INHERITANCE OF COMPLEMENTARY DWARFING FACTORS IN WHEAT [1]

By V. H. FLORELL, formerly *associate agronomist*, and J. FOSTER MARTIN, *assistant agronomist, Division of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

The occurrence of dwarfs in cereal and other plant hybrid populations is being reported by an increasing number of investigators. In most cases in the cereals it has been observed in connection with hybridization experiments for economic improvement. The crosses reported in this paper were produced incidentally in a wheat-breeding program, the main object of which was the production of improved bunt-resistant varieties. Complete dwarfing occurred in the F_1 generation of eight crosses, although dwarfs more commonly are found as segregates in the F_2 generation.

The dwarf condition in plants apparently is due to genetic factors, to chromosome abnormalities, or to other causes that interfere with normal height development. It is now generally recognized that dwarfing of the kind usually encountered in intraspecific hybrids is governed chiefly by factor interactions but that the ratios obtained usually are modified to some extent by irregular chromosome behavior.

The presence of dwarfs in wheat crosses which first appear in the F_2 generation has been explained by a number of investigators by the interaction of two factors, a factor for normal height, *N* (or *I*), which when present inhibits the dwarfing factor, *D*. In these experiments the F_2 segregation occurred in a ratio of 13 normal to 3 dwarf plants. Workers whose results with dwarfing have been explained on a two-factor basis include Hayes and Aamodt (*6*),[2] Clark and Hooker (*2*), Goulden (*5*), Stephens (*9*), Stewart and Tingey (*10*), Clark and Quisenberry (*3*), Nieves (*8*), Churchward (*1*), Tingey (*12*), and Waterhouse (*14*).

Other workers, viz, Waldron (*13*), Neethling (*7*), Florell (*4*), and Churchward (*1*), obtained segregations that indicated either three- or four-factor differences but which possibly are best explained as poor fits to the two-factor difference obtained by other workers.

Dwarfs in the F_1 generation from normal parents have been observed by a number of wheat breeders, including Waterhouse (*14*), who found dwarfs in the F_1 generation in 25 wheat crosses. Results from such dwarfs carried through the F_2 and F_3 generations were presented by Thompson (*11*).

These results were explained on the basis of the interaction of three factors. Thompson assumed the presence of the usual factor for normal, or inhibitor for dwarf, *I* (or *N*), with the dwarfing factor (*D*) and an extra inhibitor (*E*), which inhibited or neutralized the action

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[2] Reference is made by number (italic) to Literature Cited, p. 160.

of the inhibitor *I*. Thus, the dwarf plants were conditioned by the genes *IED* and *ieD*, and the normal plants by *IeD* and *IEd*.

According to Thompson's scheme the F_2 population will segregate in a ratio of 39 *D* : 25 *N*. The F_2 normal plants selected at random will produce F_3 families in a ratio of 19 true-breeding normal to 6 segregating normal and dwarf, and the F_2 dwarf plants will produce 7 true-breeding dwarf families to 32 segregating dwarf and normal.

MATERIAL AND METHODS

More than 50 crosses were made at the Idaho Agricultural Experiment Station, Moscow, Idaho, in 1931, by the senior writer and his assistants in a wheat-breeding program designed to develop improved bunt-resistant varieties of white winter wheat for the Pacific coast region. Four of these crosses and their reciprocals produced all dwarf plants in the F_1 generation. Turkey-Florence (G–326W8) was a parent in three of these crosses and Hussar-Hohenheimer (C. I. 10068 [3]) in the other. Dwarfs in the F_1 generation also were obtained in 1933 from two Arco selections (8118 and 8120) crossed with both Turkey-Florence and Hussar-Hohenheimer in 1932. Some F_1 plants of the Hussar-Hohenheimer × Jenkin cross were backcrossed to both parents in 1932.

Turkey-Florence is a white-kerneled, bunt-resistant winter wheat selected from the same cross from which Ridit was produced. The original Turkey-Florence cross was made by E. F. Gaines at the Washington Agricultural Experiment Station, Pullman, Wash., and the white-kerneled Turkey-Florence selection used in the present investigation was made by D. E. Stephens at Moro, Oreg.

Hussar-Hohenheimer (C. I. 10068) was selected by the late H. M. Woolman at Corvallis, Oreg. This wheat is a bearded, red-kerneled, white-strawed strain having a winter habit of growth.

Jenkin is a late-maturing spring variety of club wheat having tall white straw, soft white kernels, and brown chaff. Federation is a medium early spring variety having short stiff straw, soft white kernels, and brown chaff. Baart is an early spring variety having medium-tall, slender, and pliable straw and large white semihard kernels.

The Arco selections were obtained from the cross Arcadian × Hard Federation, which was made by Walter Carpenter at Moro, Oreg., in 1919. The Arco selections have short stiff straw, soft white kernels, and a winter habit with rather low winter hardiness.

Dwarf plants usually can be distinguished readily from normal plants by the much reduced height and by the abundance of grassy leaves at the base of the plants resulting from their shortened internodes. Height measurements of the F_1 and F_2 dwarfs and the parents were taken for comparison, but in the F_3 generation the dwarfs were distinguished by inspection only.

In making the crosses, pollen from a single spike was used to fertilize each emasculated spike. A good set of seed was obtained both in 1931 and 1932. The crossed kernels were sown 4 inches apart in 5-foot rows spaced 1 foot apart, between a row of each of the parents. Fairly vigorous F_1 hybrid plants were obtained in both 1932 and 1933,

[3] C. I. refers to accession number of the Division of Cereal Crops and Diseases, formerly Office of Cereal Investigations.

although there was some winter-killing of tender strains in both years. In 1932 Baart winter-killed, and a somewhat reduced stand was obtained in both the Federation and Jenkin parents. Good stands were obtained in the F_1 hybrids and vigorous plants were produced in the hybrids as well as in the parents that survived.

The height of each of the hybrid and parent plants studied was obtained by measuring the height of the earliest culm. The length of spike of the earliest culm also was measured and the average weight of kernel in milligrams was determined from the weight of 100 kernels from each plant.

Most of the F_1 plants produced seed fairly abundantly. Dwarf plants that did not produce spikes were designated as grass plants or grassy dwarfs. Seeds from F_1 dwarf and parent plants were sown in late October at the rate of 100 kernels per row in 16-foot rows 1 foot apart. Emergence did not take place before the winter snows began, and fall-stand counts could not be made in 1932.

A good snow covering was present during most of the winter months, but only fair winter survival was obtained. The dwarfs showed most evidence of winter injury. The growing season again was favorable so that vigorous plants were obtained from most of the surviving individuals.

At harvest time, plant height, length of spike, and average weight of kernel per plant were obtained as in the F_1 generation. Seed of good quality again was obtained from most of the dwarfs as well as from the parent plants.

In the fall of 1933, this experiment was transferred to the Pendleton Field Station, Pendleton, Oreg., where the crop was grown and the data were taken by the junior writer. Seed from about 25 to 35 dwarf F_2 plants and from about 35 to 70 normal F_2 plants was selected at random from each of four crosses to continue the experiments in the F_3 generation. About 75 to 100 kernels, in some instances fewer, from each plant were sown in 16-foot rows 1 foot apart. Reasonably satisfactory emergence occurred, but some of the weaker plants were lost during the winter. Limited moisture and hot weather in the spring caused many dwarfs to die prematurely and rendered identification difficult. These conditions also limited the height of some weaker normal plants.

EXPERIMENTAL DATA

THE F_1 GENERATION

The average height of culm, length of spike, and weight of kernel of four dwarf F_1 wheat crosses and of their normal parents, at Moscow, Idaho, in 1932, are presented in table 1. Similar data, except for kernel weights, for four additional crosses, in 1933, are also given.

The average height of the dwarfs in 1932 was about 15 to 17 inches; that of Turkey-Florence 44 inches, of Jenkin 43 inches, and of Federation 33 inches. The standard deviations of the heights of the F_1 hybrids were similar to those of the normal parents but were relatively larger owing to dwarfness of the plants. The mean height of the F_1 dwarfs in 1933 ranged from about 10 to 13 inches. The parents likewise were shorter than in 1932, owing to dry weather at maturity and to poor soil. The F_1 dwarfs and parents of two of these crosses are shown in figure 1.

TABLE 1.—*Average culm height, spike length, and kernel weight of eight dwarf F_1 wheat crosses and their normal parents, at Moscow, Idaho, 1932 and 1933*

Year and parent or hybrid	Plants	Mean and standard deviation: Culm height	Spike length	Kernel weight
1932	*Number*	*Inches*	*Cm*	*Mg*
Turkey-Florence	6	45.17± 1.47	11.67±1.92	47.50±1.92
F_1 hybrid	15	16.92±10.40	7.03±2.43	39.77±6.11
Jenkin	9	43.44± 2.87	6.60± .78	45.80±4.40
Turkey-Florence	8	44.63± 2.99	10.94±1.63	46.25±1.66
F_1 hybrid	7	15.43± 2.91	8.50±1.29	37.56±4.32
Federation	11	32.86± 5.45	8.64±1.91	42.73±5.04
Turkey-Florence	6	41.33± 2.83	9.92±1.17	37.00±1.15
F_1 hybrid	7	15.71± 3.57	8.00±1.36	----------
Baart [1]	0	----------	----------	----------
Hussar-Hohenheimer	9	39.56± 8.17	11.06±1.69	45.00±3.49
F_1 hybrid	8	14.88± 7.77	9.81±3.39	----------
Jenkin	2	38.50±10.59	6.00±1.42	47.00±1.42
1933				
Hussar-Hohenheimer	8	33.38± 2.98	8.94± .47	----------
F_1 hybrid	10	9.70± 2.12	9.15±1.59	----------
Arco (sel. 8120)	9	28.56± 3.25	7.67±1.86	----------
Turkey-Florence	1	36.00	10.00	----------
F_1 hybrid	1	13.00	9.00	----------
Arco (sel. 8120)	3	30.00± .00	7.88± .41	----------
Arco (sel. 8118)	3	32.33± 3.11	8.33± .58	----------
F_1 hybrid	3	12.00± 4.20	7.67± .82	----------
Turkey-Florence	4	39.00± 2.35	10.25±1.50	----------
Arco (sel. 8118)	13	29.13± 3.43	8.00±1.21	----------
F_1 hybrid	13	10.69± 5.30	8.69± .80	----------
Hussar-Hohenheimer	12	36.58± 2.22	9.33±2.48	----------

[1] Winter-killed.

The length of the main spike of the F_1 dwarfs was intermediate in some crosses but less than that of either parent in others.

The average weight of kernel is given for only two crosses, but in both cases it is definitely less than in either parent.

The first generation of the Hussar-Hohenheimer × Jenkin backcrosses was grown at Moscow, Idaho, in 1933. The proportion of normal to dwarf plants expected in the backcross to either parent was 1:1. Thirty-five mature plants were obtained from the backcross to Hussar-Hohenheimer, of which 17 were dwarf and 18 normal. This was close to the expected result. Seven plants, all normal, were obtained from the backcross to Jenkin, the number of plants apparently being too small to give the expected segregation.

The mean height of the dwarf plants, not including two grassy plants, was 10.47±5.84 inches, and that of the normal plants 32.94±5.88 inches. The mean height of the Hussar-Hohenheimer parent (28 plants) was 31.14±8.73 inches, and that of the Jenkin parent (4 plants) 32.00±4.69 inches. The mean height of the 7 normal plants obtained by backcrossing the F_1 with Jenkin was 31.86±9.21 inches.

THE F_2 GENERATION

The number of seeds of the different crosses sown and the plants harvested in the F_2 generation were as follows: Turkey-Florence × Jenkin, 688 sown and 394 (57.3 percent) harvested; Turkey-Florence × Federation, 381 sown and 139 (36.5 percent) harvested; Turkey-Florence × Baart, 366 sown and 147 (40.2 percent) harvested; Hussar-Hohenheimer × Jenkin, 410 sown and 137 (33.4 percent) harvested.

It is evident that all of the crosses suffered serious winter injury, since in favorable seasons survivals of over 90 percent are not uncommon. The data on normal and dwarf plants in the F_2 generation are presented in table 2. According to Thompson's three-factor hypothesis, these crosses should have given dwarf and normal plants in a ratio of 39 D:25 N. This ratio was indicated only in Turkey-

FIGURE 1.—Dwarf F_1 hybrid and parental plants at Moscow, Idaho, 1933. In foreground: *a*, Hussar-Hohenheimer; *b*, dwarf hybrid; *c*, Arco; *d*, Turkey-Florence; *e*, dwarf hybrid; *f*, Arco.

Florence × Baart, in which the deviation was 3.3 times the probable error. Only in this cross did the number of dwarfs exceed the number of normal plants.

TABLE 2.—*Number of normal and dwarf plants in the F_2 generation in four wheat crosses at Moscow, Idaho, 1933*

Cross	F_1 families	F_2 plants					
		Total	Observed		Calculated[1]		Deviation
			Normal	Dwarf	Normal	Dwarf	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Turkey-Florence × Jenkin and reciprocal	6	394	245	149	154	240	91±6.5
Turkey-Florence × Federation	4	139	83	56	54	85	29±3.2
Turkey-Florence × Baart	3	147	70	77	57	90	13±4.0
Hussar-Hohenheimer × Jenkin and reciprocal	6	211	137	74	82	129	55±4.8

[1] Based upon the ratio of 39 dwarf to 25 normal.

It seems probable that winter-killing destroyed the greater portion of the dwarf segregates. The number of normal plants did not exceed the number that might be expected from a reasonably good survival, whereas the number of dwarf plants was decidedly less. Dwarf plants are less vigorous than normal plants, and therefore more likely to be injured by unfavorable conditions.

The mean height of the dwarfs in the F_2 generation ranged from 12 to 15 inches. A number of somewhat taller dwarfs, which probably represented heterozygotes, were classified as intermediate dwarfs. These had the typical dwarf characteristics in most respects but were 28 to 34 inches in height. There was little or no overlapping in the height of the dwarf, intermediate-dwarf, and normal classes.

THE F_3 GENERATION

Seed from normal and from dwarf F_2 plants was selected at random for growing at Pendleton, Oreg., in the F_3 generation. A fairly large population was produced by the normal F_2 plants, but the dwarf progenies suffered from winter-killing.

The normal F_2 plants, according to the three-factor hypothesis, should produce in the F_3 generation a ratio of 19 true-breeding normal (tall) families to 6 segregating families. Two of the families should segregate in a ratio of 3 normal to 1 dwarf, and 4 families in a ratio of 13 normal to 3 dwarf plants. The dwarf F_2 plants should produce segregations in the F_3 generation of 7 true-breeding dwarf to 32 segregating families. Four types of segregation for dwarf and normal plants should occur among the 32 segregating families in the following ratios: 16; 3 : 1; 4, 13 : 3; 4, 9 : 7; and 8, 39 : 25.

The ratio of true-breeding to segregating families from both normal and dwarf F_2 plants was close to the calculated results (table 3). A study of the relative number of normal and dwarf plants in individual rows (families) from normal F_2 plants showed, however, a deficiency of dwarf plants in nearly all rows, based on the expected ratios 3 : 1 and 13 : 3. A number of these rows from each of the 4 crosses contained only 1 to 4 dwarfs among 50 or more plants. These may be normal progenies in which some chromosomal aberration has resulted in the production of dwarfs. Thompson (*11*) grew F_4 progenies from normal plants selected from four F_3 families, each of which likewise had given but few dwarfs. He found dwarfs in the progeny of but a single plant and concluded that such F_3 rows were in reality true-breeding normals.

TABLE 3.—*Behavior in the F_3 generation of the progenies of F_2 plants of four wheat crosses at Pendleton, Oreg., 1934*

Cross	Progenies of normal F_2 plants						Progenies of dwarf F_2 plants					
		Observed		Calculated [1]				Observed		Calculated [3]		
	Total	Normal	Segregating	Normal	Segregating	Deviation [2]	Total	Dwarf	Segregating	Dwarf	Segregating	Deviation [2]
	No.	*No.*	*No.*	*No.*	*No.*		*No.*	*No.*	*No.*	*No.*	*No.*	
Jenkin × Turkey-Florence and reciprocal	50	40	10	38.0	12.0	2.0±2.04	36	3	33	6	30	3±1.55
Turkey Florence × Federation	61	44	17	46.4	14.6	2.4±2.25	29	1	28	5	24	4±1.39
Turkey-Florence × Baart	51	39	12	38.8	12.2	.2±2.06	33	2	31	6	27	4±1.49
Hussar-Hohenheimer × Jenkin and reciprocal	38	24	14	28.9	9.1	4.9±1.78	25	8	17	4	21	4±1.29
All crosses	200	147	53	152.0	48.0	5.0±4.07	123	14	109	22	101	8±2.87

[1] Based upon the ratio of 19 true-breeding normal to 6 segregating.
[2] Probable errors calculated by the formula $0.6745\sqrt{pqn}$.
[3] Based upon the ratio of 7 true-breeding dwarf to 32 segregating.

If the families having a low number of dwarfs are included with the true-breeding normal families, a very good fit for the 19 true-breeding to 6 segregating lines is obtained.

The number of true-breeding dwarf families was less than the expected 7:32 ratio in three of the crosses and above the expected number in one cross. Deviations from the calculated number were less than three times the probable error in all crosses. The somewhat small number of dwarf families possibly may be accounted for by a higher mortality in the F_2 among the homozygous than among the heterozygous dwarf plants.

When the distributions for the individual rows in the various crosses were examined for conformity to the expected ratios, it was evident that the families could not be separated accurately into the expected types of segregation. However, a number of the families from normal F_2 plants, particularly in Jenkin × Turkey-Florence and Turkey-Florence × Federation crosses, segregated in satisfactory 3:1 and 13:3 ratios. It is clear that the dwarf plants suffered considerable killing.

The F_3 segregations in the Turkey-Florence × Baart cross are shown by individual families in table 4.

TABLE 4.—*Number of normal and dwarf plants in F_3 families from F_2 normal plants in the Turkey-Florence × Baart cross at Pendleton, Oreg., 1934*

Plants from normal F_2 plants				Plants from dwarf F_2 plants			
Normal	Dwarf	Total	Breeding behavior	Dwarf	Normal	Total	Probable breeding group
Number	*Number*	*Number*		*Number*	*Number*	*Number*	
46	17	63	Segregating	13	4	17	3 *D*:1 *N*.
53	17	70	do	26	8	34	Do.
36	27	63	do	21	6	27	Do.
47	27	74	do	48	20	68	Do.
70	7	77	do	46	18	64	Do.
78	6	84	do	70	25	95	Do.
56	11	67	do	36	13	49	Do.
59	6	65	do	51	17	68	Do.
63	14	77	do	42	18	60	Do.
58	10	68	do	35	9	44	13 *D*:3 *N*.
69	6	75	do	30	23	53	9 D:7 N.
74	3	77	Normal with few dwarfs	39	48	87	Do.
68	2	70	do	40	43	83	Do.
57	2	59	do	29	38	67	Do.
78	1	79	do	47	32	79	Do.
80	1	81	do	15	20	35	Do.
[1] 2,966	0	[1] 2,966	All normal [1]	19	26	45	Do.
				34	32	66	Do.
				37	31	68	Do.
				8	15	23	Do.
				34	50	84	Do.
				19	32	51	Do.
				9	21	30	Do.
				16	33	49	Do.
				53	28	81	39 *D*:25 *N*.
				48	21	69	Do.
				43	27	70	Do.
				43	28	71	Do.
				45	20	65	Do.
				40	27	67	Do.
				35	16	51	Do.
				[2] 171	0	171	True-breeding dwarf.

[1] 35 rows. [2] 2 rows.

All segregating families grown from the dwarf F_2 plants had a fairly good proportion of dwarfs, but according to expectation there should have been a preponderance of dwarf plants in all of the families that segregated. This was the case in the majority of the families only in the Turkey-Florence × Baart cross, data for which are shown in table 4. In this cross families were obtained that indicated the expected segregating dwarf to normal ratios of 3:1, 13:3, 9:7, and 39:25. The proportion of families segregating into 3:1 and 13:3 ratios was less than the calculated values, owing to shortages of dwarf plants.

Two families in the Hussar-Hohenheimer cross were all dwarf except for one normal plant in one family and two normal plants in the other. It is probable that these plants were the results of natural crossing by normal plants. Tingey (*12*) showed that a fairly high percentage of natural crossing on dwarf plants by pollen from normal plants may occur.

DISCUSSION

When a combination of parents gives rise to a new character expression such as dwarfness in the F_1 generation, it is evident that some sort of complementary-factor relationship is responsible. It has been shown by a number of investigators that dwarfing in wheat is due to a dominant factor *D* for dwarfing and that this factor is hypostatic to a factor *I* (or *N*) for normal height. A number of normal wheats have been shown to possess the dominant *IIDD* factors, and other normal varieties the recessive *iidd* factors. To explain the production of dwarfs in F_1 from normal varieties, Thompson (*11*) assumed a third factor (*E*) for the dwarf-factor complex, which inhibits or neutralizes the *I* factor.

This scheme satisfactorily explains the general situation where F_1 dwarfs are produced from normal parents. Contrary to Thompson's point of view, however, a modified complementary-factor scheme also may be used to explain the results obtained in the crosses described by the writers and by Thompson (*11*) without assuming an inhibitor-of-an-inhibitor relationship, if his *E* factor is assumed to be a second factor for dwarfing which is not capable of producing dwarfs alone, or in the absence of *I*, but which with *D* suppresses the expression of the *I* factor. The factors *D* and *E* would thus represent different capacities for dwarfing, and the factors *IIDD* would be contributed by one parent and the *EE* factor by the other parent when dwarfs are produced in the F_1 generation. This factor hypothesis would produce the same segregations as in Thompson's scheme.

The occurrence of occasional aberrant dwarf plants in apparently normal families has been elucidated by the cytological researches of both Goulden (*5*) and Thompson. Thompson (*11, p. 346*) states that—

> In view of the difficulty in formulating a completely satisfactory genetic interpretation, one might be inclined to attribute dwarfishness to chromosome irregularity. Such a proceeding would not be justified, however, since the F_1, though dwarf, had the full complement of 21 chromosomes as did dwarfs of later generations. It seems clear that dwarfness is due to genetic factors.

He concludes that the appearance of occasional unexpected dwarf plants may very well be due to the chromosome irregularities observed.

The duplication of chromosome sets (or genoms), which is believed to have taken place in the evolution of wheat, makes it entirely possible that chromosome homology may exist to a greater or less degree among at least some of the chromosome pairs. As stated by Goulden

(*5*), "There may in some cases be sufficient affinity between chromosomes that are not strictly homologous to bring about different types of pairing." Irregular pairing would result in occasional factor combinations that would afford opportunity for expression of the dwarf factor.

The results of the experiments reported in this paper indicate the genotypic composition for dwarfing in the wheat varieties used. The three-factor combination includes the normal (or dwarf-inhibiting) factor (*I*), a dominant factor (*D*), and a complementary dwarfing factor (*E*). The only parental combinations of factors which together would yield a dwarf F_1 progeny from normal parents would be *IIDDee* and *iiddEE*.

Turkey-Florence crossed with Jenkin, Federation, Baart, and the two Arco selections 8118 and 8120 produced all dwarfs in F_1, as did Hussar-Hohenheimer crossed with Jenkin, and the Arco selections. The genotypes of Turkey-Florence and Hussar-Hohenheimer must be identical, since crosses with the same varieties gave similar results. Also the five varieties with which these two were crossed must have the same genotype for the same reason. Tingey (*12*) showed in his studies, where two factors for dwarfing were involved, that the genotype of Federation was *IIDD*. The senior writer (*4*), in his studies of dwarfs in backcrosses, found that Jenkin contained the dominant factor *IIDD* and Quality the recessive factors *iidd*. Since Baart and the two Arco strains produced the same results as Jenkin and Federation, all must have had the dominant factors *IIDD*.

The third factor, *EE*, must have been contributed by Turkey-Florence and Hussar-Hohenheimer. The genotype for dwarfing of Jenkin, Federation, Baart, and the two Arco selections apparently is *IIDDee* and that of Turkey-Florence and Hussar-Hohenheimer *iiddEE*.

SUMMARY

Dwarfs were obtained in the F_1 generation in eight crosses between normal (tall) varieties of wheat at Moscow, Idaho, in 1931 and 1932. Turkey-Florence was used in five crosses, and Hussar-Hohenheimer in three crosses. In 1931 Turkey-Florence was crossed with Jenkin, Federation, and Baart, and Hussar-Hohenheimer was crossed with Jenkin. In 1932 both Turkey-Florence and Hussar-Hohenheimer were crossed with the two selections of Arco.

The height of F_1 dwarf plants averaged from 15 to 17 inches, and that of the normal parents from 33 to 44 inches. The average weight of kernel of F_1 dwarf plants was less than that of the parents.

The segregation of dwarf and normal plants was studied in the F_2 and F_3 generations in the four crosses made in 1931. Winter-killing caused considerable loss of F_2 plants. The heaviest losses seemingly occurred among the dwarfs.

The number of normal plants, based on a three-factor difference and a ratio of 39 dwarf to 25 normal plants, was close to the expected in one of the F_2 crosses.

The expected ratio of true-breeding to segregating families from both normal and dwarf F_2 plants was verified by the F_3 results. Satisfactory fits were obtained in all crosses. In general, dwarfs in individual families were too few in number to satisfy the expected ratios.

Dwarf F_1 plants from crosses between normal varieties indicate complementary factors. To explain the results on a complementary-factor basis, a second dwarfing factor, *E*, may be assumed, which, with the established *D* factor, is dominant over *I*. The *E* factor alone, unlike the dominant *D*, is not capable of producing dwarfs in the absence of *I*.

The genotype of the varieties Turkey-Florence and Hussar-Hohenheimer, accordingly, is *iiddEE*, and that of the other varieties used *IIDDee*.

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