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M. F. MILLER, *Director*

Amphidiploids in the Seven-Chromosome *Triticinae*

E. R. SEARS

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Field Crops Department, Missouri Agricultural Experiment Station,
and the Division of Cereal Crops and Diseases, Bureau of
Plant Industry, United States Department of
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INTRODUCTION

Although amphidiploidy has long been recognized as a factor in plant evolution, only through the recent discovery of convenient and reliable methods for inducing polyploidy have its many problems become subject to experimental attack. Theories regarding the origin of existing species as amphidiploids of other existing species can now be tested by synthesis of amphidiploids from the putative parents, as Beasley (1940) has done with cultivated cotton. Studies of such resynthesized species, supplemented by investigations of other amphidiploids, promise to add considerably to knowledge of the processes of evolution. Furthermore, among the multitude of amphidiploids now producible, some may be of agronomic or horticultural value.

Only comparatively few amphidiploids may be expected to have either practical or theoretical value. It is therefore important that criteria be developed, if possible, for predicting beforehand from studies of the prospective parent species, or of the undoubled hybrids, the characteristics of the amphidiploids.

The production and study of amphidiploids in the *Triticinae*† was undertaken as a possible means of contributing to the development of such criteria. By confining the study to amphidiploids resulting from various combinations of a few parent species, all of which had the basic chromosome number for the group, several of the variables were eliminated which presumably have accounted in part for the diversity of results reported for other amphidiploids.

Eighteen amphidiploids obtained from ten different species of the *Triticinae* with $n = 7$ have been subjected to morphological and

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*Research Associate, Field Crops Department, Missouri Agricultural Experiment Station, and Associate Geneticist in the Division of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture.

†A sub-tribal designation (Hutchinson, 1934) applying to the genera *Agropyron*, *Triticum*, *Aegilops*, *Secale*, and *Haynaldia*.

cytological study. The present paper deals primarily with the production of these amphidiploids and with their morphology in comparison with the parent species and the undoubled hybrids. In another publication (Sears, 1941) the cytology, fertility, and constancy of the same 18 amphidiploids are considered in relation to the cytological characteristics of the respective undoubled hybrids, with special emphasis on the problem of predicting the fertility of amphidiploids.

PRODUCTION OF AMPHIDIPLOIDS BY COLCHICINE TREATMENT

In the production of amphidiploids by use of colchicine, the high mortality which follows certain types of treatment is an important consideration, since the crosses are frequently so difficult to make that only a few hybrid seeds are available. Particularly with grasses, where treatments are ordinarily administered to seeds rather than to established plants, the survival has been too low (Sears, 1939; Myers, 1939) to encourage the risk of seeds from a difficult cross. Raw (1939) reduced the risk somewhat by propagating his plants vegetatively before treating them; but his treatments, which involved uprooting the plants and placing them in an aqueous solution of colchicine, killed much of his material. Kasparyan (1940) obtained a tetraploid spike of *Triticum monococcum* x *T. persicum* by treating the crowns of established plants with 0.2% colchicine in agar.

In the present study several methods of using colchicine have been tried. Two of these, involving treatment of very young seedlings and of potted plants, respectively, have been effective in inducing chromosome doubling, with comparatively low mortality.

Treatments of Germinating Seeds with Aqueous Solutions of Colchicine

In previous experiments (Sears, 1939) germinating seeds were immersed in 0.05% or 0.1% colchicine solution for 24 hours. Of 26 treated seeds of *Triticum monococcum* x *Aegilops uniaristata,* two survived, and one of these produced a partially tetraploid plant. Although survival was somewhat higher with certain other hybrids, the average mortality for 29 hybrids was 74%.

To test the possibility of lowering this high mortality rate while retaining the effectiveness of the treatment, 14 germinating seeds of *T. monococcum* x *Ae. uniaristata* were immersed for 24 hours in 0.02% colchicine. Of these, seven survived, but none showed tetraploid sectors. Treatments at this concentration for 48 hours resulted in the death of all of the 15 seeds used.

Somewhat more favorable results, though rather variable, have been obtained by placing germinating seeds on blotters soaked in colchicine solution, as suggested by Myers (1939). Table 1 summarizes the results of these treatments. Most of the hybrids showed low survival after 24 hours treatment with 0.05% colchicine solution. *Ae. umbellulata* x *T. aegilopoides,* which survived best (six seedlings out of eight), differed markedly from its reciprocal, of which all 12 individuals were killed. The data for 0.02% treatments suggest that such a concentration might increase the survival without lowering the incidence of tetraploidy; but the results just given for seeds immersed in 0.02% colchicine do not support this view.

TABLE 1.—RESULTS FROM TREATMENT OF GERMINATING SEEDS ON BLOTTERS SOAKED IN COLCHICINE SOLUTION.

Hybrid	Concentration of Colchicine, in Percentage	Hours Treated	No. Seedlings Treated	No. Seedlings Surviving	No. Plants with Tetraploid Sectors
Triticum monococcum x *Aegilops uniaristata*	.02	24	5	4	1
" " x " "	.02	49	5	1	1
" " x " "	.05	24	39	1	1
" " x " "	.05	36	7	1	0
" " x " "	.05	49	5	1	0
Ae. umbellulata x *T. aegilopoides*	.05	24	8	6	3
T. aegilopoides x *Ae. umbellulata*	.05	24	12	0	0
Ae. caudata x *Ae. umbellulata*	.05	24	23	6	5
Ae. speltoides x *Ae. uniaristata*	.05	24	14	1	1
27 other hybrids*	.05	24	294	10	0

*All within the seven-chromosome *Triticinae.*

Treatments of Seedlings with Mixtures of Colchicine and Lanolin

Low mortality and a relatively high incidence of tetraploidy have resulted from the application of mixtures of colchicine and lanolin to the base of the coleoptile of very young seedlings. In the winter of 1938-39, seedlings of *Triticum monococcum* x *Aegilops uniaristata* were used for such treatments. These seedlings, which were growing in Petri dishes, had developed coleoptiles 8-11 mm in length, from which no leaves had yet emerged. The colchicine-lanolin mixtures were prepared by putting powdered colchicine into melted anhydrous lanolin and stirring until cool. Mixtures containing colchicine in concentrations (by weight) of 0.5%, 1.0%, and 2.0%, respectively, were applied to three lots of 15 seedlings each, care being taken to keep the colchicine mixture from the roots. Twenty-four hours later the seedlings were transferred to soil, without removal of the mixture.

In contrast to the behavior of seedlings treated with aqueous solutions of colchicine, there was little difference between the growth of the treated hybrids and that of the controls. The first leaf of some treated plants was slightly roughened and irregular, but no abnormality was observed in subsequent growth.

Thirteen of the 15 seedlings survived the 2.0% treatment, and eight of these had tetraploid sectors. From the 1.0% and 0.5% treatments, 14 and 15 seedlings, respectively, survived, but only two plants at 1.0% and one at 0.5% had 4n sectors. Twenty-three control plants had no 4n sectors.

Tetraploid sectors usually included several entire spikes. Heads partially tetraploid were rarely observed.

From the number of tetraploid (fertile) and diploid (sterile) spikes, the approximate size of the 4n fraction of each plant was calculated (Table 2). There is some indication that the lanolin-colchicine treatments, which were made on seedlings about one day older than most of those treated with aqueous colchicine, resulted in smaller tetraploid sectors than did the aqueous treatments. The difference is of questionable significance, however, because of the small number of plants.

TABLE 2.—SIZE OF TETRAPLOID SECTOR IN PLANTS OF *Triticum monococcum* x *Aegilops uniaristata* TREATED AT DIFFERENT SEEDLING STAGES.

Length of Coleoptile When Treated	Type of Treatment	Approximate Fraction of Plant 4n
2-3 mm	Immersion .05%	.25
2-3 mm	Blotter .02%	.42
2-3 mm	Blotter .02%	.73
Average for 2-3 mm		.467
7-8 mm	Blotter .05%	.03
8-11 mm	Lanolin .5%	.29
8-11 mm	Lanolin 1.0%	.03
8-11 mm	Lanolin 1.0%	.06
8-11 mm	Lanolin 2.0%	.03
8-11 mm	Lanolin 2.0%	.06
8-11 mm	Lanolin 2.0%	.09
8-11 mm	Lanolin 2.0%	.14
8-11 mm	Lanolin 2.0%	.45
8-11 mm	Lanolin 2.0%	.45
8-11 mm	Lanolin 2.0%	.46
8-11 mm	Lanolin 2.0%	.61
Average for 7-11 mm		.225

In the winter of 1939-40, seedlings of five different hybrids (some involving species of *Triticinae* with $n = 14$) were treated with mixtures of colchicine in lanolin. With 1.0% colchicine 14 out of 15 seedlings survived, with 2.0% 14 out of 21, and with 4.0% none out of 19. Among the survivors of the 1.0% and 2.0% treatments, three and four plants, respectively, were partially tetraploid.

The superiority of seedling treatments made with colchicine in lanolin over those made with aqueous solutions is probably due to the decreased injury to the roots. Concentrations of colchicine high enough to induce tetraploidy in shoots are usually lethal to roots. For germinating seeds it is doubtful that simple aqueous treatments can be devised which will have a satisfactorily low lethality yet will be effective in inducing tetraploidy. Glotov (1939), however, increased the survival of colchicine-treated seedlings of camphor-yielding basil by subjecting them to heteroauxin treatment.

Where a dozen or more hybrid seeds are available, the treatment of seedlings with colchicine in lanolin can be considered an advantageous method of producing tetraploids. For smaller numbers of seeds, however, it is less satisfactory than the more laborious but more dependable potted-plant technique, which is next to be described.

Colchicine Treatments of Potted Plants

Potted plants of 20 different sterile hybrids in the seven-chromosome *Triticinae* have been subjected to colchicine treatments. In 18 of these, amphidiploid sectors have resulted.

The method of handling and treating the hybrids was as follows: Young plants were each divided into several parts, so as to increase the number of individuals available for treatment. When these separates were well established, but not yet beginning to "joint", the soil was cleared away from the base of the plants, and the crowns were packed with absorbent cotton (Fig. 1). The pots were then transferred to a chamber in which high relative humidity was maintained, and each morning and night the cotton was saturated with a 0.5% aqueous solution of colchicine. After from two to five days,

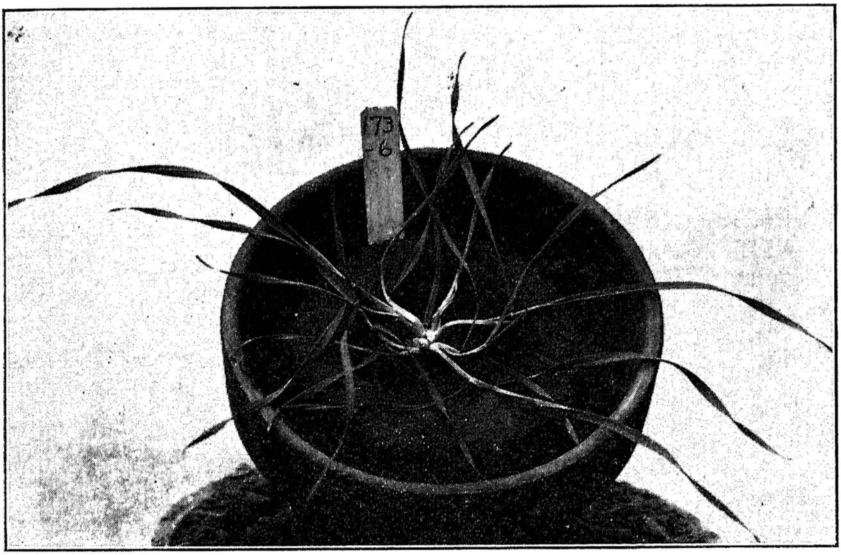

Fig. 1.—Hybrid plant prepared for colchicine treatment. The soil has been cleared away from the base of the plant, and the crown packed with absorbent cotton. The removal of soil next to the sides of the pot permits the plant to be watered without the cotton becoming wet.

the pots were brought back into the greenhouse, the cotton was removed, and the soil was replaced to its original level.

Sixty-five plants of 20 different hybrids were treated in this manner during the winter of 1938-39 (Table 3). Although the growth of most of these plants was retarded for a time by the treatment, only five died, and three of these were of the same hybrid, *Triticum aegilopoides* x *Haynaldia villosa.* (Of two plants of this hybrid given a similar treatment in 1939-40, both survived and became partially tetraploid.) Thirty-nine of the 60 surviving plants, representing 17 different hybrids, developed tetraploid sectors.

TABLE 3.—RESULTS OF TREATMENTS OF POTTED PLANTS IN 1938-39. THE THREE FIGURES IN EACH ENTRY REPRESENT, RESPECTIVELY, THE NUMBER OF PLANTS TREATED, THE NUMBER WHICH SURVIVED THE TREATMENT, AND THE NUMBER WITH 4n SECTORS.

Hybrid	Treatments with Aqueous Colchicine			Treatments with Colchicine in Lanolin
	42 Hours	88 Hours	114 Hours	
Triticum monococcum x *Aegilops comosa* ..	1-1-0	1-1-0	1-1-0	----
T. aegilopoides x *Ae. comosa*	----	1-1-0	1-1-0	----
**T. aegilopoides* x *Ae. squarrosa*	1-1-1	3-3-3	1-1-1	----
†*T. aegilopoides* x *Ae. umbellulata*	2-2-2	1-1-1	2-2-2	1-1-0
T. aegilopoides x *Ae. uniaristata*	1-1-0	1-0-0	1-1-1	----
**T. aegilopoides* x *Haynaldia villosa*	2-2-0	1-0-0	3-1-0	----
Ae. caudata x *Ae. speltoides*	2-2-0	1-1-1	2-2-1	2-2-1
Ae. caudata x *Ae. squarrosa*	----	1-1-1	1-1-1	----
Ae. caudata x *Ae. umbellulata*	1-1-1	----	1-1-1	1-1-0
Ae. caudata x *Ae. uniaristata*	----	1-1-1	1-1-1	----
Ae. comosa x *Ae. uniaristata*	----	1-1-0	1-1-1	----
Ae. sharonensis x *Ae. caudata*	1-1-1	----	1-1-1	----
Ae. sharonensis x *Ae. umbellulata*	1-1-1	1-1-1	1-1-1	----
Ae. sharonensis x *Ae. uniaristata*	2-2-0	1-1-1	2-2-2	1-1-0
Ae. speltoides x *T. monococcum*	1-1-0	1-1-1	2-1-1	1-1-1
Ae. speltoides x *Ae. sharonensis*	2-2-0	1-1-0	2-2-2	1-1-0
Ae. speltoides x *Ae. umbellulata*	----	----	1-1-1	----
Ae. speltoides x *Ae. uniaristata*	1-1-0	1-1-1	1-1-1	----
Ae. umbellulata x *Ae. uniaristata*	----	1-1-1	1-1-0	----
Ae. umbellulata x *H. villosa*	1-1-1	1-1-1	1-1-1	----

*Includes hybrids involving derivatives of *T. monococcum* x *T. aegilopoides.*
†Includes reciprocal hybrids.

Four plants (not included in the table) were treated for two days as described, but were not kept in the humid chamber. Of these, none produced tetraploid sectors.

The application of mixtures of colchicine and lanolin to the bared bases of the tillers was less effective than the use of aqueous solutions of colchicine. In 1938-39 seven plants from six different hybrids were treated with 5.0% colchicine-lanolin and were then kept for two days in the moist chamber. Only two of these developed tetraploid sectors, while 16 out of 26 plants from the same six hybrids treated with aqueous colchicine became partially tetraploid. In 1939-40, five out of 26 plants from seven different hybrids (mostly involving species with $n = 14$) showed chromosome doubling after colchicine-lanolin treatments, compared with 20 out of 32 after treatments with aqueous colchicine. (In the 1939-40 treatments with colchicine-lanolin, 4.0% colchicine was used instead of 5.0%, plants were not placed in the moist chamber, and four days instead of two elapsed before the soil was replaced about the base of the plants.)

Treatments with an aqueous solution of colchicine for four or five days were apparently more effective than two-day treatments. Of 19 plants of 14 different hybrids treated for 42 hours (1938-39 data), only seven had tetraploid sectors; while of 35 plants of the same 14 hybrids treated for 88 or 114 hours, 25 had tetraploid sectors. The difference in rate is on the border-line of statistical significance.

In contrast to the large sectors of tetraploid tissue which occurred in material treated in the seedling stage, the sectors here were predominantly small. Sometimes only one or two anthers were involved, although a few sectors included an entire spike. The most frequent type of effect involved two or three spikelets on the same side of the rachis, but numerous other sectors included spikelets on both sides of the rachis or parts of spikelets on both sides.

Nearly every plant had a number of fertile sectors. These sectors were larger in the later spikes. The number of seeds obtained per plant ranged from 0 to 69, fewer on the average than from plants treated as seedlings.

The treatment of potted plants with aqueous solutions of colchicine was more generally satisfactory than any of the other colchicine techniques tested. Because the plants were propagated vegetatively before treatment, this method greatly increased the chance of obtaining an amphidiploid when only a very few hybrid seeds were available. The tetraploid sectors were relatively small, but since the plants concerned were sterile hybrids, 4n sectors involving as little as a part of one anther were easily recognized by their fertility.

MORPHOLOGY OF AMPHIDIPLOIDS IN COMPARISON WITH PARENT SPECIES AND F_1 HYBRIDS

The possible value of amphidiploidy as a tool for plant breeding and genetic research depends to a considerable extent upon the development of criteria for predicting the characteristics of amphidiploids from studies of the proposed parent species. Without such criteria, amphidiploids needed for specific purposes must be produced largely on a trial-and-error basis.

The remainder of this paper will be concerned chiefly with the problem of predicting the morphological characteristics of amphidiploids. This problem may readily be divided into two parts, (1) predicting the characteristics of the hybrid between two species, and (2) predicting the effects of chromosome doubling on that hybrid. Considerable information bearing on the first part of the problem is already available, in the nature of data on the morphological characteristics of many hybrides and their parents, but additional information is needed before general rules can be established, particularly concerning hybrid vigor. As for the effects of chromosome doubling, the few available data are somewhat conflicting.

A study of a group of interrelated hybrids with the same low chromosome number, and comparisons of these hybrids with the parent species and the derived amphidiploids, might contribute substantially to the solution of the problem of predicting the morphological characteristics of amphidiploids. Accordingly, the 18 hybrids in the seven-chromosome *Triticinae* whose amphidiploid offspring had been carried at least one generation beyond the tetraploid sectors on the F_1 plants were compared in detail with the amphidiploids and with the parental species. The resulting information not only bears on the general problem concerned, but also constitutes, as it is presented, fairly adequate descriptions of the amphidiploids, many of which are essentially new species. Only three, *Aegilops speltoides* var. *ligustica* x *Ae. umbellulata* (Kihara, 1937; Sears, 1939), *Triticum monococcum* x *Ae. uniaristata* (Sears, 1939), and *Ae. caudata* x *Ae. umbellulata* (Sears, 1939) have been reported previously.

Parental Material

The seven-chromosome species of *Triticinae* used in this investigation belong to three genera, *Triticum, Haynaldia,* and *Aegilops.*

Two species of *Triticum* were used, *T. monococcum* L. and *T. aegilopoides* Forsk. Some investigators have considered these two types as members of a single species, but Percival (1921) and others believe their differences are great enough to justify specific rank. They are closely related cytologically (L. Smith, 1936). Morphologically they differ by a complex of characters, including fragility of spike, pubescence of rachis, and size of seed. They also differ physiologically in crossability with other genera and in viability of certain intergeneric hybrids (Sears, 1940 and unpublished).

Material from both species was provided by Dr. Luther Smith of this laboratory. The variety of *T. aegilopoides* used was *baidaricum* Flaksb., while the *T. monococcum* material was a derivative line obtained from a cross of var. *flavescens* Körn. x var. *vulgare* Körn. In addition, some use was made of derivative lines from crosses of *T. monococcum* x *T. aegilopoides.*

Haynaldia villosa (L.) Schur was obtained from Mr. W. J. Sando, Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, Washington, D. C.

Seven species of *Aegilops* were used. Concerning the classification of five of these, *Ae. caudata* L. var. *polyathera* Boiss., *Ae. sharonensis* Eig var. *typica* Eig, *Ae. squarrosa* L. ssp. *eusquarrosa* Eig var. *typica* Eig. *Ae. umbellulata* Zhuk., and *Ae. uniaristata* Vis., there is no difference of opinion among recent monographers of the genus (notably Zhukovsky, 1928; and Eig, 1929). The other two species, *Ae. comosa* Sibth. and Smith and *Ae. speltoides* Tausch, have been treated differently by various investigators.

Ae. comosa Sibth. and Sm. ssp. *Heldreichii* (Boiss.) Eig var. *subventricosa* Boiss. is given specific rank by Zhukovsky as *Ae. Heldreichii* Holzm. (error for (Boiss.) Nyman). Kihara (1937), however, points out that the *Ae. comosa* and *Ae. Heldreichii* of Zhukovsky differ cytologically by only a reciprocal translocation, and that hybrids between the two types are fully fertile. Since the morphological differences are variable and relatively small, it seems best to consider with Eig (1929) that *Heldreichii* is a sub-species of *Ae. comosa.*

The remaining species, *Ae. speltoides* Tausch, has two varieties, *ligustica* (Savign.) Fiori and *Aucheri* (Boiss.) Bornm., according to Eig's early writings (1927). In his 1929 monograph, however, Eig gives vars. *ligustica* and *Aucheri* specific rank as *Ae. ligustica* (Savign.) Coss. and *Ae. speltoides* Tausch, respectively. Zhukovsky (1928) applies *Ae. speltoides* Tausch to the *ligustica* type, and designates the other variety *Ae. Aucheri* Boiss. Although Zhukovsky thereby conforms to the practice of most previous monographers, this classification is based, as Eig (1929) points out, on a misinterpretation of Tausch's (1837) original description of *Ae. speltoides.* Undoubtedly Tausch was describing the *Aucheri* type.

Ae. speltoides var. *Aucheri* differs from var. *ligustica* in that the former is awnless except for the apical spikelet, is fragile at the base of the spike only instead of at every node, and has fewer spikelets and longer rachis segments. The two types are found growing side by side in the same geographic range, however, and in spite of the striking morphological differences between them have frequently been placed by taxonomists in the same species. Recent evidence (Miczynski, 1927; Schiemann, 1928; Eig, 1929; Kihara and Lilienfeld, 1932) that genetically only a single, Mendelian factor is concerned (var. *Aucheri* being the recessive type) strengthens the argument against the varieties being elevated to specific rank. (Intermediate types recently obtained at this laboratory suggest that two or more closely linked genes are involved.) Furthermore, cytological observations on the varietal hybrid give no indication of other than complete homology of chromosomes.

Aegilops caudata, Ae. comosa, Ae. sharonensis, Ae. speltoides var. *ligustica* (strain II), *Ae. umbellulata,* and *Ae. uniaristata* were obtained from Dr. Elizabeth Schiemann of the Institut für Vererbungsforschung der Landwirtschaftliche Hochschule, Berlin-Dahlem, Germany. *Ae. speltoides* var. *ligustica* (strain I) and *Ae. speltoides* var. *Aucheri* were obtained from K. A. Flaksberger, Leningrad, U. S. S. R.

In the present investigation the variety *Aucheri* of *Ae. speltoides* was used hardly at all. Where the varietal name is omitted, therefore, var. *ligustica* is referred to unless otherwise stated. No distinction will ordinarily be made between the two strains of var. *ligustica.*

Comparison of Amphidiploids with Undoubled Hybrids

In no hybrid was there an apparent morphological difference between the diploid and tetraploid parts of the same plant—either in the length of tillers, in the size, texture or color of leaves, or in the size or morphology of spikes. As far as material was available for comparison, amphidiploid plants produced from seed on the tetraploid sectors seemed not to differ from the sectors themselves.

The photographs in Figures 2 to 19 show both diploid and tetraploid spikes from the 18 hybrids under consideration. Except for Figures 3, 6, and 16, the 4n spikes are from second-generation, wholly amphidiploid plants. In several of the photographs, the 2n and 4n spikes are not comparable as to size, since only later, less vigorous spikes remained on certain F_1 plants when the photographs were made. Direct comparisons of 4n spikes with herbarium specimens of vigorous 2n spikes showed no appreciable differences which could not be accounted for by the presence of seeds in the amphidiploid spikes.

All tetraploid sectors on the F_1 plants were identified solely by fertility of the florets, particularly the anthers. Diploid anthers on all but one of the hybrids contained less than five per cent good pollen and did not dehisce. *Ae. speltoides* x *Ae. sharonensis* had about 12% non-aborted pollen on the diploid, enough to cause occasional anthers to open; but 4n anthers had over 90% non-aborted pollen and were easily identifiable.

In agreement with previous observations (Sears, 1939), no difference in size or spacing of stomata could be found between 2n and 4n *T. monococcum* x *Ae. uniaristata.* One sectorial plant had an average frequency per unit area of 18.5 stomata (2n) and 21.4 stomata (4n), while another had 27.7 (2n) and 26.8 (4n). In *T. aegilopoides* x *Ae. umbellulata,* the average frequency of stomata per unit leaf area was higher in the 2n leaves, but some 4n leaves did not differ significantly from comparable 2n leaves. In two other hybrids, *Ae. caudata* x *Ae. umbellulata* and *Ae. speltoides* x *Ae. umbellulata,* stomata were larger and wider spaced in 4n leaves.

The fact that periclinal chimeras of diploid and polyploid tissues have been found following colchicine treatment in *Datura* by Satina, Blakeslee and Avery (1940), in peaches by Dermen (1941), and in cranberries by Dermen and Bain (1941) suggests that the supposed 4n epidermis of *T. monococcum* x *Ae. uniaristata* was actually 2n (or vice versa), thus explaining the apparent correspondence of 2n and 4n stomatal size in this hybrid. Unless periclinals occur in considerable frequency, however, this explanation is scarcely plausible. Measurements of stomata were made from two different plants, each with a fertile sector involving about one-half the plant. Two leaves from the fertile sector and two from the sterile portion of one plant were examined, and one from each portion of the other plant.

Comparison of Amphidiploids with Parent Species

Since there were no noticeable differences in morphology or vigor between the diploid hybrids and their amphidiploid derivatives, a comparison of the amphidiploids with their parent species not only showed how various specific and generic characters behaved in crosses, but also revealed the extent to which hybrid vigor occurred.

As far as practicable, the comparisons were made by means of actual measurements, and these data are presented under the heading "Quantitative Data." Information concerning characters difficult or (less often) impossible of exact measurement is given under "Qualitative Data."

QUANTITATIVE DATA

The quantitative data (Table 4) were obtained from two or more plants, where this was possible. As a rule the first two tillers to appear on a plant were measured for culm length at maturity, and the spikes from these culms, frequently supplemented by spikes from additional vigorous tillers, were used for the remaining determinations and measurements. For the determination of average culm length (from soil level to base of spike), at least two plants were used, except with *Triticum aegilopoides, Aegilops caudata, Haynaldia villosa, Ae. speltoides* x *Ae. umbellulata,* and *Ae. umbellulata* x *H.*

TABLE 4.—QUANTITATIVE DATA FROM AMPHIDIPLOIDS IN THE SEVEN-CHROMOSOME *Triticinae* AND FROM THEIR PARENT SPECIES.

Species or Amphidiploid	Days to Pollen Shedding	Average Culm. Length in Inches	Av. Length of Rachis Segments, mm	Total No. Spikelets per Spike		No. Rudimentary Spikelets at Base of Spike	Maximum No. Fertile Florets per Spikelet	Seed Size	
				Range	Av.			Av. Length in mm	Av. Width in mm
Triticum aegilopoides	141	25.5	3.55	19-29	20.3	0-4	2	6.8	1.48
T. monococcum	± 75	30.0	2.3	20-32	24.0	0-3	2	7.55	1.70
Aegilops caudata	170	16.0	12.4	8-9	8.3	2-3	3	7.6	1.65
Ae. comosa	±210	---	9.1	4-5	4.2	1	3	5.1	2.16
Ae. sharonensis	119	23.5	8.5	11-12	11.7	0	3	6.9	1.90
Ae. speltoides	141	29.1	5.75	20-21	20.5	0	3	4.95	1.57
Ae. squarrosa	146	10.8	8.3	11-15	12.7	0-2	3	5.1	2.18
Ae. umbellulata	±175	11.9	6.8	7-9	7.7	3-4	3	5.2	1.74
Ae. uniaristata	220	12.8	7.35	6-8	7.1	2-3	3	4.7	2.14
Haynaldia villosa	141	28.0	2.05	31-32	31.5	0	3	4.4	1.05
T. aegilopoides x *Ae. squarrosa*	121	23.5	8.4	16-18	16.8	0-1	2	7.4	2.16
T. aegilopoides x *Ae. umbellulata*	136	17.0	7.25	10-13	11.3	2-3	2	6.7	1.77
T. aegilopoides x *Ae. uniaristata*	132	20.9	7.7	11-14	13.3	1-3	3	7.9	1.95
T. monococcum x *Ae. uniaristata*	114	20.0	6.2	11-14	12.5	3-4	3	7.45	2.13
Ae. caudata x *Ae. speltoides*	154	19.4	10.0	11-14	12.5	1-2	3	7.95	1.82
Ae. caudata x *Ae. squarrosa*	143	12.2	12.65	8-11	8.8	0-3	3	8.5	2.33
Ae. caudata x *Ae. umbellulata*	158	14.0	11.3	8-10	8.8	2-3	3	8.4	2.33
Ae. caudata x *Ae. uniaristata*	159	16.2	11.8	7-9	7.8	2-3	3	8.35	2.66
Ae. comosa x *Ae. uniaristata*	231	13.2	10.05	4-6	5.2	2	3	6.9	2.93
Ae. sharonensis x *Ae. caudata*	129	18.5	12.3	10-11	10.7	2-3	3	9.6	2.24
Ae. sharonensis x *Ae. umbellulata*	105	16.4	9.6	10-11	10.3	3-4	3	7.9	2.58
Ae. sharonensis x *Ae. uniaristata*	114	20.1	9.6	9-10	9.6	3-4	3	8.6	2.76
Ae. speltoides x *T. monococcum*	223	18.0	4.8	24-31	27.0	0-1	3	6.75	1.75
Ae. speltoides x *Ae. sharonensis*	132	23.8	8.7	13-14	13.7	0	3	7.6	2.26
Ae. speltoides x *Ae. umbellulata*	144	15.5	9.0	10-12	11.7	2	4	6.8	2.25
Ae. speltoides x *Ae. uniaristata*	131	23.7	8.5	9-13	11.3	1	4	7.2	2.33
Ae. umbellulata x *Ae. uniaristata*	229	15.0	7.55	7-8	7.7	2-3	3	6.3	2.66
Ae. umbellulata x *H. villosa*	205	21.5	5.85	16-17	16.5	2-3	--	--	---

villosa, the average being 2.6 plants per species or amphidiploid. For the other determinations (except days to pollen shedding) spikes from more than one plant were used except with *Ae. comosa, Ae. speltoides, Ae. speltoides* x *Ae. umbellulata,* and *Ae. umbellulata* x *H. villosa,* the average being 2.9 plants and 7.6 spikes. No amphidiploid plants were used which had other than 14 pairs of chromosomes.

For *Ae. caudata* x *Ae. speltoides,* amphidiploids from two different sources were used. The data for days to pollen shedding, culm length, and seed size were obtained from a line whose *speltoides* parent was apparently var. *Aucheri* (or a type between *Aucheri* and *ligustica*) rather than var. *ligustica. Aucheri* differs little from *ligustica* in these respects, however.

DAYS TO POLLEN SHEDDING

Days to shedding, as given in table 4, represents the number of days between planting of the seed and first opening of anthers. Plants of the various species were started September 27, 1939 (except *Ae. uniaristata,* planted September 21), and the amphidiploids September 23. The plants were all grown in the same greenhouse in as nearly the same location as possible. Since most of the families were quite uniform in date of shedding, the date used was that recorded for the earliest plant in each family. In another season actual dates might have been considerably different, but it is unlikely that the order of flowering would have been changed materially. Data from other years are available for the parental species listed, and they regularly show the same order of flowering. Those entries in the table preceded by the sign "±" were calculated from data obtained in previous years, no directly comparable material being available in 1939-40.

Somewhat arbitrarily, a difference of nine days in shedding date was selected at the minimum for significance. Smaller differences may well be significant, also, particularly where amphidiploids were a few days earlier than the parent species, for it is doubtful that the earlier planting of the amphidiploids made a corresponding difference in date of maturity. The photoperiod was evidently the controlling factor for flowering in most of the plants.

Six of the 18 amphidiploids were nine days or more earlier than either parent. *Triticum aegilopoides* x *Aegilops squarrosa* showed the greatest increase over the earlier parent (20 days). The other five amphidiploids, with their respective increases, were: *Ae. caudata* x *Ae. umbellulata* (12 days), *Ae. caudata* x *Ae. uniaristata* (11), *T. aegilopoides* x *Ae. uniaristata* (9), *Ae. sharonensis* x *Ae. umbellulata* (14), and *Ae. speltoides* x *Ae. uniaristata* (10). The early maturity of the last four amphidiploids is the more remarkable since each had one relatively very late parent.

Of the remaining 12 amphidiploids, four matured at approximately the same time as the early parent. These were *T. aegilopoides* x *Ae. umbellulata, Ae. caudata* x *Ae. squarrosa, Ae. sharonensis* x *Ae. uniaristata,* and *Ae. speltoides* x *Ae. umbellulata.* Two others, *T. monococcum* x *Ae. uniaristata* and *Ae. sharonensis* x *Ae. caudata,* were somewhat later than the early parent, but were much nearer to it than to the late parent. Two amphidiploids, *Ae. caudata* x *Ae. speltoides* and *Ae. speltoides* x *Ae. sharonensis,* were approximately intermediate.

The remaining four amphidiploids were later than either parent. Two of these (*Ae. comosa* x *Ae. uniaristata* and *Ae. umbellulata* x *Ae. uniaristata*) were hybrids involving types similar to each other in growth habit as well as in date of maturity. Their lateness, if genuine (only 11 and 9 days, respectively, different from late parents), may perhaps be explained as related to hybrid vigor, since each showed some coarseness of plant parts, particularly in the spike. The other two amphidiploids were intergeneric crosses, both much later than either parent. *A. umbellulata* x *H. villosa,* which was 30 days later than the late parent, was abnormally low in chromosome pairing and fertility (see Sears, 1941). Its lateness may perhaps be attributed to a physiological upset arising from the incompatibility of the parental genoms. However, the plants were of good vigor. *Ae. speltoides* x *T. monococcum,* the remaining amphidiploid, was 82 days later than the late parent. Although its culms were of reduced length and it was the only amphidiploid whose seeds were not larger than those of both parents, it was reasonably fertile, and fairly regular in chromosome pairing. A general coarseness of its culms and spikes suggests that some hybrid vigor was present.

LENGTH OF CULM

In length of culm, which is frequently used as a measure of hybrid vigor, only one amphidiploid, *Aegilops umbellulata* x *Ae. uniaristata,* exceeded both parent species, and one, *Ae. speltoides* x *Triticum monococcum,* fell below both parents. Two others, *T. aegilopoides* x *Ae. squarrosa* and *Ae. speltoides* x *Ae. uniaristata,* exceeded the parental average significantly, while *Ae. speltoides* x *Ae. umbellulata* was significantly below the average. Of the remaining 12 amphidiploids studied, one equalled the parental average, four exceeded it, and seven fell below it, none of the deviations being significant, however, with the few data available.

LENGTH OF RACHIS SEGMENTS

Every amphidiploid exceeded the average of its parent species in length of rachis segments. Five out of 18 significantly exceeded both parents (*Ae. comosa* x *Ae. uniaristata, Ae. sharonensis* x *Ae. umbellulata, Ae. sharonensis* x *Ae. uniaristata, Ae. speltoides* x *Ae. umbellulata, Ae. speltoides* x *Ae. uniaristata*). Intergeneric amphidiploids tended to show greater increases over parental averages than did interspecific amphidiploids (although none exceeded the longer parent significantly). This may have been due to the greater differences in length which existed between the parents of the intergeneric crosses, coupled with partial dominance of longer segments.

In determination of average length of rachis segments, segments adjacent to rudimentary spikelets were not measured, since they are of reduced length. Neither was the short segment above the first fertile spikelet of such types as *Ae. umbellulata* included.

NUMBER OF SPIKELETS

For the total number of spikelets, both average and range are given, while for the number of rudimentary spikelets, only range is given. Where one number of rudimentary spikelets was found in a large majority of the spikes, that number is in bold-faced type in Table 4. In some species and amphidiploids, the rudimentary spikelets were not sharply delimited from the normal, fertile spikelets, but showed a gradual transition into them. This was particularly true of the two species of *Triticum*.

No amphidiploid averaged lower than both parents in total number of spikelets. Only one, *Aegilops speltoides* x *Triticum monococcum,* exceeded both parents, and the difference there was not significant, since small numbers of spikes were studied (2 of *Ae. speltoides,* 6 of *T. monococcum*, and 9 of the amphidiploid) and the average of the amphidiploid fell within the range of *T. monococcum*. Of the remaining 17 amphidiploids, nine had within ten per cent of the average number of spikelets of the parents. The other eight (*T. aegilopoides* x *Ae. umbellulata, T. monococcum* x *Ae. uniaristata, Ae. caudata* x *Ae. speltoides, Ae. caudata* x *Ae. umbellulata, Ae. speltoides* x *Ae. sharonensis, Ae. speltoides* x *Ae. umbellulata, Ae. speltoides* x *Ae. uniaristata, Ae. umbellulata* x *H. villosa*) had 15 to 20 per cent fewer spikelets than the average of the parent species.

The number of rudimentary spikelets at the base of the spike was intermediate in most of the amphidiploids. A few amphidiploids, however, tended to resemble the parent with more rudimentaries, including three (*T. monococcum* x *Ae. uniaristata, Ae. sharonensis* x

Ae. umbellulata, Ae. sharonensis x *Ae. uniaristata*) which apparently exceeded both parents slightly.

NUMBER OF FERTILE FLORETS PER SPIKELET

Except the two species of *Triticum* which had two fertile florets per spikelet, all the parent species had three fertile florets. Of the five amphidiploids involving *Triticum* species, three had three fertile florets, and two had two fertile florets.

In two amphidiploids, *Aegilops speltoides* x *Ae. umbellulata* and *Ae. speltoides* x *Ae. uniaristata,* rare seeds were found in the fourth floret, whereas this floret was not fertile in the parents. Since total fertility was lower in these amphidiploids than in the parents, it is possible that the occasional fertility of the fourth florets was a compensatory response to the considerable sterility of the other florets.

SIZE OF SEED

In size of seed, calculated as the product of length by breadth, every amphidiploid exceeded the average of its parent species, and all but one, *Aegilops speltoides* x *Triticum monococcum,* exceeded both parents. Twelve of the 17 amphidiploids with available seed exceeded both parents in both length and breadth. In most cases the increase over the parental average, which ranged from 15% increase for *Ae. speltoides* x *T. monococcum* to 105% for *Ae. sharonensis* x *Ae uniaristata,* would be still greater if the comparisons had been based on volume or weight; for there was no apparent tendency for seeds of any amphidiploid to be relatively shallow.

The intergeneric crosses showed less increase over parental averages than did the interspecific amphidiploids. With one exception, *Ae. caudata* x *Ae. speltoides,* every one of the 12 interspecific amphidiploids had more increase than did any of the five intergeneric amphidiploids. Since increased seed size is a common characteristic of autotetraploids, it is probable that some of the increase here may be due to polyploidy rather than to hybrid vigor.

QUALITATIVE DATA

The following comparisons of the amphidiploids with their parent species involve primarily the characters used by taxonomists in separating the species and genera concerned. In addition, pubescence and coloration, which are of relatively minor importance taxonomically, are considered.

As far as possible, the data are presented in tabular form (Table 5).

TABLE 5.—QUALITATIVE DATA FROM AMPHIDIPLOIDS IN THE SEVEN-CHROMOSOME *Triticinae* AND FROM THEIR PARENT SPECIES.

Species or Amphidiploid	Adherence of Glumes	Fragility of Rachis			Black Color in Spike	Pubescence			Split Palea
		At Every Node		At Base of Spike					
		Above Junct. of Spklt. with Rachis (Type I)	Below Junct. of Spklt. with Rachis (Type II)	(Type Ia)		Rachis	Glumes	Stem Nodes	
Triticum aegilopoides	−	+			+	+	−	+	+
T. monococcum	−	±			−	−	−	+	+
Aegilops caudata	+			+	+	+	+	−	−
Ae. comosa	±			+	−	+	+	−	−
Ae. sharonensis	+	+			−	−	−	−	−
Ae. speltoides	+	+			−	+	+	−	−
Ae. squarrosa	+		+		−	+	+	−	−
Ae. umbellulata	−			+	+	−	+	−	−
Ae. uniaristata	±			+	−	+	+	−	−
Haynaldia villosa	−	+			−	+	+	−	−
T. aegilopoides x *Ae. squarrosa*	−	(−)	(−)		+	+	+	−	−
T. aegilopoides x *Ae. umbellulata*	−	(−)		±	+	+	+	+	−
T. aegilopoides x *Ae. uniaristata*	−	(−)		+	+	+	+	+	−
T. monococcum x *Ae. uniaristata*	−	±		+	−	+	+	+	−
Ae. caudata x *Ae. speltoides*	+	(−)		+	+	+	+	−	−
Ae. caudata x *Ae. squarrosa*	+	(−)	(−)	+	+	+	+	−	−
Ae. caudata x *Ae. umbellulata*	±			+	+	+	+	−	−
Ae. caudata x *Ae. uniaristata*	+			+	+	+	+	−	−
Ae. comosa x *Ae. uniaristata*	±			+	−	+	+	−	−
Ae. sharonensis x *Ae. caudata*	+	±		±	−	+	+	−	−
Ae. sharonensis x *Ae. umbellulata*	±	+		+	+	−	+	−	−
Ae. sharonensis x *Ae. uniaristata*	+	+		+	−	+	+	−	−
Ae. speltoides x *T. monococcum*	±	+			+	+	+	+	−
Ae. speltoides x *Ae. sharonensis*	+	+			−	+	+	−	−
Ae. speltoides x *Ae. umbellulata*	±	(−)		±	+	+	+	−	−
Ae. speltoides x *Ae. uniaristata*	+	(−)		±	−	+	+	−	−
Ae. umbellulata x *Ae. uniaristata*	−			+	+	+	+	−	−
Ae. umbellulata x *H. villosa*	−	(−)		±	+	+	+	−	−

TABULAR DATA

Adherence of Glumes

In Table 5 complete freedom of seeds is indicated by the sign "—". The sign "±" means that some seeds are free and some are adherent, while "+" shows that all normal seeds in primary or secondary florets are adherent. (Shriveled seeds and seeds in tertiary florets may be free.)

Non-adherence of glumes in *Ae. umbellulata* and *Triticum* was dominant to the adherent condition of *Ae. squarrosa,* but was partially recessive to the adherence of *Ae. caudata, Ae. sharonensis,* and *Ae. speltoides.* The intermediate adherence of *Ae. uniaristata* was recessive to both adherence and non-adherence in other species.

Fragility of Rachis

There are three types of fragility among the species of *Triticinae* used. In the first of these, which may be spoken of as type I, the fracture occurs above the junction of the spikelet with the rachis, and the rachis segment then forms a continuation of the lower end of the spikelet. In type II the fracture occurs below the junction of spikelet and rachis, leaving the rachis segment appressed to the back of the spikelet. In type Ia the fracture takes place above the junction of spikelet and rachis as in type I, but it occurs only at the base of the spike, below the first fertile spikelet. Types I and II tend to be progressively less fragile from the tip to the base of the spike, but are still fairly fragile at the base (although in table 5, to avoid confusion, no entry is made for them in the "at base of spike" column).

In the table the sign "+" signifies fragility such that mature spikes are inclined to break of their own weight; "±" indicates that tension is necessary for fracture; and "(—)" means that breakage occurs only with difficult.

Hybrids involving different species with the same type of fragility (either I or Ia) were always like the parents in fragility, even in the one intergeneric cross, *Ae. speltoides* x *T. monococcum* (type I). This evident correspondence of factors for fragility is not surprising, since *Ae. speltoides* is closely related to the *Triticums,* and since all the type Ia species used were species of *Aegilops* closely related to each other.

Only one amphidiploid involved parents of types I and II fragility, *T. aegilopoides* x *Ae. squarrosa.* This amphidiploid tended to be non-fragile, although spikes were slightly fragile both above and below the junction of spikelet with rachis.

Hybrids between types I and Ia were usually intermediate in fragility, although to an extent varying with the particular parent. Crosses involving *T. aegilopoides, Ae. speltoides,* or *H. villosa* and various *Aegilops* species of type Ia were all slightly fragile within the spike and fully fragile or nearly so at the base. Similar hybrids involving *Ae. sharonensis* or *T. monococcum* (which is less fragile than any of the other type I species) were appreciably more fragile within the spike. In fact, *Ae. sharonensis* x *Ae. umbellulata* and *Ae. sharonensis* x *Ae. uniaristata* usually broke between the first and second fertile spikelets.

Only one hybrid, *Ae. caudata* x *Ae. squarrosa,* involved parents of types Ia and II. Spikes of this amphidiploid normally fracture at the base, but some fragility of both type I and type II exists within the spike (Table 5). The basal fracture takes place above the junction of spikelet and rachis, and this sort of fragility (type I) occurs also to a small extent within the fertile portion of some spikes. It affects only the lowest two or three spikelets, however, and these progressively less going up the spike. The tendency toward fragility below the junction of spikelet and rachis (type II) is approximately the same at all the nodes of the spike. In its fragility behavior, therefore, this amphidiploid may be considered as intermediate to its parents: Both type I and type II fragility are present but are of reduced intensity, and the tendency which occurs in *Ae. caudata* toward basal localization of the fracture is also present but modified. As might be expected, this tendency toward localization introduced by the type Ia parent affects only type I fragility and not type II.

Kihara (1940) reported that F_1 spikes of *Ae. caudata* x *Ae. squarrosa* were practically non-fragile. Perhaps the infertility of his F_1 material was responsible for the difference from the present results, or perhaps this hybrid was one of those which he harvested prematurely. One other hybrid which is listed by Kihara as practically non-fragile, *Ae. speltoides* x *Ae. caudata,* has proved in the present study (in the reciprocal combination) to show fragility at the base of the spike, as well as slight fragility of type I within the spike.

There is little support in this study for Kihara's (1940) observation that *Ae. caudata* shows less dominance of fragility type in crosses than do other *Aegilops* species with type Ia fragility. Hybrids of *Ae. sharonensis* with *Ae. caudata* were slightly less fragile at the base than were crosses of *Ae. sharonensis* with *Ae. umbellulata* or *Ae. uniaristata,* but were also less fragile in the fertile portion of the spike. Hybrids of *Ae. speltoides* with *Ae. caudata, Ae. umbellulata* and *Ae. uniaristata* were all quite similar in fragility.

Black Color in Spike

The presence of black color in the spike is not constant for any one species, and is therefore of little value for description of species and genera. Several other factors detract from its usefulness. It varies considerably with environmental conditions. It is complicated by differences in the fundamental color of the spike upon which the black is superimposed. It is distributed differently in different species; for example, in *Triticum aegilopoides* and *Aegilops umbellulata* black color may affect the awns only or may spread down onto the glumes in streaks or spots, while in *Ae. caudata,* spikes are uniformly pigmented but may vary among themselves in intensity of the pigment.

Almost every amphidiploid involving a parent species with black color was also pigmented, although sometimes to a reduced degree. The only exception was *Ae. sharonensis* x *Ae. caudata,* which had non-pigmented spikes in spite of the coloration of *Ae. caudata. Ae. speltoides* x *T. monococcum* was pigmented although neither parent has black color. *Ae. speltoides,* however, does tend under certain conditions to become somewhat darker than the typically non-pigmented species, such as *Ae. sharonensis* or *Ae. uniaristata.*

Pubescence

As it occurs on stem nodes, pubescence is a characteristic which helps to distinguish the genus *Triticum* from *Aegilops* and *Haynaldia.* On glumes and rachis, it is of little importance taxonomically, pubescent and non-pubescent types frequently existing within the same species. In Table 5 the pubescent condition is indicated by "+" and non-pubescence by "—". No effort was made to distinguish between degrees of pubescence, although differences in degree were rather large in the material.

With one exception, *T. aegilopoides* x *Ae. squarrosa,* hybrids involving *Triticum* as one parent had pubescent nodes. Two other hybrids, however, *T. aegilopoides* x *Ae. umbellulata* and *Ae. speltoides* x *T. monococcum,* had much reduced pubescence.

Pubescence of rachis and glumes was found in every amphidiploid where one or the other parent was pubescent, although frequently somewhat reduced in extent or in length of individual hairs.

Split Palea

A tendency for the palea to be split at maturity of the seed is characteristic of species of *Triticum.* As is evident in Table 5, this tendency was completely lacking in hybrids of *Triticum* with species of *Aegilops.*

ADDITIONAL DESCRIPTIVE DATA

Some details about the amphidiploids and their parent species which could not be presented in tabular form are given below. Data on size and shape of spike are omitted, since this information can be obtained from the photographs.

Description of Parent Species

Triticum aegilopoides and *T. monococcum* (Figs. 2 and 5).—These species differ from all species of *Aegilops* in the possession of a strong keel on the outer or "empty" glume plus a well-defined secondary keel. In both species the apical spikelet is rarely fertile, and is frequently rudimentary. The empty glume is characterized by the presence of a short tooth as a continuation of the primary keel and a shorter tooth on the secondary keel. The lemma, or outer flowering glume, has a central awn flanked on each side by a short tooth.

Aegilops caudata (Fig. 6).—Empty glumes of lateral spikelets are long, narrow, non-keeled, and bidentate, with one tooth stretching out into an awn or awn-like projection. Apical empty glumes taper into a single, long, strong awn. Lemmas of lateral spikelets are papery and flexible, are slightly longer than the empty glumes, and have three short beaks, of which the central is strongest. The lemma of the first floret of the apical spikelet is similar, but that of the second floret is rounded, without teeth.

Ae. comosa (Fig. 10).—Empty glumes of the lateral spikelets are broad, non-keeled, and somewhat inflated at the tip, with two divergent, broad-based teeth, one of which is usually broader than the other and is sometimes stretched out into a short awn. The two empty glumes of the apical spikelet differ, one dividing into three awns (central strongest) and one being single-awned. Lateral lemmas have two or three very short beaks, while apical lemmas have a long tooth or short awn flanked by two short teeth.

Ae. sharonensis (Fig. 11).—Lateral empty glumes are keeled and have a horizontal upper margin, with a tooth or short awn on one corner, and a strong shoulder or short tooth on the other. The apical empty glume has a central short tooth, plus a shoulder or very short tooth on each side. Lemmas are tough and hard, with a central awn and two short teeth.

Ae. speltoides (Fig. 6).—Lateral empty glumes, which are short and trapezoid and keeled, have a small tooth near one corner of a horizontal, thickened margin. The apical empty glumes are rounded, with no teeth. Lateral lemmas are almost twice as long as the empty glumes and have a single awn with a shoulder on each side. Apical lemmas are also one-awned, but lack the shoulders.

Ae. squarrosa (Fig. 2).—Glumes are non-keeled, with horizontal, thickened margin and no teeth. Lateral lemmas have a tooth or awn on one corner and a square shoulder on the other. Apical lemmas have a central awn with a shoulder or blunt, short tooth on each side.

Ae. umbellulata (Fig. 3).—From none to three apical spikelets may be sterile. Empty glumes are short, obovate, non-keeled, abruptly inflated, and have a broadly horizontal margin with three to five awns. Lemmas have three awns. The first rachis segment above the lowest fertile spikelet is considerably shortened.

Ae. uniaristata (Fig. 4).—Lateral empty glumes, which are somewhat inflated, divide into a broad, strong awn and a broadly triangular tooth. Both apical empty glumes taper into a single, broad awn. Lemmas are similar to those of *Ae. comosa,* laterals having two, sometimes three, beaks, and apicals having a central tooth or short awn with a short tooth on each side. The apical spikelet is usually infertile.

Haynaldia villosa (Fig. 19).—Empty glumes have two strong keels, the two joining to form a single awn, which is flanked on each side by a shoulder or short, blunt tooth. They are not inflated. Lemmas, which are about twice as long as the empty glumes, have a central awn plus a papery tooth on each side.

Description of Amphidiploids

In the following descriptive notes concerning the amphidiploids, only those characters are mentioned in which the parent species differ.

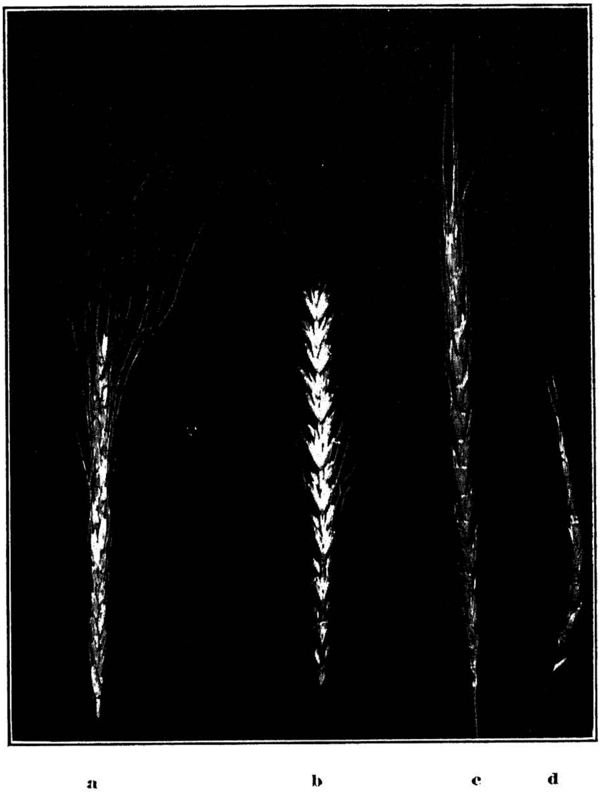

Fig. 2.—Spikes of (a) *Triticum aegilopoides*, (d) *Aegilops squarrosa*, and (b) their diploid and (c) tetraploid hybrids. x ½.

T. aegilopoides x *Ae. squarrosa* (Fig. 2).—The apical spikelet is fertile. Empty glumes have a strong keel plus a strong vein. The lateral glume has a slightly thickened margin, with a tooth on the keel stronger than that on the primary keel of *T. aegilopoides*, and a tooth on the vein weaker than that on the secondary keel of *T. aegilopoides*. Apical empty glumes have a central tooth and two weaker laterals, of which one tends to disappear. Lemmas have a strong central awn, flanked by two teeth, which are reduced and rounded in lateral spikelets.

Fig. 3.—Spikes of (a) *T. aegilopoides*, (d) *Ae. umbellulata*, and (b) their 2n and (c) 4n hybrids. x ½.

T. aegilopoides x *Ae. umbellulata* (Fig. 3).—The rachis segment above the first fertile spikelet is intermediate in length between the parents, but varies considerably. The apical spikelet is fertile. Empty glumes are slightly inflated and have a strong keel plus two strong veins. Lateral glumes have a horizontal margin with two awns or three (of which the central is shortest) and sometimes a tooth on each corner in addition. Apical glumes are similar, except that the central awn may be strongest. Lemmas have a central awn with a tooth or short awn on each side.

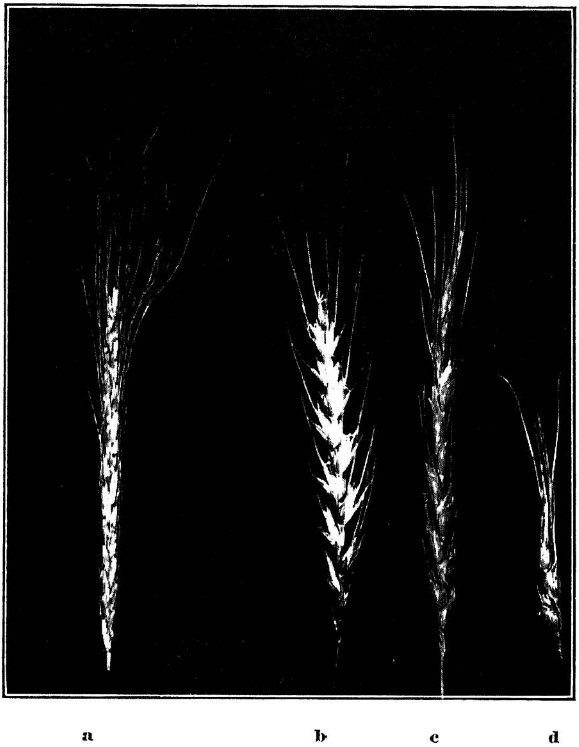

Fig. 4.—Spikes of (a) *T. aegilopoides,* (d) *Ae. uniaristata,* and (b) their 2n and (c) 4n hybrids. x ½.

T. aegilopoides x *Ae. uniaristata* (Fig. 4).—The apical spikelet is rarely fertile. Empty glumes, which have a strong keel and a strong vein, are very slightly inflated. On lateral spikelets, these glumes have a short awn on the keel, a tooth on the strong vein, a shorter tooth on the corner next to the rachis (reduced or lacking in both parents), and sometimes a very short tooth between the keel and the strong vein. The apical empty glume usually has an awn with a tooth on each side, but sometimes the awn is split into two for part or all of its length, and occasionally one of the flanking teeth is absent. Lemmas have a central awn and two teeth (longer on apical spikelets).

Fig. 5.—Spikes of (a) *T. monococcum*, (d) *Ae. uniaristata*, and (b) their 2n and (c) 4n hybrids. x ½.

Fig. 6.—Spikes of (a) *Ae. caudata*, (d) *Ae. speltoides*, and (b) their 2n and (c) 4n hybrids. x ½.

T. monococcum x *Ae. uniaristata* (Fig. 5).—This hybrid is like the preceding one except for a lack of color in the spike, a reduction of pubescence of the rachis, and a shorter central awn on the lemmas of lateral spikelets.

Ae. caudata x *Ae. speltoides* (Fig. 6).—Glumes are more or less intermediate to the parent species in size and shape. Lateral empty glumes are keeled and have a slightly thickened margin, with an awn in one corner and a tooth or shoulder on the other. Apical glumes have an awn similar to that of *Ae. caudata* but shorter, and tend to have a shoulder on each side of the awn. Lateral lemmas are hard in texture, are about one-third longer than the empty glumes, and have a central short awn plus two flanking shoulders or beaks. Apical lemmas are similar, except that the first floret bears a strong awn and the second usually a somewhat weaker awn.

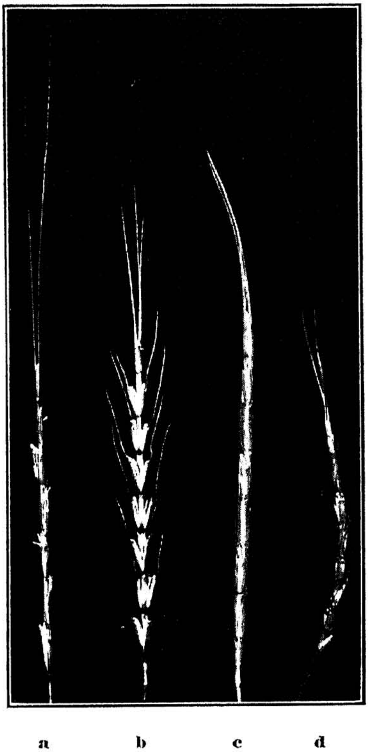

Fig. 7.—Spikes of (a) *Ae. caudata,* (d) *Ae. squarrosa,* and (b) their 2n and (c) 4n hybrids. x ½.

Ae. caudata x *Ae. squarrosa* (Fig. 7).—Lateral empty glumes are slightly thickened at the margin and have one short awn plus a prominent shoulder. Apical glumes taper into a fairly strong awn. Lateral lemmas have a central tooth with a strong and a weak shoulder. The apical lemma (fertile floret) has a strong awn and two teeth.

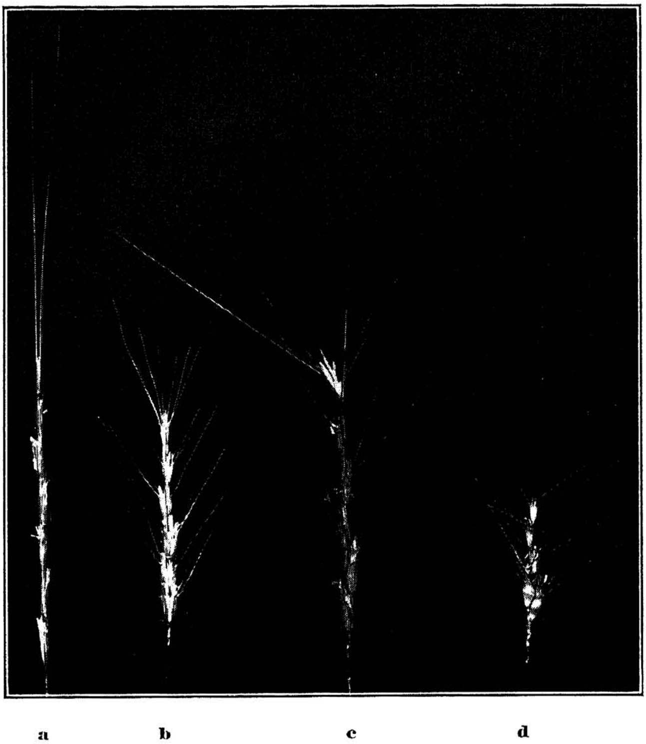

Fig. 8.—Spikes of (a) *Ae. caudata*, (d) *Ae. umbellulata*, and (b) their 2n and (c) 4n hybrids. x ½.

Ae. caudata x *Ae. umbellulata* (Fig. 8).—This amphidiploid is very similar to an existing species, *Ae. triuncialis* (var. *typica*). The amphidiploid differs, however, in that spikes are fragile at the base only, while the wild species is fragile also at other nodes (type I fragility). *Ae. triuncialis* planted a month later shed pollen a month earlier. It had slightly longer tillers, fewer spikelets, smaller seeds, and was somewhat more fertile. Hybrids of *Ae. triuncialis* var. *typica* with the amphidiploid show that, as anticipated by Senjaninova-Korczagina (1932), chromosome homologies are by no means perfect. An average of 2.36^{I}, 9.64^{II}, 1.04^{III}, $.64^{\mathrm{IV}}$, $.04^{\mathrm{V}}$, and $.08^{\mathrm{VI}}$ was found in 25 microsporocytes. Pollen was 72.5% aborted (400 grains), and only three seeds were set on five plants. Senjaninova-Korczagina believed the chromosomes of *Ae. caudata* x *Ae. umbellulata* to have more homology with *Ae. triuncialis* var. *persica* than with var. *typica*, but Iwata (1938) found that the two varieties of *Ae. triuncialis* have almost identical chromosome complements.

The rachis segment above the first fertile spikelet of the amphidiploid is not noticeably shortened. Empty glumes of lateral spikelets are slightly inflated. They have two awns separated by a shorter awn or a tooth and sometimes flanked on one side by a shoulder or short tooth. Apical empty glumes have three awns, of which the central one is stronger than any other on the spike. Lemmas have three teeth or short awns, of which the central is strongest and may become a full-length awn on the first floret of the apical spikelet.

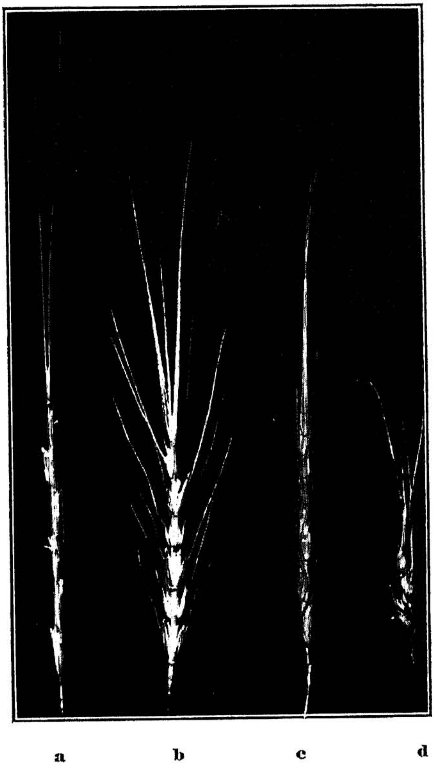

Fig. 9.—Spikes of (a) *Ae. caudata*, (d) *Ae. uniaristata*, and (b) their 2n and (c) 4n hybrids. x ½.

Ae. caudata x *Ae. uniaristata* (Fig. 9).—The apical spikelet is fertile. Lateral empty glumes have an awn and a tooth, not quite as broad as in *Ae. uniaristata*. Apical empty glumes taper into long, very strong awns, as in both parents. Lemmas have two beaks and a very short tooth.

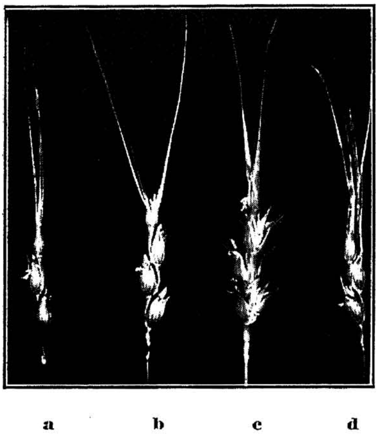

Fig. 10.—Spikes of (a) *Ae. comosa,* (d) *Ae. uniaristata,* and (b) their 2n and (c) 4n hybrids. x ½.

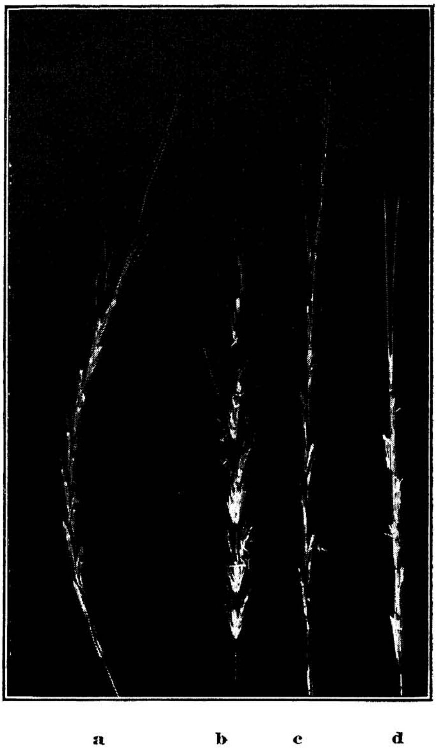

Fig. 11.—Spikes of (a) *Ae. sharonensis,* (d) *Ae. caudata,* and (b) their 2n and (c) 4n hybrids. x ½.

Ae. comosa x *Ae. uniaristata* (Fig. 10).—The awn of the outer glume of the lateral spikelet of *Ae. uniaristata* is absent, but the teeth are longer than in *Ae. comosa* and tend to curl over. The glume itself is somewhat nearer flat than in either parent. The apical empty glumes are typically three-awned, with the central awn of the upper outer glume slightly longer than that of the lower, about twice as long as the awns flanking itself, and about four times as long as those flanking the central awn of the lower glume. However, the side awns of the upper glume may be completely absent, and the central awn of the lower glume may be partially or entirely split into two. Lemmas have two or three very short teeth, as in both parents.

Ae. sharonensis x *Ae. caudata* (Fig. 11).—Outer glumes of lateral spikelets are keeled, but otherwise are more like *Ae. caudata.* They have two teeth, one of which stretches into an awn on some spikelets. Apical empty glumes have a long, strong awn with a tooth on each side. Lemmas are tougher than in *Ae. caudata.* Laterally they have a central tooth with shoulders or very short teeth, while apically they have an awn in the center and teeth on each side.

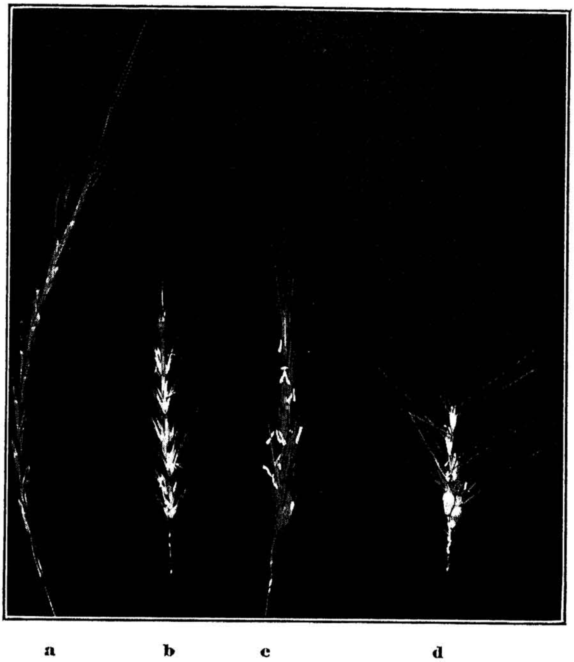

Fig. 12.—Spikes of (a) *Ae. sharonensis*, (d) *Ae. umbellulata*, and (b) their 2n and (c) 4n hybrids. x ½.

Ae. sharonensis x *Ae. umbellulata* (Fig. 12).—The rachis segment is of normal length above the first fertile spikelet. The apical spikelet is fertile. Lateral empty glumes, which are not keeled and not inflated, have three awns, of which the central one is shorter and frequently considerably reduced. Often there is a shoulder or tooth on each corner, also. Apical empty glumes are similar, except that the central awn is stronger than the others and is sometimes separated from one or both of them by a short tooth. Lemmas have a central awn, with a short awn on each side.

Fig. 13.—Spikes of (a) *Ae. sharonensis*, (d) *Ae. uniaristata*, and (b) their 2n and (c) 4n hybrids. x ½.

Ae. sharonensis x *Ae. uniaristata* (Fig. 13).—Empty glumes of lateral spikelets are very little inflated. They have a strong vein instead of a keel. On one corner is a beak or short awn, while the rest of the upper margin consists of a broad, blunt tooth with or without a very short tooth on the side toward the awn. The apical empty glume has a central awn and two beaks or teeth. Lateral lemmas have a central beak or short awn, flanked by a tooth and a shoulder or very short tooth. Apical lemmas have a central awn and two short teeth.

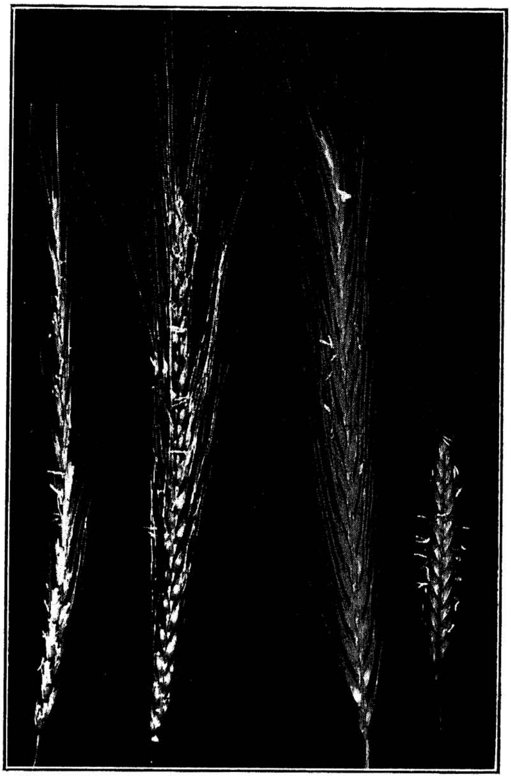

Fig. 14.—Spikes of (a) *Ae. speltoides,* (d) *T. monococcum,* and (b) their 2n and (c) 4n hybrids. x ½.

Ae. speltoides x *T. monococcum* (Fig. 14).—Empty glumes of lateral spikelets have a strong keel and one or two strong veins. The upper margin of these glumes has a small tooth near one corner, a central slight projection, and a shoulder on the other corner. The apical empty glume has a small tooth on each corner, one much reduced. Lemmas have a single awn, with a shoulder or tooth on each side in some lateral spikelets.

Fig. 15.—Spikes of (a) *Ae. speltoides,* (d) *Ae. sharonensis,* and (b) their 2n and (c) 4n hybrids. x ½.

Ae. speltoides x *Ae. sharonensis* (Fig. 15).—Empty glumes of lateral spikelets resemble *speltoides,* but the margin is not so thick and fits more snugly to the lemma. Apical empty glumes are rounded like those of *speltoides.* Lemmas have a central awn usually flanked by a very short tooth.

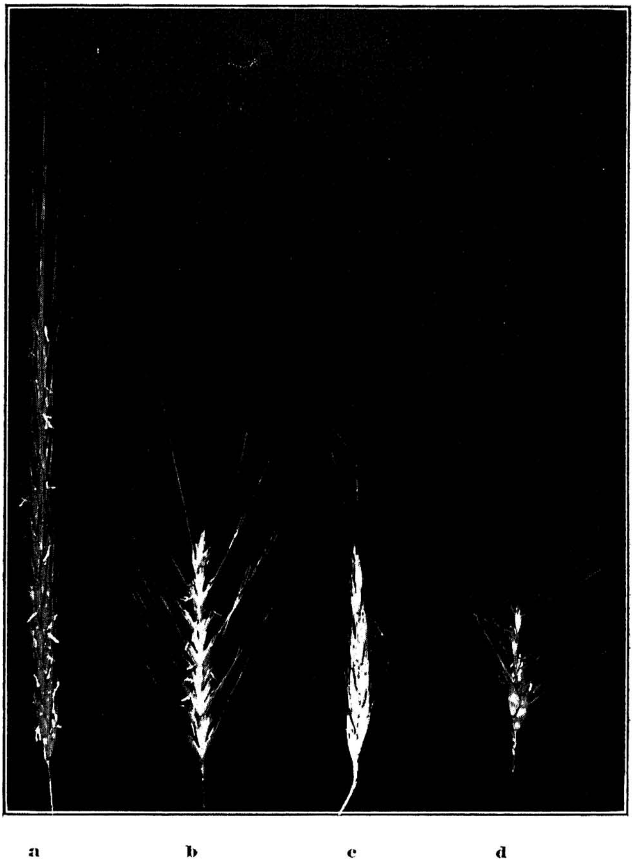

Fig. 16.—Spikes of (a) *Ae. speltoides*, (d) *Ae. umbellulata*, and (b) their 2n and (c) 4n hybrids. x ½.

Ae. speltoides x *Ae. umbellulata* (Fig. 16).—Rachis segments are of normal length above the first fertile spikelet. The apical spikelet is frequently fertile. Empty glumes of lateral spikelets are very slightly inflated, have a strong vein, and have two or three awns (rarely four), with the corner awns strongest. Apical empty glumes have three awns, of which the center one is much stronger than the others.

Fig. 17.—Spikes of (a) *Ae. speltoides*, (d) *Ae. uniaristata*, and (b) their 2n and (c) 4n hybrids. x ½.

Ae. speltoides x *Ae. uniaristata* (Fig. 17).—Empty glumes of lateral spikelets are strongly keeled, are somewhat thickened on their upper margin, and have an awn or beak, flanked on each side by a weaker tooth or a shoulder. The apical empty glumes have a rather short awn, with a tooth or a shoulder (square or rounded) on each side. Lateral lemmas bear an awn slightly longer than that on the empty glume, with a tooth on each side. Apical lemmas have a strong awn, sometimes with a very small tooth on each side.

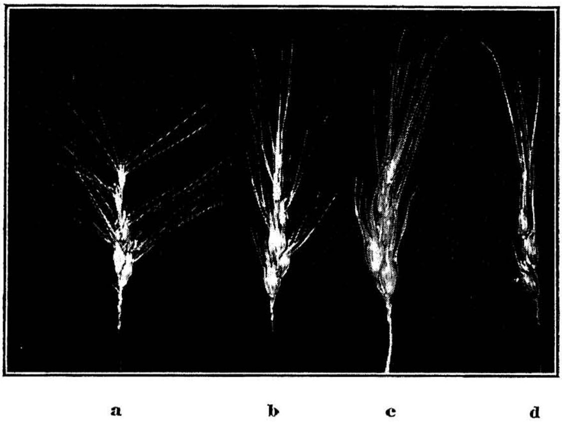

Fig. 18.—Spikes of (a) *Ae. umbellulata*, (d) *Ae. uniaristata*, and (b) their 2n and (c) 4n hybrids. x ½.

Ae. umbellulata x *Ae. uniaristata* (Fig. 18).—The apical spikelet is occasionally fertile. The rachis segment above the first fertile spikelet is shorter than those elsewhere in the fertile portion of the spike, but not so short as in *Ae. umbellulata*. Empty glumes of lateral spikelets have a horizontal margin, with three, or sometimes two, awns. Apical glumes regularly have three awns, of which the one next to the rachis is rather weak.

Fig. 19.—Spikes of (a) *Ae. umbellulata*, (d) *Haynaldia villosa*, and (b) their 2n and (c) 4n hybrids. x ½.

Ae. umbellulata x *Haynaldia villosa* (Fig. 19).—The rachis segment above the first fertile spikelet is sub-normal in length, but quite variable. Empty glumes of lateral spikelets have a keel plus two strong veins, and are not inflated; two awns are present, with a shoulder outside each, and sometimes a third, shorter awn between the other two. The apical empty glume has a single awn flanked by shoulders. Lateral lemmas are about one-third longer than the empty glumes, and bear a central awn and two short or long teeth. Apical lemmas are similar, but the flanking teeth are always short.

DISCUSSION

Effect of Chromosome Doubling

Tetraploid sectors have now been observed in 19 hybrids (including *Triticum aegilopoides* x *Haynaldia villosa,* for which amphidiploid data are not yet complete) in the seven-chromosome *Triticinae.* In no hybrid were the tetraploid sectors noticeably different from the rest of the plant in morphology, in size, or in time of maturity. Even stomatal size, which has been a sensitive indicator of polyploidy in other material, was the same in the 2n and 4n tissues of one of the four hybrids in which stomata were measured. It is possible that the increases observed in seed size of the amphidiploids over the parent species may be attributed to chromosome duplication, but hybrid vigor can scarcely be dismissed as a possible cause of at least part of this increase.

Although it is true that the tetraploid sectors obtained were frequently rather small, particularly in the material treated as potted plants, nearly every hybrid had one or more completely tetraploid spikes, all of which were very similar to diploid spikes. It might be argued that differences occurred between 2n and 4n tissues which were dependent on the plant as a whole and were therefore not expressed in 4n sectors on 2n plants. This, however, would be contrary to the results obtained by various investigators in other groups of plants. H. Smith (1939), for instance, found a striking difference between the 2n and 4n portions of a colchicine-treated hybrid between *Nicotiana glutinosa* and *N. glauca.* Furthermore, in the present study, spikes on amphidiploid plants of the next generation showed no appreciable differences from 4n and 2n spikes on the F_1 hybrid; and no general tendency appeared in the next generation toward late maturity, which usually accompanies 4n size increases (Müntzing, 1936).

The failure of fertile sectors of treated plants to differ morphologically from infertile portions of the same plants might be due to the occurrence of periclinal chimeras in such high frequency that tissues arising from the various germ layers were substantially independent of each other in degree of polyploidy. As nearly as could be determined, however, plants grown from the seeds produced by treated plants did not show appreciable differences from 2n hybrids. Such an explanation does not suffice, therefore, to reconcile the present data with those of other investigators who have found striking changes associated with tetraploidy.

In the lack of changes due to tetraploidy, these amphidiploids differed from most of those which have been studied previously. Even elsewhere in the *Triticinae,* vigor due to tetraploidy may be found in amphidiploids—for example, *Triticum vulgare* x *Secale cereale.* Autotetraploids of *T. monococcum,* which was one of the species used in the present study, show distinct differences from the diploid (Dorsey, 1939). Müntzing (1936) concluded from his survey of natural and induced polyploids that chromosome doubling nearly always results in quantitative increases in the plant body. East (1936), however, suggested that the quantitatively different tetraploids are special cases, not common in most plant groups (particularly the monocotyledons), and that chromosome determinations made at random, rather than on forms which differ morphologically, would reveal numerous instances of indistinguishable tetraploids. He cited work on *Tradescantia* (Anderson and Sax, 1936), where three different tetraploid forms could not be distinguished from the corresponding diploids without cytological analysis.

Subsequent to the enunciation of these opposing views, tetraploids of many species have been obtained artificially, by the use of colchicine. According to Dermen (1940), the tetraploids have been distinguishable from the diploids in every case but one (Lapin, 1939; *Ocimum canum* x *O. gratissimum*). The differences usually involve an increase in one or more dimensions of certain plant parts (particularly thickness of leaves), but the 4n plant as a whole may be smaller than the diploid (H. Smith, 1939; *Nicotiana glauca, N. rustica, N. tabacum*).

Possibility of Predicting Amphidiploid Characteristics

In the characters which were studied only qualitatively, the amphidiploids were approximately intermediate to their respective parent species, almost without exception. Only one character, unsplit palea, showed consistent dominance. Pubescence and black color in the spike were dominant as regards presence or absence, but the degree or extent of pubescence or coloration seldom equalled that found in the "dominant" parent. The presence of a keel tended to dominate, though the secondary keel of *Triticum* usually became only a strong vein in the hybrids, and the weak keel of *Aegilops sharonensis* (and, to a lesser degree, that of *Ae. speltoides*) disappeared in certain crosses, particularly those with *Ae. umbellulata.* In such pattern effects as shape of spike and shape of glumes, and in such other taxonomically important characteristics as fragility of rachis, position and length of awns, and adherence of glumes, intermediacy was regularly observed. This prevalence of the intermediate condition agrees with

East's (1935) conclusion from his work with *Nicotiana,* that the factors responsible for differences between species and genera do not exhibit dominance in hybrids.

In the characters which were studied quantitatively, the amphidiploids were usually intermediate to their parent species, also. Little evidence was found of hybrid vigor; only in length of rachis segments and in size of seeds was any general tendency observed toward an increase over the parental average. Since increased seed size is perhaps attributable to polyploidy rather than to hybridity, and since length of rachis segments is possibly too specific a character to serve as an indicator of general hybrid vigor, it might be said that little or no hybrid vigor of the conventional sort was present in these particular hybrids and amphidiploids. It must be admitted, however, that none of the quantitative characters studied, with the possible exception of culm length, is a satisfactory measure of general hybrid vigor. It is probable that determinations of total plant weight, for example, would show increases in some of the hybrids. Furthermore, there seems good reason to consider the earliness of certain of these amphidiploids as an expression of hybrid vigor. The essential phenomenon of hybrid vigor, as Luckwill (1939) and others have shown, is an increase in growth rate during some part of the life cycle. Therefore, the attainment of a given size through a more rapid growth rate over a shorter period of time is a type of hybrid vigor. Although in the present experiment no data on plant weight are available to prove that a size equal to that of the parents was attained, it is believed that some or all of the amphidiploids which showed increased earliness did equal their parent species in size and therefore had hybrid vigor.

Certain predictions concerning the characteristics of amphidiploids are thus found to be possible from studies of the prospective parental species. The amphidiploids tend to be intermediate in all respects, except for unsplit paleas, longer spikes (due to increased length of rachis segments), larger seeds, and either earlier or later maturity. Greater increases over parental average for spike length are found for intergeneric amphidiploids, while seed size behaves in opposite fashion, with greater increases for interspecific amphidiploids. Early maturity is more common than late maturity, with lateness perhaps to be looked for mostly in very wide hybrids.

Amphidiploids produced in other genera and families may be expected to be intermediate to their parents in most respects, but such strict intermediacy in size as found here is likely to prove rather rare. Some degree of hybrid vigor has usually been met with in interspecific and intergeneric hybrids. Possibly the early-maturity type of hybrid vigor found here will appear in other families or orders of plants, and it may prove possible to predict from the family, genera, and species concerned in a particular cross what kind of hybrid vigor will occur—whether involving early, intermediate, or late maturity, and whether resulting in final vegetative increases or not. But it seems unlikely that the amount of heterosis can be predicted with much accuracy. East (1936) has pointed out that hybrid vigor tends to increase with genetic dissimilarity of the parent species, but that too great diversity may result in genetic disharmony which cancels the heterosis or even results in dwarf hybrids. Such disharmony is scarcely predictable, particularly since it may be caused by a single gene (Hollingshead, 1930; Lehmann, 1939; Sears, 1940), which is confined, perhaps, to a single race within a species, and which has no recognizable expression until combined with a particular foreign genom.

SUMMARY

A high incidence of tetraploidy, accompanied by relatively little killing, has followed (1) the use of 2.0% colchicine in lanolin on coleoptiles of germinating seeds and (2) the repeated application of 0.5% aqueous colchicine solution to the crowns of potted plants. The latter method is better adapted to hybrid material, since plants may be propagated vegetatively before treatment.

Nineteen hybrids involving species of *Triticum, Aegilops,* and *Haynaldia* with $n = 7$, and including seven intergeneric crosses, have given rise to amphidiploids. In none were the 4n sectors distinguishable other than by their fertility and, in some instances, by larger stomatal size, nor have differences appeared in the 18 amphidiploids which have been carried one or more generations further.

In the various morphological characters studied, the amphidiploids were generally intermediate to their parent species. Unsplit palea, the only consistent exception, was always dominant. Some amphidiploids exceeded both parents in time of maturity, length of rachis segments, and size of seeds. These increases, particularly that in time of maturity, may be manifestations of hybrid vigor. Increased seed size is probably to some extent an effect of chromosome doubling.

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