 57 plants from the most fertile of the F_2 plants, 6860-8. Chromosome numbers in the family derived from plant 6860-6 varied from 14 to 29 (table 3). This was expected, since the seed parent 6860-6 was exposed to both *T. durum* and *Ae. speltooides* pollen and was itself partially male fertile. Nine of the derivatives had a high number of chromosomes (21-29) and can be considered products of crosses to $n = 14$ pollen. Morphologically, they resembled the triploid hybrid more than they did *Ae. speltooides* and were marked by high sterility (tables 5, 6).

Three plants had chromosome numbers of 14-15. They showed six or seven bivalents in meiosis plus an additional trivalent or univalent. Morphologically, they resembled *Ae. speltooides*. These plants can be considered as products of crosses to $n = 7$ or $n = 8$ pollen.

In contrast to the family derived from F_2 plant 6860-6, in which a wide range of chromosome numbers was segregated, the family derived from F_2 plant 6860-8 contained mainly diploid $2n = 14$, or almost diploid $2n = 15$ or 16, individuals (table 3). Plants of this family must be considered to have arisen from crosses to $n = 7$ or $n = 8$ pollen. Since anthers in the 6860-8 parent dehisced, most of the progeny were presumably products of self-pollination. Chromosome pairing in $2n = 14$ plants was considerable but not completely regular (11.07-13.03 chiasmata per cell). Most of the $2n = 15$ plants were apparently trisomic and a single trivalent was observed frequently. Pollen fertility and seed set were normal or almost normal (tables 5 and 6). All the progenies of 6860-8 resembled *Ae. speltooides* rather closely in general growth habit, morphology and ear shape.

In summary: as in the previous combination ABS^I , the third-generation hybrid derivatives ABS combination also showed an almost complete stabilisation at the diploid level. This was unexpected since pairing behaviour of triploid F_2 plants of the ABS combination still resembled that of the triploid F_1 . The high pairing observed in F_1 and F_2 ABS plants indicated that chromosome exchange was taking place and thus the *speltooides*-like diploid ($2n = 14$) individuals obtained in F_3 were presumably introgressants.

4. DISCUSSION

The data obtained suggest that tetraploid to diploid introgression can occur in wheats. As in diploid to tetraploid introgression (Vardi and Zohary, 1967; Vardi, 1970), the occasional gametes produced in the triploid F_1 hybrid, which are genomically more or less balanced, are necessary for this process. When such ABS^I gametes are produced in *T. durum* $\times$ *Ae. longissima* triploids and roughly AB gametes in *T. durum* $\times$ *Ae. speltooides* triploids, products of the backcross to the respective diploid parent will be mainly tetraploid, or almost tetraploid, $ABS^I S^I$ plants in the first combination and more or less triploid ABS plants in the second combination. Rare trivalents in F_2 samples from the ABS^I combination and quadrivalents in the samples of the ABS combination indicate that intergenomic chromosome exchange has occurred during the meiosis of the F_1 triploid hybrids (tables 1 and 2). It is assumed that these exchanges take place between homoeologous chromosomes. One of the main subsequent problems in tetraploid to diploid introgression is an excess of chromosomes which have to be eliminated before stabilisation at the diploid level can occur.

(i) In the *durum* $\times$ *longissima* combination, complete or almost complete elimination of A and B genomes is achieved already in F_3 . Stabilisation at the diploid level is indicated by the full or almost full fertility of F_3 plants and their close morphological resemblance to *Ae. longissima*. In an F_2 plant, 6857-59 ($2n = 23$), which gave rise to viable diploid F_3 products, cytological data (table 1) indicate that there were only relatively minor donations, if any, from the A and B genomes of wheat. As seen from table 1, this F_2 plant produced only bivalents and univalents.

Another *durum* × *longissima* F_2 plant, 6859-51 ($2n = 28$), showed an average of 0.46 trivalent per cell in M_I (table 1). The single third-generation derivative obtained from F_2 plant 6859-51 differed morphologically from the 6859-57 family. This segregant bore close resemblance to a local single-awned or asymmetrically awned form of *Ae. longissima*, which occurs sporadically on both sides of the Jordan Rift Valley (Judean Hills, Moab, Gilead). This wild *Ae. longissima* form differs from the typical *Ae. longissima* described by Eig (1929) in its more delicate spike morphology and in its single or asymmetrical awns which carry two lateral teeth on their adaxial side. It is noteworthy that some of the sites of this *longissima* morph are areas in which *Ae. longissima* and *T. dicoccoides* form mixed populations. This wild morph may represent an established product of an introgression process similar to that witnessed under experimental conditions in the 6859-51 line.

(ii) In the *durum* × *speltoides* combination there is a parallel rapid elimination of chromosomes and the main products in the third hybrid generation are diploid ($2n = 14$) or almost diploid ($2n = 15$ or 16). Here the F_3 plants resemble typical *Ae. speltoides* morphologically. This indicates a relatively small donation from the *A* genome.

Homoeologous exchanges in the *ABS* F_1 triploid may be a contributing factor to the relatively low fertility in the second hybrid generation. This is without doubt one of the reasons why the various F_2 plants ($2n = 21$ and $2n = 22$) showed variation in chromosome pairing and fertility (table 2). Because of these homoeologous exchanges in F_1 *ABS* triploids, it is impossible to determine the genomic constitution of F_2 plants through cytological observations, as is possible in most *ABS* F_2 plants. Without information on the genomic make-up of F_2 plants it is difficult to account for diploidy in the third hybrid generation. Diploid F_3 plants can be the result of either genomic segregation or lethal duplication which leads, during meiosis of the F_2 seed parent, to an elimination of chromosomes. Such processes may have led to diploids in the third-generation plants of the 6860-8 family.

That the *speltoides*-like 6860-8 F_3 plants bear a modified genome and differ from true *speltoides* plants is indicated by their lower chiasma frequency (11.00-13.03 chiasmata per cell as against 13.65 chiasmata per cell in *Ae. speltoides*) and by occasional univalents. Similar relatively low pairing was also observed in F_4 hybrids obtained from crosses between *speltoides*-like F_3 ($2n = 14$) individuals of families 6860-6 and 6860-8 and within family 6860-8. On the other hand, when the same *speltoides*-like F_3 parent plants were crossed with true *Ae. speltoides*, pairing in the resulting hybrids was fully normal. In 23 such hybrids, chiasma frequency per cell varied from 12.67 to 13.87. Thus, pairing was lower in the crosses between two recombined genomes (*speltoides*-like × *speltoides*-like) than in crosses between a recombined and a pure *Ae. speltoides* genome (*speltoides*-like × *Ae. speltoides*). Yet, in both series of crosses, 5B suppressor alleles were present, as was verified by crossing *speltoides*-like F_3 plants with *T. aestivum* (unpublished data). In other words, the *speltoides*-like individuals are evidently introgressants, but the pure *Ae. speltoides* genome cancels the pairing irregularities caused by introgression. However, in nature any such processes of introgression would result in crosses between true *Ae. speltoides* and *speltoides*-like introgressants, both being outcrossed. Within a few generations derivatives of such crosses would achieve normal pairing and be cytologically indistinguishable from *Ae. speltoides*.

The data presented confirm that interspecific triploid hybrids in the wheat (*Triticum-Aegilops*) group do act as bridges for tetraploid to diploid gene transfer. When such transfers, or transfers in the reverse direction, take place in nature the recombined products become almost indistinguishable morphologically and cytologically from their diploid or tetraploid parents within only a few generations. Such introgression enriches natural genetic variation. Thus, if the *B* genome of wheat is a modified genome, as suggested by Kimber and Athwal (1972), it is possible that the two diploid species used in this experiment contributed to the *B* genome. Tetraploid to diploid introgression may also explain the appearance of local forms, such as the *Ae. longissima* form described here, and the comparatively large morphological variation in diploids that are related to polyploids. Examples of such polyploid-diploid species pairs are *Ae. triuncialis* and *Ae. umbellulata*, *T. dicoccoides* and *T. boeoticum*, and *Ae. cylindrica* or *Ae. crassa* and *Ae. squarrosa*. Thus, polyploid to diploid introgression can enrich the very diploid which gave rise to the polyploid.

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