INVIABILITY OF INTERGENERIC HYBRIDS INVOLVING TRITICUM MONOCOCCUM AND T. AEGILOPOIDES¹

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INTRODUCTION

WITH the development in recent years of colchicine techniques and other reliable methods for doubling chromosome number in plants, interspecific and intergeneric hybrids which formerly could not be maintained because of their sterility can now easily be rendered fertile and true-breeding. The ready source of essentially new species thereby made available is rather strictly limited, however, by the failure of many crosses between reasonably close relatives to yield viable hybrids.

Noteworthy progress has recently been made toward extending the limits of crossability. The discovery by LAIBACH (1925) that the embryos of certain inviable hybrid seeds can be dissected out and grown on artificial media, coupled with the recent development by VAN OVERBEEK, CONKLIN, and BLAKESLEE (1942) of methods for culturing extremely young embryos, should permit many otherwise impossible crosses to be made. Certain other devices, notably the style-shortening technique of MANGELSDORF and REEVES (1931) and the mixed pollinations of BEASLEY (1940), have served in special instances to make possible the production of hybrids.

An important barrier to hybridization which cannot be overcome by any of the foregoing methods is the lethality of hybrid seedlings. In the genus *Crepis*, BABCOCK and NAVASHIN (1930) reported that 19 out of 103 interspecific hybrids were abnormal or weak, in most cases dying before reaching the flowering stage; and EAST (1935a) found 14 inviable types in 77 hybrid combinations in *Nicotiana*. The very early stage at which some hybrid seedlings die makes it probable that there are numerous comparable instances where the embryo dies before maturity of the seed. Such lethal embryos would presumably not be subject to removal from the seed and successful culture on an artificial medium.

Only an indirect method is yet available for overcoming the lethality of hybrid embryos or seedlings, and this is the substitution of varieties or strains which give viable hybrids. This method has thus far been utilized in isolated instances only. Genetic studies may indicate whether or not it is generally applicable.

The present report deals chiefly with the genetics of the lethality of hybrids

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between *Triticum monococcum* and *Aegilops umbellulata*. Also included are data on the semi-lethality of hybrids of *T. aegilopoides* with *Ae. bicornis* and on non-crossability of *T. monococcum* with *Haynaldia villosa*.

REVIEW OF LITERATURE

HOLLINGSHEAD (1930) was the first to analyze genetically a difference between varieties or strains in viability of their hybrids with another species. She found in certain strains of *Crepis tectorum* a single factor which caused inviability of hybrids with *C. capillaris*, *C. leontodontoides*, and presumably with *C. bursifolia*, but which was without apparent effect in *C. tectorum* itself. A similar situation, except that the affected hybrids were merely sickly and of reduced vitality rather than inviable, was observed by LEHMANN (1939) in crosses of two biotypes of *Epilobium hirsutum* with *E. adenocaulon*. MELCHERS (1939) found that a single factor in *Hutchinsia alpina* resulted in inviability of hybrids with *H. brevicaulis*, the inviability being expressed so early as to result in the production of empty, non-germinable seeds. SEARS (1940) reported a single factor in *Triticum monococcum* to be responsible for inviability of hybrids with *Aegilops umbellulata*.

The foregoing studies have shown the constitution of only one parent of each inviable hybrid. Presumably each other parent also carries some genetic imperfection, else its genome would make the hybrid viable. Each parent of the semi-lethal hybrid between a strain of *Gossypium arboreum* and various strains of *G. herbaceum* and *G. arboreum* has been found by HUTCHINSON (1932) and SILOW (1941) to possess a single, dominant gene for hybrid inviability. When both parents are considered, two complementary factors are thus involved. Analysis of both parents was possible in this case because they were closely enough related that their hybrid, which occasionally lived to flower, produced viable seed.

KOSTOFF (1936) found that *Nicotiana rustica* var. *texana* formed viable hybrids with *N. glauca*, while *N. rustica* var. *humilis* × *N. glauca* gave hybrids which died as early embryos; but no genetic analysis was attempted. MANGELSDORF and REEVES (1939) noted that occasional plants of *Zea mays* × *Tripsacum dactyloides* were extremely weak and slow to develop.

In animals, also, factors for inviability of interspecific hybrids have been discovered. CROW (1941, 1942) found in a strain of *Drosophila aldrichi* a gene, or possibly a series of genes, on the X chromosome which had no noticeable effect within the species but which acted as a dominant semi-lethal in crosses with *D. mulleri* and probably with *D. mojavensis* and *D. arizonensis*. A similar gene or set of genes was suspected to be effective in *D. mulleri* × *D. mojavensis*.

MATERIALS

The einkorns, the varieties of *Triticum* with seven pairs of chromosomes, are usually classified into two species, *T. monococcum* L. and *T. aegilopoides* Bal. ex Körn. (incorrectly listed as *T. aegilopoides* Forsk. by SEARS 1941a). However, interspecific crosses are easily made, and the hybrids are of normal fertility (SMITH 1936). When *T. aegilopoides* var. *baidaricum* Flaksb. is crossed

with other varieties of the *aegilopoides-monococcum* complex, the F_1 plants have a ring of four chromosomes at meiosis and show considerable sterility. The sterility is not due to the ring, however, but to one or a few genetic factors, since some plants in F_2 form varietal hybrids which possess the ring but are almost fully fertile, while others have no ring but are largely sterile (SMITH unpublished). *T. aegilopoides* var. *Thaoudar* (Reut.) Percival is often given specific rank as *T. Thaoudar* Reut.

T. aegilopoides was represented in this investigation by the varieties *baidaricum*, *pubescentinigrum* Flaksb., *Pancici* Flaksb., and *Thaoudar*, and *T. monococcum* by the varieties *flavescens* Körn. and *Hornemanni* (Clem.) Körn. and by F_4 to F_6 lines of var. *vulgare* Körn. $\times$ var. *flavescens*. Also used were F_3 and F_4 lines of *T. monococcum* var. *vulgare* $\times$ *T. aegilopoides* var. *baidaricum* and of (*T. aegilopoides* var. *baidaricum* $\times$ var. *pubescentinigrum* F_1) $\times$ (*T. monococcum* var. *vulgare* $\times$ *T. aegilopoides* var. *baidaricum* F_1). These lines, which had been subjected in segregating generations to selection for characters mostly from *T. aegilopoides*, will be referred to hereafter as *T. aegilopoides* derivatives. They and the *T. monococcum* *vulgare-flavescens* lines were obtained from DR. LUTHER SMITH.

Seed of *Aegilops umbellulata* Zhuk. was obtained from DR. ELIZABETH SCHIEMANN of the INSTITUT FÜR VERERBUNGSFORSCHUNG DER LANDWIRTSCHAFTLICHE HOCHSCHULE, Berlin-Dahlem, Germany. *Haynaldia villosa* (L.) Schur came from MR. W. J. SANDO of the U. S. DEPARTMENT OF AGRICULTURE, Washington, D. C. *Ae. bicornis* (Forsk.) Jaub et Spach was supplied by MR. C. O. JOHNSTON of the U. S. DEPARTMENT OF AGRICULTURE, Manhattan, Kansas. Each of these three species has seven pairs of chromosomes.

HYBRIDS WITH *AEGILOPS UMBELLULATA*

Viable Hybrids

Hybrids of *Ae. umbellulata* with *T. aegilopoides* vars. *baidaricum*, *pubescentinigrum*, *Pancici*, and *Thaoudar*, and with the *T. aegilopoides* derivatives, were normal, viable plants. Amphidiploids of var. *baidaricum* $\times$ *Ae. umbellulata* have been produced and described (SEARS 1941a). Chromosome pairing in the sterile, non-doubled hybrids averaged 5.78 univalents, 2.88 bivalents, and 0.82 trivalents per microsporocyte (SEARS 1941b).

Inviabile Hybrids

Hybrids of *Ae. umbellulata* with all tested varieties and derivative lines of *T. monococcum* were inviable, irrespective of which species was used as the female parent. Hybrid seeds were easily obtained as a rule. Only one seed was formed on seven pollinated spikes of var. *Hornemanni* and but four on two spikes of var. *flavescens*, but some of the derivative Triticum material yielded up to 50 percent seed set on some spikes—that is, 10 to 15 seeds. Seeds were of normal size and plumpness.

Two distinct types of lethality were observed, one being expressed much earlier than the other.

FIGURE 1. Early-dying, inviable hybrids of *T. monococcum* $\times$ *Ae. umbellulata*, showing the range in size attained and some of the abnormalities which occur. $\times 1.65$.

FIGURE 2. (b to d) Late-dying, inviable hybrids, shown with their parents, (a) *Triticum monococcum* and (e) *Aegilops umbellulata*, at a time when growth had ceased in the hybrids. $\times 0.42$.

FIGURE 3. (a) An extreme late-dying hybrid of *T. monococcum* $\times$ *Ae. umbellulata* in comparison with (b) a younger viable hybrid with a comparable amount of top growth. $\times 0.22$.

Early-Dying Hybrids

When *Ae. umbellulata* was crossed with *T. monococcum* var. *flavescens* or with certain derivatives of hybrids between var. *flavescens* and *T. aegilopoides*, death occurred shortly after germination. Figure 1 shows some typical hybrids.

The stage at which development ceased varied from almost immediately after the pericarp was broken to when two stunted leaves were present. It is probable that death occasionally occurred before the testa was broken, since seeds which failed to germinate were somewhat more common than in normal material. Approximately half of the seedlings were visibly abnormal, particularly in a tendency toward multiplication of the number of shoots. As many as five separate coleoptiles were noted in a single seedling, two of these emerging from the bottom, or furrowed, side of the seed. If a single coleoptile was present, it was sometimes enlarged or forked. Roots were usually absent, though a single, very short root, usually with a bulbous tip, was occasionally formed.

Only four seeds were obtained of *T. monococcum* var. *flavescens* × *Ae. umbellulata*, and two of these failed to germinate, while the other two died at an extremely early stage. It is believed that a larger population would have contained some seedlings which would die at somewhat later stages, for there was no indication in F_2 populations from var. *flavescens* × *T. aegilopoides* that the variation in time of death of hybrids with *Ae. umbellulata* was due to the segregation of modifying factors introduced by the *aegilopoides* parent.

Late-Dying Hybrids

Hybrids of *Ae. umbellulata* with the *T. monococcum* *vulgare-flavescens* derivatives survived distinctly longer than did the hybrids with var. *flavescens* described in the preceding section. Practically all seeds germinated without delay, and some seedlings grew at an approximately normal rate until the third leaf appeared, or later. Other individuals showed a slow rate of elongation of the coleoptile and a delayed emergence of the first leaf, but all developed at least two leaves, and these were of considerably greater size than the two leaves sometimes produced on the early-dying type of hybrid. Figures 2b, 2c, and 2d show typical late-dying hybrids at their final size, while figure 3a is of a hybrid which attained unusually large size. Retardation of growth was the first symptom of inviability, and this retardation, once initiated, became increasingly severe, until in from three to seven weeks after planting, no further development occurred. Leaves tended to be darker green than normal until growth ceased; then they gradually turned brown, beginning with the youngest ones. Leaves were stiffer than normal. The amount of root growth was approximately normal for the amount of top development (fig. 3). No seedlings were observed with multiple shoots or other abnormality such as described for the early-dying type; but some plants developed a tiller in the axil of the coleoptile, whereas under the same conditions this tiller did not develop on any plant of either parent or of the viable hybrid.

The single seed obtained of *T. monococcum* var. *Hornemanni* × *Ae. umbellulata* produced a plant which survived to such a stage as definitely to exclude this hybrid from the early-dying group. In fact, its development, under rather unfavorable conditions, was such as to suggest an ability to survive longer than even the late-dying hybrids.

Genetic Data on Viability vs. Inviability
 Hybrids of *Ae. umbellulata* with F₁ Plants

A *T. monococcum vulgare-flavescens* derivative, carrying the potentiality for producing late-dying hybrids with *Ae. umbellulata*, was crossed with a *T. aegilopoides* derivative, which had the ability to produce viable hybrids with *Ae. umbellulata*. Two plants from this F₁ (designated F₁ No. 1) were then crossed with *Ae. umbellulata*. One produced 16 viable and ten late-inviable off-

TABLE 1
Viability of hybrids between Aegilops umbellulata and plants
of F₂ No. 1 (late-inviable vs. viable).

F ₂ PLANT	HYBRIDS WITH <i>Ae. umbellulata</i>	
	NO. VIABLE	NO. INVIABLE
P39-78.1- 5	10	
-11	10	
-16	8	2
-18	7	2
- 1	3	3
-14	4	2
- 3	2	2
- 7		11
-10		3
-17		2
- 2		1
- 6		1

spring from 35 seeds, and the other gave three viable and five late-inviable plants from 12 seeds. The totals, 19 viable and 15 inviable, are a good fit to a 1:1 ratio and a rather poor fit to a 3:1 ratio (odds of 42:1 against this large a deviation, according to WARWICK'S (1932) tables). This suggests that the two *Triticum* lines differ by a single factor which causes hybrids with *Ae. umbellulata* to die.

A similar test was made of the early-dying type, through a cross of *T. aegilopoides* var. *pubescentinigrum* × *T. monococcum* var. *flavescens* (F₁ No. 2). From three F₁ plants, 45 seeds were obtained in crosses with *Ae. umbellulata*. These produced 41 hybrids, of which 20 were viable and 21 early-inviable.

Hybrids of *Ae. umbellulata* with F₂ Plants

From F₂ No. 1, which came from a cross of a *T. monococcum vulgare-flavescens* derivative × a *T. aegilopoides* derivative, 12 plants were tested in crosses with *Ae. umbellulata*, with the results shown in table 1. Two plants produced only viable hybrids, five produced both viable and late-inviable hybrids, and five produced only late-inviable hybrids. Four of the last group, however, were not

tested sufficiently to prove that they could not produce viable hybrids. This is a satisfactorily close approach to the expected one-factor ratio of 1 homozygous for the viability factor: 2 heterozygous: 1 homozygous for the inviability allele. In the segregating families a total of 24 plants were viable and 11 inviable. Although this is a considerable deviation from the expected 1:1 ratio, as large a deviation would occur by chance in four trials out of 100. Between the inviable hybrid offspring of different plants, and among the inviable offspring of

TABLE 2
*Viability of hybrids between Aegilops umbellulata and plants of
F₂ No. 2 (late-inviable vs. viable).*

F ₂ PLANT	HYBRIDS WITH <i>Ae. umbellulata</i>	
	NO. VIABLE	NO. INVARIABLE
P40-78.3- 8	10	
- 1	9	
- 7	5	
- 4	4	6
- 5	5	5
-10	7	3
-14	2	8
-18	5	5
-17	6	3
- 9	4	3
- 2	3	3
- 6	2	2
-19		8*
-22		8*
-13		1

* Five of these observations were based on tests of F₂ plants.

certain individual plants, there was considerable variation in the amount of growth which occurred, but all plants were within the limits previously described for late-dying hybrids.

Results from F₂ No. 2, which was similar to the above except that *T. aegilopoides* var. *pubescentinigrum* was used as one parent instead of the *T. aegilopoides* derivative, are given in table 2. Of 15 F₂ plants, three produced only viable hybrids with *Ae. umbellulata*, nine gave both viable and late-inviable, and three (from one of which only one hybrid was obtained) yielded only late-inviable hybrids. This is a reasonable approach to a 1:2:1 ratio. In the nine segregating families there were 38 viable and 38 inviable hybrids, a perfect 1:1 ratio.

F₂ No. 3 was obtained from *T. monococcum* var. *flavescens* × *T. aegilopoides* var. *baidaricum*—that is, from early-inviable × viable. F₂ plants were tested in crosses with *Ae. umbellulata*, with the results shown in table 3. Of ten plants, two produced only viable hybrids (but were insufficiently tested to prove them

TABLE 3

*Viability of hybrids between Aegilops umbellulata and plants of
F₂ No. 3 (early-inviable vs. viable).*

F ₂ PLANT	HYBRIDS WITH <i>Ae. umbellulata</i>	
	NO. VIABLE	NO. INVIABLE
P39-78.2- 9	2	
- 3	1	
- 2	5	2
- 7	12	13
-14	4	3
- 8	2	4
-10	5	1
-13	1	1
-15	1	1
- 4		8*

* Six of these observations were based on tests of F₃ plants.

homozygous), seven produced both viable and early-inviable hybrids, and one produced only early-inviable hybrids. Again the fit to a 1:2:1 ratio is satisfactory. In the segregating families 30 hybrids were viable and 25 inviable—very close to a 1:1 ratio.

Genetic Data on Early vs. Late Inviability

A derivative plant homozygous for the factor causing early inviability of hybrids with *Ae. umbellulata* was crossed with another derivative plant homozygous for the factor for late inviability. From the resulting F₁ one individual was crossed with *Ae. umbellulata* and 64 seeds were obtained. Of these, 61 germinated, and 28 were of the early-dying and 33 of the late-dying type. No more than the usual variation appeared within each group, with the result that the two classes were sharply separated. Less variation than usual was, in fact, observed in the late-dying group. The 28:33 segregation is a good fit to a one-factor difference for early versus late inviability.

The one-factor difference between early and late inviability may be explained in either of two ways: (1) by two factors, L^e and L^l , for early- and late-inviability, respectively, which, together with the factor l for viability of hybrids, form an allelic series; or (2) by one pair of basic factors, L and l , for inviability and viability, plus a pair of modifiers, M^e and M^l , which cause death to occur early or late, respectively. Data are available which show the first hypothesis to be the correct one.

On the modifier theory, the *T. monococcum* varieties which produce early-dying hybrids with *Ae. umbellulata* would be $LL M^e M^e$, and the varieties giving late-dying hybrids would be $LL M^l M^l$. Since no early-dying hybrids were obtained when *Ae. umbellulata* was crossed with late-inviable × viable material

(F₁ No. 1, F₂ No. 1, F₂ No. 2), *T. aegilopoides* had to be $ll\ M^1M^1$. If this was true, however, the early-inviable $\times$ viable material (F₁ No. 2, F₂ No. 3) was $LL\ M^eM^e \times ll\ M^1M^1$ and should have produced as many late-dying as early-dying hybrids with *Ae. umbellulata*. Since this material produced no late-dying hybrids, the modifier hypothesis appears incorrect. However, different varieties of *T. aegilopoides* were used in the early-inviable $\times$ viable crosses than in the late-inviable $\times$ viable material, thereby making possible an explanation based on some varieties of *T. aegilopoides* being $ll\ M^1M^1$ and others being $ll\ M^eM^e$. To test this theory, derivative plants homozygous for the inviability factor were taken from F₂ No. 1 and F₂ No. 2. On the modifier hypothesis these derivatives had to be $ll\ M^1M^1$. They were crossed with a derivative plant, homozygous for the early-inviability gene, from F₂ No. 3. This plant had to be $LL\ M^eM^e$, and the hybrids $Ll\ M^eM^1$. These hybrids yielded no late-dying offspring, however, when crossed to *Ae. umbellulata*, thereby definitely disproving the modifier hypothesis. Out of 54 seeds, 51 germinated, and these produced 31 viable and 20 early-inviable seedlings.

A series of alleles may then be assumed, L^e causing early-inviability in hybrids with *Ae. umbellulata*, L^l causing late-inviability, and l permitting viability. The varieties of *T. monococcum* are L^eL^e or L^lL^l and *T. aegilopoides* is ll .

Sources of the Inviability Alleles

The allele for early inviability occurred only in *T. monococcum* var. *flavescens*. Only early inviability was found in this variety, but all of the material tested originated from a single plant.

The late-inviability allele occurred only in derivative lines from a cross of var. *flavescens* $\times$ var. *vulgare*, and presumably came from var. *vulgare*. That all of the lines tested were homozygous for this allele is attributable to the circumstance that they all originated from the same F₂ plant. Since the *flavescens* material used in making this cross was not itself tested in hybrids with *Ae. umbellulata*, there is a possibility that the *flavescens* parent rather than var. *vulgare* contributed the late-inviability gene.

A Modifier or Modifiers of Late Inviability

On the theory that the considerable variation observed in the expression of the late-inviability gene might be due to modifying factors, an effort was made to select for extreme late inviability of hybrids with *Ae. umbellulata*. Plant P39-78.1-16 from F₂ No. 1 was chosen, because the two inviable hybrids it yielded were the longest-lived of any in that particular F₂ test. Six F₃ plants were grown, of which five produced inviable hybrids (plus viable hybrids in two instances) with *Ae. umbellulata*. These were of only average late inviability.

Selections from F₂ No. 2, however, very strongly indicated the existence of a modifier or modifiers. Plant P40-78.3-19, whose three hybrids with *Ae. umbellulata* showed a wide range in time of death, and P40-78.3-22, which produced one medium late-dying and two very late-dying hybrids, were grown in F₃. Hybrids of F₃ plants with *Ae. umbellulata* were scored for size attained, as

indicated by the number of tillers formed. Results are shown in table 4. The mean numbers of tillers per plant, 0.90 ± 0.27 and 3.35 ± 0.39 , are different to a highly significant degree. No further study has been made of the extreme late-dying strain to determine the number of modifying factors involved or their possible reaction with the early-inviability gene.

The modifier (or modifiers) was probably derived from *T. aegilopoides* var. *pubescentinigrum*, one of the parents of the F_2 concerned. However, the other

TABLE 4
The final number of tillers produced by hybrids between *Ae. umbellulata* and the offspring of two plants selected from F_2 No. 2.

PARENT PLANT	NUMBER OF HYBRIDS WITH <i>Ae. umbellulata</i>	NO. WITH INDICATED NO. OF TILLERS							AVE. NO. TILLERS
		0	1	2	3	4	5	6	
P40-78.3-19	10	6	1	1	2				0.9
-19	1			1					2.0
-19	10	7		1	2				0.8
Total	21	13	1	3	4				0.90
P40-78.3-22	2						2		5.0
-22	8	1	1	2	1		2	1	3.0
-22	10	1			6	1	1	1	3.3
Total	20	2	1	2	7	1	5	2	3.35

parent, an untested F_4 plant from a *flavescens-vulgare* cross, may possibly have been the source of the modifier.

Mode of Action of the Inviability Factors

Two methods may be suggested by which a factor might cause inviability of a hybrid: (1) by failure to produce some substance essential to the proper development of the hybrid plant, or (2) by some positive action antagonistic to the foreign genome. Evidence is available which favors the former interpretation of the *Triticum monococcum*-*Aegilops umbellulata* inviability. The multiple hybrids (*T. monococcum* × *Ae. uniaristata* 4n) × *Ae. umbellulata* and (*T. aegilopoides* × *Ae. umbellulata* 4n) × (*T. monococcum* × *Ae. uniaristata* 4n) are viable, although each contains an inviability factor and an *Ae. umbellulata* genome. If inviability were due to antagonism between an inviability gene and the *umbellulata* genome, this antagonism might be expected to cause lethality regardless of what additional genomes were present.

The absence of an antagonistic action suggests, then, that death of the hybrid is due to a deficiency of some essential substance. It is not unreasonable to assume that this deficiency is based in turn on a chromatin deficiency.

Production of the somewhat more critical multiple hybrid *T. monococcum* $\times$ (*T. aegilopoides* $\times$ *Ae. umbellulata* 4n) was attempted extensively in both directions, but yielded only inviable seeds, such as commonly follow 2n-4n crosses in the Triticinae. In both the multiple hybrids obtained, the inviability factor involved was the one which produces late-dying hybrids with *Ae. umbellulata*.

HYBRIDS WITH *AEGILOPS BICORNIS*

When crossed with *Ae. bicornis*, certain varieties of einkorn produce inviable or poorly viable offspring. These are characterized by the premature death of

FIGURE 4. (a) The viable hybrid *Triticum monococcum* $\times$ *Aegilops bicornis* in comparison with (b) the semi-lethal hybrid *T. aegilopoides* $\times$ *Ae. bicornis*. $\times 0.13$.

leaves and by a general lack of vigor. Only two or three spikes are produced at best (fig. 4).

Hybrids of *Ae. bicornis* with *T. aegilopoides* vars. *baidaricum* and *pubescens-tinigrum* are of the inviable type, and hybrids with *T. monococcum* var. *flavescens* and the *flavescens-vulgare* derivatives are viable. This situation, being opposite to that observed for hybrids with *Ae. umbellulata*, makes it doubtful that the *umbellulata* inviability factor is concerned in the inviability of hybrids with *Ae. bicornis*. Proof that the factorial basis is different is the fact that F_3 plants from certain individuals in F_2 No. 2 produced viable hybrids with both *Aegilops* species and that others produced inviable hybrids with both. Furthermore, *T. monococcum* var. *Hornemanni*, which produced an inviable hybrid with *Ae. umbellulata*, gave inviable hybrids also with *Ae. bicornis*. *T.*

aegilopoides vars. *Pancici* and *Thaoudar* produced an approximately intermediate type of hybrid with *Ae. bicornis*.

The genetic data available suggest that inviability is due to a single factor. Two F_1 plants from the cross *T. aegilopoides* var. *pubescentinigrum* $\times$ *T. monococcum* var. *flavescens* were hybridized with *Ae. bicornis*, 53 seeds being obtained. Of the 37 of these which germinated, 20 were viable and 17 inviable. This is a close approach to a 1:1 ratio and deviates significantly from a 3:1 ratio. The inviable plants were quite similar to those obtained from *Ae. bicornis* $\times$ *T. aegilopoides*, with little variation among themselves.

TABLE 5

Crossability with Haynaldia villosa of plants from F₂ No. 2 (viable versus late-inviable) in relation to viability of hybrids between the same plants and Ae. umbellulata.

F ₂ PLANT	HYBRIDS WITH <i>Ae.</i> <i>umbellulata</i>	NO. SPIKES POLLINATED BY <i>H. villosa</i>	AVERAGE SEED SET PER SPIKE
P40-78.3- 4	Segregating	3	6.3
- 5	Segregating	4	0.0
-10	Segregating	2	0.0
-14	Segregating	3	3.3
-18	Segregating	3	4.0
-17	Segregating	3	0.0
- 9	Segregating	2	0.0
- 2	Segregating	3	13.7
- 6	Segregating	1	6.0
- 8	Viable	2	1.0
- 1	Viable	3	0.0
- 7	Viable	1	17.0
-19	Invisible	2	5.0
-22	Invisible	2	1.0
-13	Inv. or segr.	1	0.0

CROSSABILITY WITH HAYNALDIA VILLOSA

Whereas *T. aegilopoides* vars. *baidaricum* and *pubescentinigrum* produced viable hybrids with *Haynaldia villosa*, the *T. monococcum* *vulgare-flavescens* derivatives produced no seeds when pollinated by *H. villosa*. Furthermore, the *T. aegilopoides* derivatives, which produced viable hybrids with *Ae. umbellulata*, were crossable with *H. villosa*, although there was a possibility for them to have inherited non-crossability from *T. monococcum*, from which they were in part derived. These circumstances suggested that the same factor which caused inviability of hybrids with *Ae. umbellulata* might also prevent crossability with *H. villosa*, through being effective so early as to cause death of immature embryos and seeds.

To test this possibility, the plants in F_2 No. 2 were pollinated by *H. villosa*. Table 5 summarizes the results. The data show that the factor for inviability of hybrids with *Ae. umbellulata* is not responsible for non-crossability with *H. villosa*. Plants 19 and 22 were inviable with *Aegilops* and crossable with *Haynaldia*, while plant 1 did not cross with *H. villosa* and yet formed viable hybrids with *Ae. umbellulata*.

The fact that nine out of 15 F_2 plants were crossable with *H. villosa* suggests that a single factor for crossability may be operating. The approach to a 3:1 ratio is reasonably good and may actually be better than indicated, since more extensive trials of the six sterile combinations might have shown one or more to belong in the fertile group.

DISCUSSION

Genetic data are now available concerning several inviable interspecific and intergeneric hybrids. Only in *Gossypium*, however, has the inviable hybrid itself been subjected to analysis, and this hybrid cannot be considered a typical inviable F_1 , since the parents are quite closely related. In every other instance the data merely show that two strains or varieties of one species differ by a single factor in the viability of their hybrids with a second species. There is therefore no direct evidence as to how many genetic factors may actually be concerned in bringing about the inviability of the hybrids. Inviability could depend on several cumulative factors, perhaps deficiencies, from each parent species, all necessary to bring about inviability. Any variety lacking one of these factors would produce viable hybrids with the other species, and this factor would be the only one detectable unless other varieties of still different constitution were available. Some of the inviability factors would have to be compensated for in the parent species, in order that this species be viable. These compensating factors would need to be recessive, since they are inactive in the species hybrid.

The number of factors involved in interspecific inviability probably depends to a considerable extent upon the degree of differentiation of the species at the time when the factors appeared. If the factors arose more or less accidentally after the two species were established, as a result of these species becoming more and more diverse, then several or many factors are indicated, since the inheritance of other interspecific differences have proved to be complex (EAST 1935b, and others). If, on the other hand, the inviability factors arose before the two types became differentiated into species, and served as aids to isolation, then simple, complementary factors might be expected. Complementary inviability factors which could serve as varietal isolating mechanisms favoring speciation have been reported in *Gossypium* (HUTCHINSON 1932; SILOW 1941), *Hordeum* (WIEBE 1934), and *Triticum* (CALDWELL and COMPTON 1943).

If several factors or deficiencies are ordinarily responsible for hybrid inviability, it might be anticipated that differences of two or more factors might be found between varieties in the viability of their hybrids with another species. Such differences would tend to be rare, however, because the only varieties which can be analyzed are those which are closely enough related to yield fer-

tile, normally segregating hybrids with each other; and such closely related varieties usually differ in comparatively few factors.

SUMMARY

Two alleles have been identified in *Triticum monococcum* which act as dominant lethals in hybrids with *Aegilops umbellulata*, but which are without effect in *T. monococcum* itself. The alleles differ in the earliness with which they cause death. A third, normal allele is present in the closely related *T. aegilopoides*. Multiple hybrids combining the normal allele and one of the inviability factors with the *Ae. umbellulata* genome are viable.

Semi-lethality occurs in hybrids of *Ae. bicornis* with certain of the *Triticum* varieties, while hybrids with another variety are viable. This inviability is apparently monofactorially determined.

Non-crossability of *T. monococcum* with *Haynaldia villosa* appears also to be simply inherited.

The existence of a single-factor difference between two varieties with respect to viability of their hybrids with another species does not establish that only a single factor is involved in the interspecific inviability. There could be several factors from each species, all necessary for inviability of the hybrid, but only one revealed by the varietal difference.

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