STERILITY IN WHEAT HYBRIDS. III. ENDOSPERM DEVELOPMENT AND F_2 STERILITY

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Crosses of wheat species with different chromosome numbers result in small or wrinkled seeds. These seeds consist of the F_1 endosperm and the embryo of the F_1 plant. Although the F_1 endosperm is usually poorly developed, the F_1 plant is even more vigorous than the parents. The F_1 plants are partially sterile and bear grains (F_2 endosperms) which vary greatly in size. Since small wrinkled grains are characteristic of partially sterile hybrids the small wrinkled grains borne on the F_1 plant might be expected to produce partially sterile F_2 plants, while the large plump grains would produce relatively fertile F_2 individuals.

It is well known that wide species crosses in wheat result in partially sterile F_1 plants and that in F_2 all degrees of sterility are found, ranging from plants which never pass the rosette stage, to those quite as fertile as the parents. A study of sterility in view of the chromosome relationships should be of value.

The parental varieties of wheat used were *Triticum durum* Desf. (Kubanka) and *T. vulgare* Vill. (Pacific Coast Bluestem). The crosses were made in 1916 and the F_1 was grown at BUSSEY INSTITUTION in 1917. The F_2 was grown in the greenhouse in 1917–1918.

WEIGHT OF SEEDS OF PARENTS AND HYBRIDS AND F_1 STERILITY

The degree of sterility, as indicated by the grains set per spikelet, and weight of grains of parents and the F_1 hybrids are shown in table 1. The F_1 plants are about one-fourth as fertile as the parents, although they are more vigorous vegetatively as indicated by the greater number of heads per plant. There is little difference in the fertility of the reciprocal hybrids. For the 30 F_1 plants the average number of grains per spikelet was found to be $0.57 \pm .03$ with a standard deviation of $0.25 \pm .02$. The sterility of the F_1 plants varied from .07 to 1.00 grain per spikelet. It appears probable that with larger numbers some F_1 individuals would

TABLE 1

Weight of grain and sterility in parents and hybrids.

NO. OF PLANTS	NO. OF HEADS	NO. OF SPIKELETS	NO. OF GRAINS	GRAINS PER SPIKELET	WEIGHT OF GRAINS IN 5-MG UNITS															NUMBER	MEAN	STANDARD DEVIATION
					2.5-7.5-	7.5-	12.5-	17.5-	22.5-	27.5-	32.5-	37.5-	42.5-	47.5-	52.5-	57.5-	62.5-	67.5-	72.5-77.5-			
					Kubanka																	
6	9	144	386	2.68					1	8	25	30	45	55	89	82	20	1		356	48.9±.3	8.9±.2
					Bluestem																	
7	23	354	789	2.23				1	2	14	27	51	115	123	100	24	2			458	45.2±.2	7.4±.2
					(Kubanka × Bluestem)F_1 endosperm																	
							2	4	7	6	4	1								24	24.4±.9	6.4±.6
					(Kubanka × Bluestem)F_1 (F_2 endosperm)																	
15	152	2323	1413	.61	4	19	31	50	106	124	138	154	183	161	175	121	103	33	11	1413	41.4±.3	14.5±.2
					(Bluestem × Kubanka)F_1 (F_2 endosperm)																	
15	131	1932	990	.51	9	22	34	50	77	109	115	123	114	110	95	70	37	19	6	990	38.1±.3	14.7±.2

be totally sterile, although the percentage of such plants would be small. The variation in sterility of the F_1 plants is apparently not due to differences in vegetative development, because the correlation between sterility, as indicated by the number of grains set per spikelet, and vegetative vigor, as indicated by the number of heads per plant, is practically zero ($r = -.08 \pm .12$).

Kubanka has somewhat larger seeds than Bluestem, but the variability of grain weight does not differ greatly although the difference is statistically significant. The grains resulting from the immediate cross (F_1 endosperm) are but little more than half as heavy as the grains of the parents and are no more variable. The grains borne by the F_1 plants[1] (F_2 endosperm) are extremely variable, with a standard deviation of nearly twice that of the parental grain weight. The average grain weight of the F_1 plants is greater when Kubanka is used as the female parent, but the difference, although statistically significant, may depend on environmental and not genetic factors.

STERILITY IN THE F_2 GENERATION

The seed from an F_1 plant of Kubanka × Bluestem was planted in the greenhouse under very uniform and favorable conditions. The F_1 plant selected was representative of all F_1 plants, both in vegetative development and sterility. Of the 84 seeds planted 6 failed to germinate, 78 seeds germinated but of these only 61 produced heads and only 47 produced grain. In the entire F_2 only 1 or perhaps 2 plants were as fertile as the parents. The descriptions of the F_1 grain (F_2 endosperm) and the resulting F_2 plants are given in table 2.

The sterility in F_2 ranged from plants which were totally sterile to one which set 2.66 grains per spikelet. The mean sterility of the 61 plants that headed was found to be .83 with a standard deviation of .64. Thus in the F_2 a larger proportion of plants is totally sterile than in the F_1. Moreover, many F_2 plants fail to develop normally and a large percentage fails to produce heads. Under field conditions probably half of the F_1 grain fails to produce viable F_2 plants, and under unfavorable climatic conditions nearly all F_1 grains fail to develop, even though standard varieties may show more than 50 percent germination under the same conditions. Much of the extreme sterility in F_2 is undoubtedly due to

[1] The mean weight and variability of seeds of parents and F_1 plants were relatively uniform, so all individuals of each class were grouped together. The variability in seed weight is not due to differences in average seed weight of individual plants.

TABLE 2

Kubanka × Bluestem—F_1 and F_2.
(*Greenhouse* 1917.)

F_1			F_2				F_1			F_2			
Grain No.	Weight in mg*	Wrinkled or plump	Height of plant in cm	No. of spikelets	No. of grains	Grains per spikelet	Grain No.	Weight in mg	Wrinkled or plump	Height of plant in cm	No. of spikelets	No. of grains	Grains per spikelet
1	15	W	127	120	156	1.30	43	45	P	96	54	62	1.15
2	20	W					44	45	P	128	80	20	.25
3	20	W					45	45	P	128	60	45	.75
4	20	P					46	45	P	117	+	0	.00
5	25	W	132	106	142	1.34	47	45	P	*9*			
6	25	W	131	90	111	1.23	48	45	P	137	148	213	1.44
7	25	W	118	72	78	1.10	49	50	W	145	66	21	.32
8	30	W	123	68	23	.34	50	50	W	109	+	0	.00
9	30	W					51	50	W	128	+	0	.00
10	30	W	124	100	200	2.00	52	50	W	54	+	0	.00
11	30	P	136	115	58	.50	53	50	W	140	100	41	.41
12	30	P					54	50	W	*14*			
13	35	W	119	92	127	1.38	55	50	W	*13*			
14	35	W	115	124	177	1.42	56	50	P	107	88	16	.18
15	35	W	130	74	6	.08	57	50	P	80			
16	35	W	128	47	125	2.66	58	50	P	30			
17	35	W	130	150	68	.45	59	50	P	115	+	0	.00
18	35	P	105	74	10	.14	60	50	P	40			
19	40	W	126	116	152	1.31	61	50	P	129	188	391	1.81
20	40	W	136	102	96	.94	62	50	P	*13*			
21	40	W	*10*				63	55	W	*14*			
22	40	W	122	122	185	1.52	64	55	W	115	151	253	1.70
23	40	W	35				65	55	W	142	102	37	.37
24	40	W	*10*				66	55	W	114	86	118	1.37
25	40	W	110	60	77	1.28	67	55	W	*14*			
26	40	W	105	80	57	.71	68	55	P	124	138	180	1.30
27	40	W	40				69	55	P	105	100	131	1.31
28	40	W	*11*				70	55	P	87	+	0	.00
29	40	W					71	55	P	147	36	52	1.44
30	40	W	127	130	183	1.41	72	55	P	145	192	306	1.60
31	40	P	106	112	73	.65	73	55	P	50	+	0	.00
32	40	P	*7*				74	60	W	130	94	111	1.18
33	40	P	100	+	0	.00	75	60	W	115	+	0	.00
34	40	P	117	80	15	.19	76	60	P	60			
35	40	P	60	+	0	.00	77	60	P	135	126	216	1.71
36	40	P	40				78	60	P	86	+	0	.00
37	45	W	132	70	50	.70	79	60	P	153	104	136	1.31
38	45	W	121	68	78	1.14	80	65	W	90	+	0	.00
39	45	W	100	130	59	.45	81	65	W	115	100	167	1.67
40	45	W	137	126	67	.53	82	65	W	155	34	10	.30
41	45	W	108	100	29	.29	83	65	P	61	+	0	.00
42	45	P	130	84	138	1.64	84	70	W	63	+	0	.00

poor vegetative development of certain plants. Such a relation is indicated by the relatively high correlation between sterility and height of the 61 F_2 plants which headed ($r = .42 \pm .07$). Among the 47 plants which set grain the high sterility of certain individuals does not seem to be due to poor vegetative development, since there is no significant correlation between height and sterility of the 47 F_2 plants ($r = .04 \pm .10$).

The 84 F_1 grains were extremely variable in weight and were also variable in shape,—whether wrinkled or plump. In table 2 the F_1 grains are arranged in order of weight and arbitrarily classified as wrinkled or plump. The average weight of the wrinkled grains was found to be but little less than the weight of the plump grains. The correlation between weight and plumpness of grain was found to be rather low ($r = .23$). The correlation was determined by a method suggested by PEARSON (1909).

Among the F_1 seeds which failed to germinate, a majority are in the lower weight classes, but among the 78 plants which grew there is little or no correlation between weight of F_1 grains and height of the resulting F_2 plant ($r = -.10 \pm .05$). The correlation is not greatly increased by using only the 61 F_2 plants which headed ($r = -.20 \pm .08$.) The size of the F_1 grain gives little indication of the probable size of the F_2 plant. The plumpness of F_1 grains has little or no effect on the size of F_2 plants. For the 78 F_2 plants the correlation between wrinkled or plump F_1 grain and height of F_2 plants was found to be only .10, and for the 61 plants which headed, $r = .10$.

A similar correlation was found between F_1 grain weight and F_2 sterility. For the 47 F_2 plants that headed, the correlation between F_1 grain weight and F_2 sterility was $.03 \pm .10$, and for all 78 plants, $r = -.19 \pm .08$. The correlation between wrinkled or plump F_1 grains and F_2 sterility was found to be .24 for the 61 F_2 plants which headed. Although small wrinkled grains are characteristic of partially sterile hybrids there is little or no correlation between F_1 grain weight or shape and the height or sterility of the resulting F_2 plants.

DISCUSSION AND SUMMARY

In a cross of Kubanka × Bluestem a male gamete with 21 chromosomes unites with an egg cell containing 14 chromosomes. In the endosperm there are 28 chromosomes of maternal origin and 21 chromosomes of paternal origin while in the reciprocal cross 42 chromosomes are contributed by the polar nuclei and only 14 by the sperm nucleus. Such unbalanced conditions of the chromosome sets might be expected to result in abnormal endosperm development, although in pure species the triploid condition of the endosperm does not result in abnormal development, unless endosperm formation itself is considered abnormal. Endosperm formation is not due simply to the triploid condition, however, because triploidy is found in the vegetative cycle of a number of plants.

The greatly increased variability of the F_1 grain (F_2 endosperm) can be attributed to differences in chromosome number, to recombinations of factors for growth, and to more or less compatible chromosome combinations. Although the maximum mixture of parental chromosomes is found in the F_1 endosperm the F_2 endosperms may in many cases be significantly smaller than F_1 endosperms, due to inharmonious chromosome relations.

Since poorly developed F_1 endosperm is associated with sterility and unusual vegetative vigor of the F_1 plant, a high degree of correlation would be expected between F_2 endosperm development and sterility and vegetative development of F_2 plants. An analysis of the data shows, however, that there is little or no correlation between F_2 endosperm development and F_2 sterility or vegetative development. Apparently the results of the peculiar chromosome relationships in endosperm formation do not indicate the nature of the chromosome relations of the accompanying embryo. This relation may be due to the greater opportunity for an unbalanced condition of maternal and paternal chromosomes in the endosperm.

The increased sterility in F_2 individuals as compared with the F_1, and especially the weak somatic development of many plants, may be attributed to chromosome combinations incompatible for vegetative development. The chromosome compatibility may depend on numerical or balanced relation of the chromosomes or on specific chromosome relationships. In F_1 plants two complete sets of chromosomes are present and the F_1 plant is unusually vigorous even though it is partially sterile. In F_2 individuals a complete set of chromosomes of either parent would rarely be found and the perfection of somatic development would be expected to vary with the completeness of the parental sets of chromosomes. Thus in F_2 many individuals are completely sterile because of weak vegetative development as well as gametic sterility.

LITERATURE CITED

PEARSON, K., 1909 On a new method of determining correlation between a measured character A, and a character B, of which only the percentage of cases wherein B exceeds (or falls short of) a given intensity, is recorded for each grade of A. Biometrika 7: 96-105.