STERILITY IN WHEAT HYBRIDS. I. STERILITY RELATIONSHIPS AND ENDOSPERM DEVELOPMENT[1]

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INTRODUCTION

Partial or complete sterility is of frequent occurrence in species crosses. Within the same genus certain species are sterile when crossed while other combinations are completely fertile. Partial sterility may cause the elimination of certain classes of gametes and prevent desired recombinations of characters in the second generation. Sterility may also cause an abnormal vegetative development. It is therefore desirable to determine the sterility relationships of the species of economic genera.

The present study of the genus Triticum will include: (1) the endosperm development in fertile and sterile crosses; (2) sterility in species crosses as determined by grains set and pollen counts; (3) hybrid vigor of F_1 plants in relation to sterility; and (4) size and variability of pollen grains in parents and F_1 plants. The second generation of species crosses and the cytological basis for sterility in wheat crosses will be treated later.

The species of wheat are divided by SCHULZ (see VON TSCHERMAK 1914) into three groups as follows:

[1] Papers from the Biological Laboratory, MAINE AGRICULTURAL EXPERIMENT STATION, No. 137.

1. The Einkorn group, consisting of *Triticum aegilopoides* and *T. monococcum.*
2. The Emmer group, consisting of *T. dicoccoides*, *T. dicoccum*, *T. durum*, *T. turgidum* and *T. polonicum.*
3. The *vulgare* group, consisting of *T. spelta*, *T. compactum*, *T. vulgare* and *T. capitatum.*

This grouping is in accord with serological relationships as determined by ZADE (1914). ZADE noted that the serum of *T. polonicum* reacted more strongly with the antigen of *T. durum* than with *T. turgidum* and *T. dicoccum.* He also called attention to the fact that in general the members of the Emmer group are resistant to rust while the *vulgare* group is susceptible.

VAVILOV (1914) classified the species of wheat according to their susceptibility or resistance to disease. His classification, applied to conditions found in Russia, is as follows:

In relation to *Puccinia triticina* Eriks.

Susceptible	*Resistant*	*Perfectly immune*
T. vulgare (a few immune races)	*T. durum*	
T. compactum	*T. polonicum*	*T. monococcum*
T. spelta	*T. turgidum*	

T. dicoccum has both susceptible and immune races. Practically the same relationship is indicated in respect to susceptibility to *Erysiphe graminis.*

VON TSCHERMAK (1914) and others have determined the degree of fertility of various species crosses. Following are VON TSCHERMAK'S results with wheat crosses:

1a. Einkorn × *vulgare* group, fully sterile.
1b. Einkorn × Emmer group, almost fully sterile.
2a. *T. dicoccoides* and *T. dicoccum* × Spelt } all weakly fertile.
2b. *T. dicoccoides* and *T. dicoccum* × *T. vulgare*, *T. compactum* and *T. capitatum* } all weakly fertile.
2c. *T. dicoccoides* and *T. dicoccum* × *T. durum*, *T. turgidum* and *T. polonicum*, weakly fertile.
2d. *T. dicoccum* × *T. dicoccoides*, weakly fertile.
2e. *T. polonicum* × *T. vulgare*, *T. compactum* and *T. capitatum*, not fully fertile.
3a. *T. durum*, *T. turgidum* and *T. polonicum* × *T. spelta*, weakly or fully fertile.
3b. *T. durum* and *T. turgidum* × *T. vulgare*, *T. compactum*, and *T. capitatum*, fully fertile.
3c. *T. spelta* × *T. vulgare*, *T. compactum*, and *T. capitatum* } all fully fertile.
3d. *T. durum*, *T. turgidum*, and *T. polonicum*, *inter se* } all fully fertile.
3e. *T. vulgare*, *T. compactum*, and *T. capitatum*, *inter se* } all fully fertile.

The Emmer group as used by VON TSCHERMAK includes *T. dicoccum*, *T. durum*, *T. turgidum*, and *T. polonicum.* The *vulgare* group includes *T*

spelta, *T. vulgare*, *T. compactum* and *T. capitatum*. *T. polonicum* is considered more closely related to *T. durum* than is *T. turgidum* or *T. dicoccum*.

BLARINGHEM (1914) crossed Einkorn with *T. durum* and *T. turgidum* and obtained F_1 plants. Some grains set on the F_1 plants, and in later generations some individuals were fertile. TSCHERMAK and others attribute the development of grains of the F_1 of Einkorn-wheat crosses as possibly due to wind-pollination.

FREEMAN (1919) studied the inheritance of quantitative characters in a cross between *T. durum* and *T. vulgare*. He found some sterility and notes the shriveled grains in the first and second generations. He also found that tall F_2 plants with wrinkled seed (like the F_1) gave a more variable F_3 in respect to height than tall F_2 plants with smooth seeds (like the parents). The plump F_2 grains also gave taller F_3 plants.

HAYES, PARKER and KURTZWEIL (1920) used crosses of *T. vulgare* with *T. durum* and *T. dicoccum* in breeding for rust resistance. They found sterility in the F_1 plants and show the amount of pollen abortion. In the cross between Emmer and *T. vulgare* the pollen sterility is less than in the F_1 of *T. vulgare* × *T. durum*. The same sterility relationship is indicated by the percentage of seed set on F_1 plants.

Crosses between wheat and rye are difficult to make and very few seeds set on the F_1 plants. LEIGHTY (1920) found a number of natural wheat-rye hybrids and in most cases they were completely sterile. Nineteen plants produced only 40 seeds or about 1 percent of the flowers set seed. A number of other writers have described wheat-rye hybrids and in all cases few grains were found on the F_1 plants.

MATERIALS AND METHODS

The wheat species and varieties used in this study were obtained from E. F. GAINES, of the WASHINGTON AGRICULTURAL EXPERIMENT STATION. The following species are represented:

Triticum vulgare
1. Pacific Coast Bluestem, a wheat of Australian origin.
2. Amby, a true beardless wheat recently introduced from Australia.
3. Marquis, a well known wheat introduced by the OTTAWA STATION of Canada.

Triticum compactum
Washington Hybrid 143, a segregate from a cross of White Track × Little Club, made by Dr. SPILLMAN in 1898.

Triticum durum
Kubanka, a Russian wheat introduced by M. A. CARLETON of the U. S. DEPARTMENT OF AGRICULTURE.

Triticum turgidum compositum
Alaska, a bearded wheat with branching head.
Triticum polonicum
Polish, a bearded wheat with very long glumes and grain.
Triticum monococcum.
Einkorn.

Pure lines of Einkorn (*T. monococcum*) and Alaska as well as the F_1 hybrids were obtained from Dr. ZINN of the MAINE AGRICULTURAL EXPERIMENT STATION.

The varieties of wheat used in this work represent six species. These six species can be divided into three groups. First, *Triticum vulgare* and *Triticum compactum* which are fertile *inter se;* and second, *Triticum durum, Triticum turgidum* and *Triticum polonicum* which are also cross-fertile *inter se*. Members of the first group crossed with members of the second group result in partially sterile hybrids. For convenience the first group will be classed as the *vulgare* group, the second group as the Emmer group. Einkorn (*T. monococcum*) constitutes a third sterility group, but this species was not used at the beginning of the present study.

The crosses for this study were made in Illinois in 1919. Wheat scab was unusually prevalent and all grain obviously infected had to be discarded. The F_1 plants were grown in Maine. Due to scab and unfavorable climatic conditions a large number of seeds failed to grow and the number of F_1 plants is not as large as desired in many cases.

In making crosses only six or eight spikelets were left on a head and the central flowers of each spikelet were removed. The remaining flowers were emasculated and the head wrapped in tissue paper both before and after pollinating. There was thus no chance for wind-pollination to occur.

In studying the behavior of the endosperm, the weight of individual grains of the parents and of fertile and sterile F_1 hybrids was determined. A glass scale used for this purpose permitted accurate and rapid work.

The degree of sterility in the hybrids was determined in two ways. (1) The number of grains per spikelet was obtained for parents and F_1 plants. (2) The percentage of sterile pollen was determined. Pollen counts were obtained by taking anthers from several plants and shaking out the pollen on a slide smeared with albumin fixative. A drop of lactic acid was added, the preparation covered and sealed with balsam. Preparations made in this way were in perfect condition after six months. In addition to differences in contents of pollen grains there was considerable variation in the size of pollen grains. In order to obtain accurate data pollen grains of parents and F_1 hybrids were measured with a Zeiss ocular micrometer.

THE F_1 ENDOSPERM IN FERTILE AND STERILE HYBRIDS

As in maize the endosperm resulting from the immediate cross contains chromosomes contributed by both parents due to double fertilization (SAX 1918). In wheat the embryo sac is derived from a single megaspore (JENSEN 1918). This megaspore is one of four megaspores resulting from the reduction divisions and contains the haploid number of chromosomes. Since in wheat the embryo sac is derived from a megaspore, the egg nucleus and the two polar nuclei each contain haploid chromosomes of identical constitution. The F_1 endosperm resulting from the immediate cross has the same chromosome constitution as the F_1 plant, plus an extra set of maternal chromosomes. The grain resulting from the immediate cross will be called the F_1 grain and the endosperm the F_1 endosperm. This grain contains the embryo of the F_1 plant. The grains borne on the F_1 plant will be designated F_2 grains and the endosperm the F_2 endosperm.

When the hybrid grains (F_1 endosperm) were examined, it was found that all combinations which later proved to be partially sterile had small wrinkled grains, while the fertile combinations had plump grains often larger than those of the female parent. Since the development of size and shape of grain is normally dependent on the female parent plant (ENGLEDOW 1920), F_1 grains were compared only with grains of the female parent.

For purposes of comparison, grains of parent varieties were selected at random from the cereal garden. In order to make the comparison with the hybrid grains more exact, a number of heads were emasculated and pollinated with pollen from another plant of the same variety. The number of grains set was too small in most cases, for accurate conclusions, so a field selection was made instead. The grains of parents of fertile crosses and sterile crosses were weighed and the means and standard deviations determined. The grains were weighed to the nearest 5-milligram unit but are recorded in classes of 5 mg. Table 1 gives the data obtained.

The Emmer group has somewhat larger grains than the *vulgare* group. The grain weight of Hybrid 143 was unusually low due to lateness in maturing and to rust infection. In comparing F_1 hybrid grain with parents only the female parent was used for reasons already stated. The average weight of the F_1 grains which produce partially sterile F_1 plants is less than the average grain weight of the female parent. In all cases these grains were wrinkled. The F_1 grains which later produced fertile F_1 plants are as a rule larger than grains of the female parent. The weights of F_1 grains are no more variable than the weight of grain of the parents.

TABLE 1

Weight of grains, of parents and F_1 endosperm.

	WEIGHT IN MILLIGRAMS (5-MG UNITS)														NUMBER	MEAN	σ
	2.5–7.5	7.5–12.5	12.5–17.5	17.5–22.5	22.5–27.5	27.5–32.5	32.5–37.5	37.5–42.5	42.5–47.5	47.5–52.5	52.5–57.5	57.5–62.5	62.5–67.5	67.5–72.5			
Parents:																	
Kubanka				1	3	8	8	8	6	8	2	2			46	39.9±1.0	9.7±0.7
Alaska			5	13	21	12	4	2							57	25.3±0.6	5.9±0.4
Bluestem		2	2	5	9	16	11	8	1						54	29.8±0.7	7.8±0.5
Amby			1	3	3	3	9	5	8	6	3				41	38.6±1.1	10.4±0.8
Hybrid 143		20	26	14	11	1	1								73	16.6±0.5	5.7±0.3
Polish				2	8	8	11	13	7	6	2	3	2		62	39.1±1.0	10.9±0.7
Marquis			4	6	9	11	8	4	2						44	28.8±0.8	7.9±0.6
Sterile crosses:																	
Bluestem × Kubanka				5	2	2									9	23.3±0.9	4.1±0.7
Kubanka × Bluestem			3	6	10	8	5	1							33	26.4±0.8	6.3±0.5
Bluestem × Alaska		2	7	20	22	8		1		1					61	23.1±0.6	6.4±0.4
Alaska × Bluestem			3	6	2	1	2								14	22.5±1.1	6.5±0.8
Kubanka × Amby	1	1	4	7	10	5	4	4	2						38	26.5±1.0	9.4±0.7
Amby × Kubanka		10	18	15	3	1									47	16.5±0.5	4.7±0.3
Kubanka × Hybrid 143			2	10	23	29	13	1	2	3	2				85	29.7±0.6	7.9±0.4
Hybrid 143 × Kubanka	2	17	17	14	5		1								56	15.7±0.5	5.8±0.4
Alaska × Amby		1	1	3	8	5	1								19	24.8±0.9	5.8±0.5
Amby × Alaska	1	4	14	18	4	1	1								43	18.2±0.5	5.4±0.4
Alaska × Hybrid 143		4	10	13	9	7	12	6							61	25.4±0.8	9.0±0.6
Hybrid 143 × Alaska	3	44	32	23	6	2									110	14.6±0.4	5.3±0.3
Polish × Hybrid 143			1	3	2	1									7	22.2±1.1	4.3±0.8
Hybrid 143 × Polish		10	17	21	5			1							54	17.4±0.5	5.4±0.4
Marquis × Kubanka		1	7	30	29	1	2								70	22.0±0.3	3.8±0.2
Marquis × Alaska		3	11	9	6	1									30	18.5±0.6	5.0±0.5
Marquis × Polish		2	10	6	4		2								24	19.2±0.9	6.4±0.6
Fertile crosses:																	
Bluestem × Amby							1		4	9	9	3			26	51.6±0.7	5.6±0.5
Amby × Bluestem			3	2	5	5	3	2	4	2					26	31.7±1.4	10.6±1.0
Bluestem × Hybrid 143							1	2	1	7	15	5	2		33	53.5±0.8	6.5±0.6
Hybrid 143 × Bluestem		11	10	18	9	4	4	1							57	20.1±0.7	7.6±0.5
Amby × Hybrid 143							5	7	12	6	1				31	43.6±0.6	5.3±0.5
Hybrid 143 × Amby			1	2	13	8	6	4							34	29.2±0.7	6.1±0.5
Marquis × Amby			2	4	4	6	12	3	4	4					39	33.6±1.0	9.5±0.7
Marquis × Hybrid 143			1	4	3	5	3	3	2						21	30.3±1.3	8.5±0.9
Kubanka × Alaska			1	2	2	8	12	18	39	25	20	15	14	6	162	48.2±0.6	11.1±0.4
Alaska × Kubanka				2	7	13	10	10	7	1					50	34.4±0.7	7.3±0.5
Kubanka × Polish				2	2	3	8	10	18	8	4	1			56	42.0±0.8	8.5±0.6

Table 2 was prepared to facilitate comparisons between grains of parents and hybrids. The average weight of grain of each parent is given as well as the difference between the grain weight of the female parent and the weight of the hybrid grain (F_1 endosperm). For example Kubanka selfed resulted in grains weighing 39.9 mg; Kubanka pollinated with Alaska pollen produced F_1 grains which weigh 8.3 mg more than Kubanka grains;

TABLE 2

Showing mean weight of grains from parents and differences between mean weight of hybrid grains (F_1 endosperm) and mean weight of grains from ♀ parent. E = Emmer group; V = vulgare group. Weight in milligrams.

♂ / ♀	Alaska E	Kubanka E	Polish E	Bluestem V	Marquis V	Hybrid 143 V	Amby V
Alaska E	25.3±0.6	+9.1±0.9		−2.8±1.3		+0.1±1.0	−0.5±1.1
Kubanka E	+8.3±1.2	39.9±1.0	+2.1±1.3	−13.5±1.3		−10.2±1.2	−13.4±1.4
Polish E			39.1±1.0			−16.9±1.5	
Bluestem V	−6.7±0.9	−6.5±1.1		29.8±0.7		+23.7±1.1	+21.8±1.0
Marquis V	−10.3±1.0	−6.8±0.8	−9.6±1.2		28.8±0.8	+1.5±1.5	+4.8±1.3
Hybrid 143 V	−2.0±0.6	−0.9±0.7	+0.8±0.7	+3.5±0.9		16.6±0.5	+12.6±0.9
Amby V	−20.4±1.2	−22.1±1.2		−6.9±1.8		+5.0±1.3	38.6±1.1

Kubanka pollinated with Bluestem pollen produced F_1 grains which weigh 13.5 mg less than Kubanka grains. All of the F_1 grains in the Emmer group are heavier than the grains of the female parent. The difference is hardly significant, however, in case of Polish × Kubanka. In the *vulgare* group all crossed grains are significantly larger than those of the female parent with the exception of Amby × Bluestem. The reciprocal cross

on the other hand produced grains much larger than those of the female parent. Both of these crosses, however, behave in a very unusual manner in the first generation which will be described later. Most of the partially sterile crosses result in grains significantly smaller than those of the female parent. In no case is the average grain weight significantly larger than that of the female parent. One of the most striking cases is that of Bluestem crossed with members of the Emmer group and with members of the *vulgare* group. When selfed the average grain weight is 29.8 mg; when pollinated with pollen from the Emmer group the average weight is 23.2 mg and when pollinated with pollen from the *vulgare* group the average weight is 52.5 mg. It appears that there is some effect of hybrid vigor in the F_1 endosperm of fertile crosses and a considerable decrease in average grain weight in the case of partially sterile crosses.

The technique used in making crosses may have some effect on the size the grain attains. Part of the head is cut off and the central florets of the remaining 6 to 8 spikelets are removed. Such mutilation may be injurious, but at the same time there are fewer grains to be developed per head. Certainly the technique used in crossing could not account for the decrease in weight of grain (F_1 endosperm) in sterile crosses and at the same time account for an increase in weight of grain in fertile crosses. Crossed grains compared with parent grains from plants subject to the same technique also show increased weight of grain of fertile crosses and decreased weight in case of grains of partially sterile crosses.

Crosses made in 1920 show that Spelt (*T. spelta*) crossed with the *vulgare* group results in plump grain and when crossed with members of the Emmer group result in small shriveled grains. Emmer (*T. dicoccum*) crossed with members of the Emmer group produced plump large grains while pollinated with pollen from the *vulgare* group only small shriveled grains resulted.

HYBRID VIGOR IN FERTILE AND PARTIALLY STERILE CROSSES

In order to determine if sterility has any effect on vegetative vigor, the parent and F_1 plants were grown under as nearly uniform conditions as possible. Due to scab infection and unfavorable climatic conditions a comparatively small number of plants survived and the numbers were too low for significant comparison in many cases. By grouping the parent plants, and F_1 plants, respectively, comparisons can be made between the two parent groups and between fertile and sterile hybrids (table 3). The grouping of varieties and crosses in this way is subject to some error, but it is believed that the conclusions to be drawn are correct.

The F_1 plants of both the fertile and partially sterile F_1 hybrids are taller than the parent plants. The fertile F_1 hybrids resulting from crosses of species in the Emmer group are slightly taller than the average of the parents. The fertile crosses between *T. vulgare* and *T. compactum* result in F_1 plants which average 7.8 ± 1.8 cm taller than the average of the parents. The parents, of course, vary considerably in height since *T. compactum* has short culms as well as club heads. It may appear that the increased height of the F_1 hybrids as compared with the average of the parents is due to dominance of the taller parent. The F_1 head shape is intermediate however, and since length of head and length of straw are positively

TABLE 3

Height of parent groups, fertile F_1 hybrids, partially sterile F_1 hybrids, and completely sterile F_1 hybrids.

PARENTS AND F_1 HYBRIDS	FREQUENCIES OF HEIGHTS IN 5-CENTIMETER CLASSES																		NUMBER	MEAN	σ
	55–60	60–65	65–70	70–75	75–80	80–85	85–90	90–95	95–100	100–105	105–110	110–115	115–120	120–125	125–130	130–135	135–140	140–145			
Emmer group....					1	3	5	16	12	19	17	8	1	1	1				84	100.7±0.7	9.2±0.5
Vulgare group...	1	5	6	15	10	13	14	20	8	3	9	1							105	85.3±0.8	12.7±0.6
Emmer × Emmer..........					1	3	4	4	9	7	9	5	3	6	1				52	103.6±1.1	12.2±0.8
Vulgare × *vulgare*	3		3	3	3	4	5	1	5	9	7	8							51	93.1±1.6	16.4±1.1
Vulgare × Emmer*..........				2	2	8	11	14	19	16	17	17	10	8	2	6			132	103.5±0.8	13.7±0.6
Alaska × Einkorn†.........													1	1	1		1	1	5	129.5±2.8	9.3±2.0

* Partially sterile.
† Almost completely sterile.

correlated (FRUWIRTH 1910) the height of F_1 plants resulting from a cross of *T. compactum* × *T. vulgare* should be intermediate unless other factors are involved. The F_1 plants resulting from crosses of members of the *vulgare* group × members of the Emmer group are partially sterile. The height of these plants, however, is 10.5 ± 1.1 cm taller than the average of the parent groups. Only five plants of Alaska × Einkorn were grown. These F_1 plants although totally sterile exceed the average height of the parents by 34.8 ± 3.0 cm. The average height of Alaska was 102.3 ± 1.1 cm while Einkorn plants were 87.0 ± 1.0 cm tall. It is evident that the partially or completely sterile F_1 plants often exceed the parents in vegetative vigor even though they originate from small wrinkled grains.

LETHAL FACTORS IN WHEAT CROSSES

The cross of Bluestem × Amby and the reciprocal might be expected to behave the same as other crosses in the *vulgare* group. These varieties when crossed with other members of the *vulgare* group produced plump grain (F_1 endosperm) and the resulting F_1 plants are wholly fertile. Twenty six grains of the cross Bluestem × Amby and 26 grains of the reciprocal cross were planted. Twelve grains of each cross were planted in the greenhouse in Illinois. They all germinated and appeared to develop normally until they reached the height of 15 to 20 cm. They then ceased to increase in height although they were vigorous and stooled excessively, often as many as 40 or 50 primary culms were formed, but in no case did a true culm develop. The plants were observed for 5 months but did not develop further. The behavior of this cross was the same when planted in the field although the plants died before the growing season was ended. The unusual growth of this cross might be attributed to factors for winter habit, but the upright habit of growth and excessive stooling are not characteristic of the early stages of development of winter wheat. In all other cases both the parent and F_1 plants developed normally and the F_1 hybrids even exceeded the parents in vegetative vigor. The uniform behavior of the F_1 plants of Bluestem × Amby and reciprocal, both in the greenhouse and under field conditions precludes any argument that external factors were involved. It is evident that in this cross we have factors which prevent the hybrid plant from developing beyond a very definite stage. This case can be analyzed by crossing the F_1 of Amby × Marquis with Bluestem.

STERILITY IN THE F_1 HYBRIDS

The degree of sterility of various crosses was determined by pollen counts and by the grain set per spikelet. The pollen grains were mounted in lactic acid and examined under a microscope. All grains which appeared to be empty were classed as poor pollen. A cytological examination would undoubtedly reveal other abnormal conditions and would increase the counts of poor pollen grains. In shaking out the mature pollen grains the heavier pollen grains will come out more readily than the small shriveled ones so that the absolute degree of sterility cannot be determined by this method. For comparative purposes the method used is considered satisfactory. The following table shows the amount of pollen sterility and grain set for parents and F_1 hybrids.

With two exceptions the grains set per spikelet on the parent plants range from 1.85 to 2.91. The grain set in case of Hybrid 143 was unusually low due to late maturity and unfavorable climatic conditions for the variety. The Einkorn used normally sets only one grain per spikelet so that 0.97 grains per spikelet is nearly a perfect set.

TABLE 4

Sterility in parent and F_1 plants as indicated by grain set and pollen development.

VARIETY OR CROSS (F_1)	GRAIN SET			POLLEN		
	Spikelets	Grains	Grains per spikelet	Total count	Poor pollen	% poor pollen
Polish	345	638	1.85	1016	16	1.6
Kubanka	398	1159	2.91	1019	19	1.9
Alaska	247	478	1.93	1015	15	1.5
Einkorn	551	535	0.97	1003	3	0.3
Bluestem	402	1036	2.58	1009	9	0.9
Amby	284	717	2.52			
Hybrid 143	179	269	1.49	770	10	1.3
Marquis	380	1039	2.73	1011	11	1.1
Semi-sterile crosses:						
Bluestem × Alaska	935	1139	1.22			
Amby × Kubanka	88	45	0.51			
Kubanka × Hybrid 143	59	29	0.49	759	94	12.4
Hybrid 143 × Kubanka	301	136	0.45	838	135	16.1
Hybrid 143 × Alaska	591	616	1.04	676	103	15.2
Hybrid 143 × Polish	328	190	0.58	1144	176	15.4
Marquis × Kubanka	182	181	0.99	737	125	17.0
Marquis × Alaska	110	211	1.92			
Marquis × Polish	96	161	1.68	834	130	15.6
Kubanka × Bluestem	127	58	0.46	1919	413	21.5
Kubanka × Marquis	46	65	1.41	469	54	11.5
Totally sterile:						
Alaska × Einkorn	127	0	0	622	608	97.7
Fertile crosses:						
Bluestem × Hybrid 143	425	1033	2.43	1004	4	0.4
Hybrid 143 × Bluestem	290	827	2.85			
Hybrid 143 × Amby	90	304	3.37			
Marquis × Amby	47	129	2.74			
Marquis × Hybrid 143	54	175	3.24			
Kubanka × Alaska	347	1239	3.57	708	9	0.9
Alaska × Kubanka	127	463	3.64			
Kubanka × Polish	381	994	2.61	1012	12	1.2

The proportion of poor pollen grains as indicated by small empty pollen grains is only about 1 percent in the parent plants. Lack of vigor, as in

case of Hybrid 143, seems to have no effect on the normal development of pollen grains. Pollen counts give more uniform results in regard to fertility than do the grains per spikelet.

All crosses between members of the two general groups,—Emmer group and *vulgare* group,—resulted in partially sterile F_1 plants. As indicated in table 4 the grains set range from 0.45 to 1.92 per spikelet. In all cases the grains borne on partially sterile F_1 plants varied greatly in size. Many grains were small and wrinkled like the F_1 endosperm, while others were even larger than the parent grains. The amount of sterility as indicated by percentage of poor pollen grains does not vary greatly in different crosses. The number of poor pollen grains in partially sterile crosses is about 15 percent as compared with approximately 1 percent for the parents. Attention is called to the fact that in the crosses Kubanka × Hybrid 143 and reciprocal and Kubanka × Marquis and reciprocal the number of grains per spikelet is greater, and the pollen sterility is less, when a member of the Emmer group is used as the female parent. The same relation is found in other crosses to be reported later. The cross of Marquis × Alaska is nearly as fertile as the parents. Unfortunately pollen counts were not made. It seems rather paradoxical to say that a partially sterile hybrid is as fertile as one of the parents. There is no question that the cross is partially sterile and would produce all degrees of sterility in the second generation. The grains on the F_1 plant of this cross vary from small shriveled grains to large plump grains. This extreme variation in size of grains on the F_1 plant is characteristic only in partially sterile crosses.

The F_1 plants of Alaska × Einkorn produce no grain and nearly all of the pollen grains are obviously poor. It is probable that none of the pollen grains are functional and that the few grains set in occasional instances are due to wind-pollination. It is assumed therefore that the female gametes are more fertile than the male gametes as is the case in most partially sterile hybrids of plants and animals.

The crosses of varieties within each general group of species give fertile F_1 plants. The grains set per spikelet are even greater than in the parent plants due to the vigor of the F_1 plants. The percentage of poor pollen is no greater than in the parents.

SIZE OF POLLEN GRAINS IN PARENTS AND HYBRIDS

While examining the pollen of parents and F_1 hybrids it was found that considerable difference existed in the size and uniformity of the pollen grains. Measurements were made with a Zeiss micrometer. Random

TABLE 5

Diameter of pollen grains of parent and F_1 plants. "Good" or "poor" after cross indicates that pollen is apparently good or poor.

VARIETY OR CROSS	DIAMETER IN MICRONS																					NUMBER	MEAN	σ
	33.5–35.5	35.5–37.5	37.5–39.5	39.5–41.5	41.5–43.5	43.5–45.5	45.5–47.5	47.5–49.5	49.5–51.5	51.5–53.5	53.5–55.5	55.5–57.5	57.5–59.5	59.5–61.5	61.5–63.5	63.5–65.5	65.5–67.5	67.5–69.5	69.5–71.5	71.5–73.5	73.5–75.5			
Kubanka					1	2	2	2	6	10	18	17	20	8	2	1		1				90	55.6±0.3	4.3±0.2
Marquis × Kubanka, good								1	3	4	9	6	6	14	12	13	12	5	9	5	7	106	63.1±0.4	6.5±0.3
Marquis × Kubanka, poor			1	1		5	2	3	4	3	4											23	48.6±0.6	4.5±0.4
Kubanka × Marquis—good					4	9	6	7	9	8	5	8	7	11	5	1	3	1				84	53.7±0.5	6.7±0.3
Marquis						1	1			1	8	6	21	16	18	12	7	1				92	60.3±0.3	4.1±0.2
Alaska						1	2	5	2	8	15	13	21	13	6	5	1	2				94	57.1±0.3	4.7±0.2
Alaska × Einkorn—poor	5	6	19	20	11	5																66	39.7±0.2	2.6±0.2
Einkorn				1	2	7	8	7	11	17	16	8	2	2	1							82	51.5±0.3	4.5±0.3
Hybrid 143							1	1		1	4	12	21	16	10	15	5					86	60.1±0.3	3.8±0.2
Alaska × Kubanka—good					2	3	5	4	9	11	14	11	18	9	14	8	4	2	3			117	57.0±0.4	6.3±0.3
Hybrid 143 × Alaska—good					1		1	4	8	9	8	10	19	4	7	8	2	1				82	56.9±0.4	5.2±0.3
Kubanka × Bluestem—good					2	2	2	2	12	8	5	5	7	10	3	8	7	4				77	57.3±0.5	7.1±0.4

samples were taken by measuring the pollen grains in each of a series of fields taken in definite areas across the slide. Table 5 shows the size and standard deviation of pollen grains of several of the parents and hybrids.

The pollen grains of Marquis and Hybrid 143 (*vulgare* group) have an average diameter of 60.2 microns. They are significantly larger than the pollen grains of Alaska and Kubanka (Emmer group) which have an average diameter of 56.4 microns. Einkorn, which belongs to a third sterility group, has pollen grains much smaller than either of the other two groups. The average diameter of Einkorn pollen grains is only 51.5 microns. The mean volume of the pollen grains for the three groups expressed in thousands of cubic microns assuming that the pollen grains are perfectly spherical, is 114 for the *vulgare* group, 94 for the Emmer group and 72 for the Einkorn. The obviously poor pollen grains in sterile or partially sterile crosses are much smaller than the good pollen grains of the parents or the hybrids. The good pollen grains of both fertile and partially sterile hybrids are about the same size as parent pollen grains with one exception. The pollen grains of the F_1 of Marquis $\times$ Kubanka are even larger than pollen grains of Marquis.

The variability in size of pollen grains is greater in the F_1 hybrids than in the parents. In all cases with the possible exception of Hybrid 143 $\times$ Alaska the difference between the standard deviation of the parents' pollen grains and those of the F_1 hybrids are significant. In the case of Marquis $\times$ Kubanka, there is a difference of 2.3 ± 0.4 and in the reciprocal cross the difference between the standard deviation of the pollen grains of the F_1 plant and the standard deviation of the average size of pollen grains of the parents is 2.5 ± 0.4. In the case of partially sterile hybrids only the apparently good pollen grains were measured except in the cases mentioned. If these poor pollen grains were included the standard deviation of the size of pollen grains of the partially sterile F_1 plants would be considerably increased, as the obviously poor pollen grains are usually small. In the fertile cross Alaska $\times$ Kubanka the difference in standard deviation between parent and F_1 pollen grains is 1.8 ± 0.4. The probability that this difference is statistically significant is over 400 to 1.

CONCLUSIONS

Crosses of wheat species which produce sterile or partially sterile F_1 hybrids also produce small wrinkled F_1 grains. Fertile crosses produce large plump grains often larger than the grains of the female parent. Both fertile and sterile or partially sterile F_1 plants are usually more vigorous than the parents. Sterile combinations which produce small wrinkled

F_1 endosperms produce large vigorous F_1 plants. The chromosome constitution of the F_1 endosperm and the F_1 plant is identical with the exception that the F_1 endosperm has an extra set of maternal chromosomes. The individual chromosomes are identical and carry the same factors.

It is evident that groups of chromosomes which are incompatible in gamete formation can function normally in the vegetative development of the plant so long as the paternal and maternal sets of chromosomes are intact. In partially sterile crosses the addition of an extra set of maternal chromosomes in case of the endosperm is correlated with abnormal development. In fertile combinations the extra set of maternal chromosomes in the endosperm causes no abnormal growth, unless endosperm formation itself is considered abnormal. In fertile wheat crosses we get hybrid vigor in both F_1 endosperm and F_1 plant as in corn. In partially sterile crosses, however, we get a reduced development of the F_1 endosperm and yet the F_1 plant is unusually vigorous. Apparently the hybrid endosperm is not always adapted to the needs of the hybrid embryo as JONES (1918) has suggested. In sterile or partially sterile wheat hybrids where the chromosomes are incompatible in gamete formation the behavior of the 3x chromosomes in the F_1 endosperm development is not comparable with the behavior of the 2x chromosomes in the corresponding F_1 plant development.

The degree of sterility of a wheat hybrid may be determined by the amount of grain set on the F_1 plant and by the amount of aborted pollen. In addition a sterile or fertile cross can be recognized at once by the size and appearance of the F_1 grain resulting from the immediate cross. Sterile or partially sterile crosses produce small wrinkled F_1 grains, while fertile crosses produce grains as large or larger than those of the maternal parent. Comparisons are made only with the grains of the female parent because the F_1 grains are also borne on the female parent and size and shape of grain is normally dependent on the mother plant only.

The sterility relationships of wheat species are in accord with SCHULZ'S taxonomic classification (see VON TSCHERMAK 1914) and with VAVILOV'S (1914) classification in respect to disease resistance. The results of the present investigation as well as other work on sterility are not in complete agreement with VON TSCHERMAK'S (1914) classification. VON TSCHERMAK classes *T. dicoccum* × *T. durum*, *T. turgidum* and *T. polonicum* as weakly fertile. *T. durum* and *T. turgidum* × *T. vulgare* and *T. compactum* are classed as fertile crosses. The first group has been found to be completely fertile and the second group in all cases has proved to give partially sterile F_1 hybrids.

In making general statements regarding the behavior of wheat species it must be remembered that species limits are arbitrary and that in many cases there is a more or less continuous series between one species and another. This overlapping of species is especially true in the species *T. durum* and *T. turgidum* and also in *T. vulgare* and *T. compactum*. *T. compactum* might well be classed with *T. vulgare* both in respect to taxonomic similarity and genetic relationship. There is some indication that different varieties of a species may not show the same sterility relations when crossed with members of another specis. It has been shown that within a sterility group one species may not react the same as another species. For instance in the Emmer group *T. dicoccum* is more fertile with *T. vulgare* than is *T. durum* (HAYES, PARKER and KURZWEIL 1920). The three sterility groups are more distinct and clearly defined than are the species within each sterility group. The members of the Emmer group are usually bearded. They are as a rule taller, have fewer culms per plant, often have solid or pithy straw, usually have more sharply keeled glumes, and in general are more disease resistant than members of the *vulgare* group. Although there may be considerable variation in the species and varieties of each sterility group the three general groups are comparatively distinct. The general sterility classification can be made as follows:

1. Einkorn group: *T. monococcum*. All varieties cross-fertile; sterile or only slightly fertile with groups 2 and 3.
2. Emmer group: *T. dicoccum, T. durum, T. turgidum* and *T. polonicum*. All species and varieties cross-fertile; partially sterile with group 3; sterile or slightly fertile with group 1.
3. *Vulgare* group: *T. spelta, T. vulgare,* and *T. compactum*. All species and varieties cross-fertile; sterile with group 1; partially sterile with group 2.

The members of each group are fertile with each other and sterile or partially sterile with members of the other two groups. *T. monococcum* is completely sterile or nearly so when crossed with members of the other two groups. Crosses between members of the Emmer group with members of the *vulgare* group result in F_1 plants which as a rule are less than half as fertile as the parents. The sterility relationships of the above species groups are based on gametic sterility and do not apply to sterility as reported in the cross of Bluestem × Amby.

The available data indicates that the size of pollen grains varies significantly in different species of Triticum. The average volume of the pollen grains expressed in thousands of cubic microns was found to be 72 for

Einkorn, 94 for Kubanka and Alaska (Emmer group) and 114 for Marquis and Hybrid 143 (*vulgare* group). It is rather remarkable that pollen-grain size is so closely correlated with the sterility relationships of the three groups of wheat species. The size of pollen grains has little or no effect on the percentage of grain set in crossing. Crosses between members of the Emmer and *vulgare* groups are about as easy to effect as crosses within each group.

The pollen grains of both fertile and partially sterile F_1 plants are more variable in respect to size than pollen grains of the parents. In the partially sterile hybrids all degrees of compatible and incompatible combinations are probably present in the pollen grains. The pollen grains of the F_1 plant contain the haploid number of chromosomes consisting in nearly all cases, of chromosomes contributed by both parents. We may assume that some combinations are unable to function and the pollen grains abort at an early stage resulting in small empty pollen grains. Other combinations are able to function more or less favorably resulting in apparently good pollen grains of varying sizes. In the fertile hybrids and to some extent in the partially sterile hybrids, the increased variation of pollen-grain size may be attributed to differences in growth factors resulting from various combinations of maternal and paternal chromosomes. Here we have a case of variation in the haploid generation due presumably to different combinations of non-homologous maternal and paternal chromosomes.

SUMMARY

1. The species of Triticum can be divided into three sterility groups as follows:

a. Einkorn group: *T. monococcum.* Varieties inter-fertile; sterile or only slightly fertile with groups b and c.
b. Emmer group: *T. dicoccum, T. durum, T. turgidum* and *T. polonicum.* Species and varieties inter-fertile; sterile or slightly fertile with group a; partially sterile with group c.
c. *Vulgare* group: *T. spelta, T. vulgare* and *T. compactum.* Species and varieties inter-fertile; sterile or slightly fertile with group a; partially sterile with group b.

2. Fertile species crosses produce F_1 endosperms as large or larger than those of the maternal parent. Sterile crosses produce small shriveled F_1 endosperms.

3. Fertile, sterile, and partially sterile F_1 plants resulting from species crosses equal or exceed the parents in vegetative vigor.

4. The average size of the pollen grains differs in different species and is correlated with the three sterility groups.

5. The pollen grains of the F_1 plants are more variable than those of the parents, due presumably to recombinations of maternal and paternal chromosomes in the haploid generation.

6. A varietal cross within the *vulgare* group produced F_1 plants which failed to develop beyond the rosette stage, presumably due to lethal or inhibiting factors.

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