IRREGULARITIES IN THE INHERITANCE OF THE HAIRY-NECK CHARACTER TRANSPOSED FROM SECALE TO TRITICUM [1]

By J. W. TAYLOR

Associate agronomist, Division of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

A preliminary paper [2] recorded the transfer of the "hairy neck" of rye (*Secale*) to wheat (*Triticum*). This transfer of a definite character is of interest inasmuch as within *Secale* there are certain economic characters, particularly winter hardiness, that are desired in the common wheats. If it can be shown that one character may be successfully transferred from one genus to the other there are good reasons to believe that other characters also may be transferred. This paper deals primarily with the genetic stability and with the behavior of these hairy-neck wheat forms in crosses with different varieties of wheat.

REVIEW OF LITERATURE

Leighty and Taylor [2] and Florell [3] report the isolation of hairy-neck lines from wheat-rye hybrids. Bleier [4] gives a comprehensive review of the work of investigators who have studied phases of the wheat-rye problem. Florell [3] has reviewed studies on the cytology of wheat-rye hybrids.

MATERIALS AND METHODS

Hairy-neck is characterized by the presence of pubescence or hairiness on the peduncle, or that portion of the culm just below the first node of the rachis (fig. 1). In rye plants and in hairy-neck wheatlike segregates from wheat-rye crosses hairiness varies from a few hairs around the apical node of the culm to a dense pubescence extending 3 or more inches below the head.

As reported by Leighty and Taylor,[5] typical wheatlike hairy-neck segregates were selected in 1923 at the Arlington Experiment Farm, near Washington, D.C., from descendants of natural wheat-rye hybrids found in 1918. Ten of these selections were grown originally, but later work was concentrated on three, designated as C, K, and H, which it is believed represent the characteristic behavior of this group of selections.

The three selections are similar to *Triticum vulgare* [6] in their principal spike characters, with the exception of the neck (or peduncle), which is hairy, as shown in figure 2. The plants are not so tall and

[1] Received for publication Nov. 18, 1933; issued June 1934.

[2] LEIGHTY, C. E., and TAYLOR, J. W. "HAIRY NECK" WHEAT SEGREGATES FROM WHEAT-RYE HYBRIDS. Jour. Agr. Research 28: 567–576, illus. 1924.

[3] FLORELL, V. H. A CYTOLOGICAL STUDY OF WHEAT-RYE HYBRIDS AND BACK CROSSES. Jour. Agr. Research 42: 341–362, illus. 1931.

[4] BLEIER, H. GENETIK UND CYTOLOGIE TEILWEISE UND GANZ STERILER GETREIDEBASTARDEN. Bibliog. Genetica 4: 321–400, illus. 1928.

[5] LEIGHTY, C. E., and TAYLOR, J. W. See footnote 2.

[6] According to the rules of botanical nomenclature the name of this species is *Triticum aestivum*, but as *T. vulgare* is in general use among agronomists and cereal pathologists and geneticists, the writer gives preference to that form.

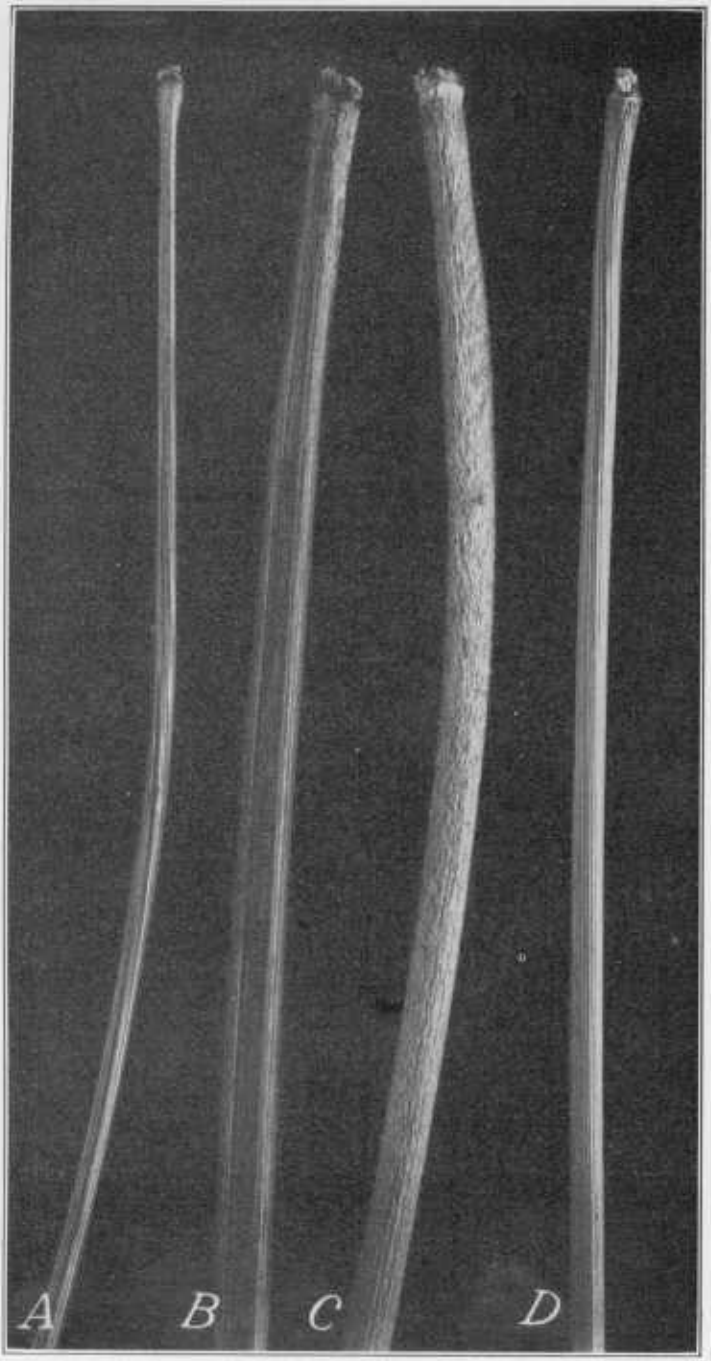

FIGURE 1.—Necks (upper portions of peduncle) of rye, wheat, and two hairy-neck wheatlike selections from wheat-rye hybrids. *A*, Abruzzes rye; *B*, Selection C; *C*, Selection H; *D*, Fulcaster wheat. × 3. *A*, *B*, and *C* are hairy.

are less vigorous than those of wheat, as is usually the case with hairy-neck segregates of wheat-rye crosses. They are more subject to natural crossing than are commercial varieties of wheat, and selfing has been necessary to maintain them. They may be described as follows:

FIGURE 2.—Heads of wheat and three hairy-neck wheatlike selections from wheat-rye hybrids. *A*, Selection K; *B*, Selection H; *C*, Fulcaster wheat; *D*, Selection C. Natural size.

SELECTION C.—Awnless, white glumes, red kernel, with hairs extending one half inch downward from the apical node.

SELECTION K.—Awned, white glumes, red kernel, with hairs extending one half inch downward from the apical node.

SELECTION H.—Awned, white glumes, red kernel, with hairs extending 4 inches or more downward from the apical node. Spike more lax than that of Selection K.

Observations regarding the stability of each of the three selections with respect to the hairy-neck character were made. Each of these selections was crossed with several varieties of soft red winter wheat grown at the Arlington Farm and the progeny were studied in such a way as to determine the nature of the segregation of the hairy-neck character in relation to other characters of the parents. The F_2 populations were grown in spaced nursery rows and the F_3 populations in 5-foot head rows. All hairy-neck plants of each F_2 population which produced sufficient seed for a test were continued in the F_3 generation. Notes on neck character and height were taken in the field. Data on sterility were obtained from the two lower florets of each spikelet of the primary head.

EXPERIMENTAL RESULTS

CONSTANCY OF THE HAIRY-NECK SELECTIONS

The constancy of the hairy-neck character was determined by selfing hairy-neck plants of each of the selections and recording the number of aberrant types appearing in the following generation. The data for Selection C, which is regarded as typical of the hairy-neck segregates, and which has been selfed since 1925, are given in table 1. It will be seen that Selection C does not stand the test of genetic purity expected of a true species. Of 3,818 plants grown during the 8 years, 262, or nearly 7 percent, were different from those of Selection C with respect to the hairy neck.

TABLE 1.—*Constancy of the hairy-neck character in progeny of Selection C selfed for 8 generations*

Year	Total plants	Plants similar to Selection C	Plants differing from Selection C	
			Variant hairy	Variant smooth
	Number	*Percent*	*Percent*	*Percent*
1924	39	92.3	7.7	0.0
1925	675	93.8	5.9	.3
1926	608	94.7	4.8	.5
1927	388	99.0	1.0	.0
1928	435	93.5	5.1	1.4
1929	227	97.8	1.8	.4
1930	423	91.0	5.9	3.1
1931	1,023	89.2	9.6	1.2
Total or average	3,818	93.1	5.9	1.0

Two aberrant types appeared, one, designated "variant smooth", indistinguishable from wheat, and the other, designated "variant hairy", almost intermediate with respect to hairy neck between Selection C and wheat. There were approximately 1 percent of the former and 6 percent of the latter. Variant smooth is easily distinguished from Selection C because it is smooth-necked and taller. Variant hairy is from 4 to 6 inches taller than Selection C when grown under favorable conditions, but the difference in height may not be apparent under unfavorable conditions. Partly for this reason it is not so readily recognized. However, there is good reason to believe that none of the conclusions arrived at herein is invalidated by errors of classification.

During the 8 years Selection C never behaved as a pure line. Variant hairy necks were found every year and variant smooth necks in 6 of the 8 years. The greatest irregularity occurred in 1931, when 110 plants of a population of 1,023 plants, or 10.8 percent, were variants. The least variation occurred in 1927, when only 1 percent were variants.

Additional data regarding the constancy of Selection C and the breeding behavior of the variants selected from it were obtained by growing in 1930 a selfed plant of Selection C and selfing the progeny and growing them in 1931. The pertinent data are presented in table 2.

The progeny of the single selfed plant in 1930 were classified as 50 similar to Selection C, 1 variant hairy, and 2 variant smooth. Only 49 of the 50 plants of Selection C indicated in table 2 were grown in 1931, 1 failing to produce sufficient seed. Each of the 49 plant rows supported the 1930 classifications, breeding typical Selection C with 7.3 percent variants. The 2 variant smooth-neck plants bred smooth, and the variant hairy-neck plant segregated in the ratio of 3 smooth to 1 hairy.

TABLE 2.—*Breeding behavior of the hairy-neck character in the progeny of a plant of Selection C during 2 generations of selfing, 1930 and 1931*

Progeny from selfed plant, 1930		Progeny from second generation of selfing, 1931			
Type	Total plants	Total plants	Type of plant		
			Selection C	Variant hairy	Variant smooth
	Number	*Number*	*Percent*	*Percent*	*Percent*
Selection C	50	384	92.7	7.0	0.3
Variant hairy	1	8	.0	25.0	75.0
Variant smooth	2	26	.0	.0	100.0

The percentage of smooth-neck plants in this particular line of Selection C in 1930 and 1931 was somewhat less (0.7 percent), and the proportion of variant hairy plants slightly more (6.4 percent) than the average shown in table 1.

During this study of the inconstancy of Selection C 30 variant hairy-neck plants were grown in head or plant rows. These produced 1,388 plants of which 321, or 23.1 percent, were hairy-necked and 76.9 percent smooth-necked, thus approximating the results, presented later, of crosses between Selection C and wheat.

The average proportion of smooth-neck plants appearing in Selection C, that is, about 1 percent, may be explained by assuming a simultaneous loss of the hairy-neck factor in 10 percent of the pollen cells and egg cells. The expected proportion of smooth-neck, variant hairy-neck (heterozygous), and Selection C types is then given by the expansion of the binomial $(1+9)^2$. The fact that the smooth-neck plants bred true and the hairy-neck plants bred like F_1 hybrids is in accord with this hypothesis. However, the average proportion of variant hairy-neck plants, approximately 6 percent, is only about one third of the number to be expected on this basis. It seems necessary to assume also differential functioning or vigor of the two types of gametes

or zygotes, or it is possible that the loss of the hairy-neck factor may occur in a somatic division in the development of the primordium for the flowers of a spike.

INHERITANCE IN CROSSES OF HAIRY-NECK SELECTIONS × WHEAT

Hybridizing the hairy-neck selections with common wheat may be expected to give further information as to the genetic irregularity of the hairy-neck character and its relation to the inheritance of certain common wheat characters. In 1923 and later, selections which from phenotypic indications were pure for the hairy-neck character of the C, K, and H selections, were crossed with common wheat varieties. The varieties chosen differed in such head characters as awnlessness and awnedness, red and white glume color, and smoothness and pubescence of glumes. The segregation of the common allelomorphs permitted observation as to the effect of an intergeneric character on their behavior.

The F_1 hybrids conformed in the more common spike characters to what would be expected in crosses of wheat varieties; that is, there was expressed the incomplete dominance of awnlessness, red glume color, and pubescent chaff. The hairy-neck character was dominant, but the hairs did not extend downward so far as in the parental selection, and the density of the hairiness was decidedly reduced. The F_1 heads appeared fully fertile and were selfed.

The hairy-neck selections were crossed with one or more of the varieties of *Triticum vulgare*, namely, Brown Fife,[7] Purplestraw, Fulcaster, Nittany, Poole, and Fultz. All except Fulcaster and Nittany are awnless, and all except Brown Fife and Poole have glabrous white glumes. Brown Fife has pubescent red glumes, and Poole has glabrous red glumes.

Glume color developed poorly, and segregates from this character were not classified, although it was evident that hairy neck was present in both the red- and white-glume segregates of the F_2 generation. The number of F_1 plants secured in each case, the number of F_2 plants that were grown, and the segregation of the latter with respect to presence of awns, pubescence of glumes, and hairy necks are shown in table 3.

The segregation with respect to awns and pubescence is what would be expected when varieties of *Triticum vulgare* possessing these characters are crossed. In the six crosses involving awn segregation, the fully awned recessive constitutes 24.4 percent of the total number of plants that were grown. In the single cross (Selection C × Brown Fife) involving pubescent and glabrous glumes, 24.1 percent of the plants had glabrous glumes. On the other hand, the segregation with respect to the hairy-neck character was quite irregular. In the five crosses involving Selection C the percentage of hairy-neck plants ranged from 17.7 to 29.2 and averaged 25. In the four crosses involving Selection K, the percentage of hairy-neck plants ranged from 30.6 to 48.2, with an average of 36.2. There were two crosses involving Selection H. In these the percentages of hairy-neck plants were 61 and 63.4, respectively, averaging 62.9.

[7] The name "Brown Fife" was given in 1922 to a strain of wheat formerly grown as Jones Winter Fife. In habit of growth and morphological characters it is somewhat similar to Grandprize.

TABLE 3.—*Segregation in the F_2 generation from crosses of 3 hairy-neck selections with varieties of common wheat at the Arlington Experiment Farm, Rosslyn, Va.*

Cross	F_1 plants	F_2 plants	F_2 plants of indicated class					
			Awnless				Awned (glabrous)	
			Pubescent		Glabrous			
			Hairy	Smooth	Hairy	Smooth	Hairy	Smooth
	Number	*Number*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Selection C × Brown Fife	1	220	12.3	63.6	5.5	18.6	0.0	0.0
Selection C × Purplestraw	2	1,365	.0	.0	26.4	73.6	.0	.0
Selection C × Fulcaster	1	168	.0	.0	22.6	57.7	6.6	13.1
Nittany × Selection C	12	343	.0	.0	15.2	58.6	5.8	20.4
Selection C × Poole	1	171	.0	.0	26.9	73.1	.0	.0
Selection K × Purplestraw	4	486	.0	.0	37.7	39.5	10.5	12.3
Selection K × Fultz	13	281	.0	.0	23.8	50.2	8.2	17.8
Fulcaster × Selection K	1	191	.0	.0	.0	.0	38.7	61.3
Poole × Selection K	8	950	.0	.0	21.9	52.1	8.7	17.3
Selection H × Fultz	1	100	.0	.0	51.0	27.0	10.0	12.0
Selection H × Fulcaster	9	383	.0	.0	.0	.0	63.4	36.6

In none of the crosses involving Selections K and H do the ratios conform to simple Mendelian inheritance. The average results for Selection C agree exactly with expectations for a monohybrid, except that hairy neck behaves as the recessive, whereas in the F_1 this character was dominant. The breeding behavior of the F_1 of Selection C × wheat is similar to that of the hairy-neck variants.

There is no indication of linkage of the hairy-neck character with either of the other characters studied except in the Selection H × Fultz cross, in which the proportion of hairy necks in a small population is approximately twice as great for the awnless segregates as for the awned.

A number of the crosses were continued into the F_3 generation. Some of these were space-planted, but the greater number were grown in 5-foot head rows. In some cases all the plants from the F_2 rows were grown, whereas in others only the hairy-neck plants were grown. The progeny of 388 smooth-neck F_2 plants were grown and all bred smooth neck. The data for the hairy-neck plants are presented in table 4.

Of the 125 F_3 lines grown from hairy-neck F_2 plants of the two crosses of Selection C, only 3, or 2.4 percent, were homozygous. If the hairy-neck character were a simple recessive, 33.3 percent should be homozygous.

Of the 83 hairy-neck F_2 plants of the cross Selection K × Fultz grown in the F_3, approximately 11 percent were homozygous hairy neck. However, of the 76 F_3 lines of the cross Selection K × Purplestraw 25 percent were homozygous. In the F_2 of Selection K × Purplestraw approximately 50 percent of the plants were hairy neck as compared to 32 percent in the cross Selection K × Fultz. In the former cross the F_2 homozygous hairy-neck plants appeared more than twice as often as in the latter cross.

TABLE 4.—*Breeding behavior of hairy-neck F_2 plants from crosses of hairy-neck selections × wheat*

Cross	F_3 lines		
	Number	Heterozygous hairy neck	Homozygous hairy neck
		Percent	*Percent*
Selection C × Purplestraw	71	98.6	1.4
Nittany × Selection C	54	96.3	3.7
Selection K × Fultz	83	89.2	10.8
Selection K × Purplestraw	76	75.0	25.0
Selection H × Fultz	54	81.5	18.5

The F_1 of Selection K × Fultz was grown in 1925 and the F_1 of Selection K × Purplestraw in 1928. The difference in percentage of homozygosity of the two crosses is believed to be due to differences in the two seasons, inasmuch as 30 of the segregating F_3 lines of Selection K × Purplestraw, involving 545 plants, were space-planted and 25.5 percent of the plants were hairy as compared to approximately 48.1 percent in the F_2 generation. The higher percentage of hairy-neck plants in the F_2 generation of this cross as compared to that of the other three crosses of Selection K × wheat, and the comparatively high percentage of F_3 homozygous hairy-neck lines, indicate conditions unusually favorable for either the formation or the functioning or both of the hairy-neck gametes of the F_1 plants.

Of the 54 F_3 lines of Selection H × Fultz, 18.5 percent were homozygous hairy-neck. Selection H crosses produced approximately 61 percent of hairy-neck plants in the F_2; that is, the hairy-neck character behaved as dominant. However, the F_3 test clearly shows a lethal factor operating to eliminate the homozygous hairy-neck type.

EFFECT OF HAIRY NECK ON PLANT CHARACTERS

The supposition of a lethal effect of the hairy-neck factor suggested the desirability of a study of sterility, seed germination, height of plant, and tillering of the crosses, especially with respect to the smooth-neck and hairy-neck segregates.

STERILITY

The percentages of sterile florets of the hairy-neck selections and of the F_1 hybrids between these and certain varieties of wheat are shown in table 5.

TABLE 5.—*Floret sterility of hairy-neck selections and of F_1 hybrids of hairy-neck selections × wheat*

Selection or F_1 hybrid	Florets	Seeds	Sterile florets
	Number	*Number*	*Percent*
Selection C	1,190	789	33.7
Nittany × Selection C	369	321	13.0
Selection C × Purplestraw	1,356	1,249	7.9
Selection K	282	159	43.6
Selection K × Fultz	536	487	9.1
Selection H	204	160	21.6
Selection H × Fultz	106	102	3.8

In Selection C, 33.7 percent of the florets were sterile, and in the F_1 hybrid of Selection C × wheat and its reciprocal, approximately 10 percent of the florets were sterile. This is about the average sterility for wheat. The average sterility of Selection K was 43.6 percent and of Selection H, 21.6 percent. The F_1 hybrids with wheat in each case were as fertile as would be expected for wheat, the sterility of Selection H × wheat being only 3.8 percent. Selection H has the highest fertility of the three selections and the same relation exists between the F_1 hybrids with wheat. It is pertinent in this connection to note that in the F_2 generation 61 percent of the plants of this cross had hairy necks as compared with 25 and 36 percent in Selections C and K, respectively (table 3). In Selection H, hairiness extends 4 inches down the peduncle as compared to approximately one half inch in the other two selections; that is, the degree of hairiness in these selections was not positively correlated with reduction of fertility as might be expected.

Seed Germination

Seed of the F_1 plants of wheat × Selection C was planted and allowed to mature. Approximately 85 percent of the planted seeds matured plants. A similar study was made of Selection K × wheat from F_2

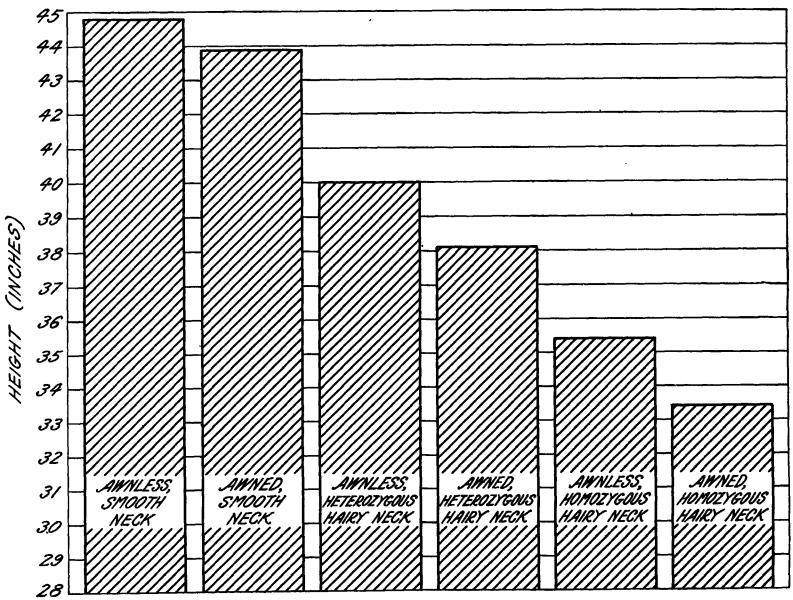

FIGURE 3.—Height of plants of different awn and neck types in the F_3 generation of the cross Selection K × wheat.

seed, as no F_1 seed was available. Conditions for germination were poor, and only 49 percent of the seed of segregating hairy-neck lines and a like percentage of homozygous hairy-neck lines matured plants. A similar planting of smooth-neck seed from the same cross matured only 48 percent of plants. In neither case is there any evidence of differential zygotic lethals.

Height of Plant

The height of a large number of plants in the F_2 and F_3 generations was measured, and the data are presented in table 6. In each of the 17 possible comparisons of the hairy-neck with the smooth-neck classes the hairy-neck plants were significantly shorter, in most cases materially so. The average height of the smooth-neck plants was 46.9 inches as compared to 41.4 inches for the hairy-neck plants. Furthermore, the homozygous hairy-neck F_3 lines were approximately from 2 to 5 inches shorter than those segregating for hairy neck. The comparative height differences in the classes obtained from the cross of Selection K × Fultz are shown graphically in figure 3. No significant differences were found between the height of the plants as a result of the presence or absence of awns.

The commonly cultivated rye varieties have hairy necks. A few strains of smooth-neck rye have been bred, the height of which is no greater than that of their hairy-neck relatives. It is probable, therefore, that the hairy-neck character in the presence of the rye-chromosome set does not adversely affect the height of the plant. The average height of the rye varieties grown at the Arlington Experiment Farm varies from 62 to 65 inches as compared with 46 and 54 inches in the wheat varieties.

Table 6.—*Average height of hairy-neck and smooth-neck plants in heterozygous and homozygous hairy-neck lines from hybrids of hairy-neck selections × wheat*

Class and hybrid	Generation	Plants	Average height of plants of indicated class			
			Awnless smooth	Awnless hairy	Awned smooth	Awned hairy
HETEROZYGOUS		*Number*	*Inches*	*Inches*	*Inches*	*Inches*
Selection K × Fultz	F_2	281	47.5±0.42	40.7±0.39	47.7±0.40	38.7±0.85
Do	F_3	1,466	44.8± .36	40.0± .38	43.9± .47	38.1± .57
Selection C × Purplestraw	F_2	1,172	44.1± .39	39.6± .45		
Selection H × Fultz	F_2	90	47.5± .55	42.8± .66	47.6± .69	40.9±1.83
Do	F_3	443	49.1± .14	45.2± .16	49.8± .11	46.9± .16
HOMOZYGOUS LINES						
Awnless hairy (Selection C × Purplestraw)	F_3			36.1± .44		
Awned hairy (Selection K × Fultz)	F_3					33.4± .80
Awnless hairy (Selection K × Fultz)	F_3			35.4± .97		
Awned hairy (Selection H × Fultz)	F_3					44.8± .80
Awnless hairy (Selection H × Fultz)	F_3			43.2± .72		

Tillering

Data on tillering were obtained for individual plants in the F_2 generation of the two crosses Selection K × Fultz and Selection H × Fultz. The former was grown on more productive land than the latter. In all cases the smooth-neck plants tillered more than did the hairy-neck plants (table 7). The differences between awned and awnless plants were not statistically significant.

TABLE 7.—*Average number of tillers per plant in F_2 classes of hairy-neck selections × wheat crosses*

Cross	Average tillers per plant in indicated F_2 class					
	Awnless			Awned		
	Hairy	Smooth	Difference	Hairy	Smooth	Difference
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
Selection K × Fultz	6.7±0.39	8.5±0.46	1.8±0.60	6.6±0.58	9.5±0.46	2.9±0.74
Selection H × Fultz	3.7± .12	5.3± .30	1.6± .32	3.4± .37	4.5± .49	1.1± .61

BACK-CROSSING F_1 HYBRIDS WITH WHEAT

Since no evidence of zygotic elimination was obtained it seemed desirable to resort to back-crossing to test for comparative functioning of male and female gametes carrying the smooth-neck and hairy-neck factors. This was done by reciprocally crossing the F_1 hybrids with wheat, only the F_1 hybrids of Selection C and Selection K being used. The resulting progeny were then classified with respect to the hairy-neck character. Errors due to self-pollinated plants were eliminated by the selection of a wheat variety in which selfing could be detected. The data are presented in table 8.

The female gametes of Selection K × Fultz, fertilized by wheat pollen, produced plants of which 16.9 percent had hairy necks, whereas the male gametes of the same hybrid, fertilizing wheat egg cells, produced but 9.0 percent of hairy-neck plants. Similarly, the female gametes of the F_1 of Selection C × wheat (Purplestraw and Nittany), fertilized by wheat pollen, produced 13.2 percent of hairy-neck plants, whereas the male gametes of the same hybrid, fertilizing wheat egg cells, produced 8.9 percent of hairy-neck plants. In all back crosses except one a larger percentage of hairy-neck plants was produced when the F_1 hybrid was used as the female parent. However, neither the functional male nor female gametes carried the hairy-neck character in the expected frequency, since in back-crossing experiments such as these the hairy-neck and smooth-neck gametes should occur in equal numbers.

TABLE 8.—*Hairy-neck and smooth-neck plants resulting from reciprocal back-crossing of the F_1 hybrid of hairy-neck selections × wheat with wheat*

F_1 hybrid	Year	F_1 hybrid as the female produced—			F_1 hybrid as the male produced—		
		Smooth-neck plants	Hairy-neck plants		Smooth-neck plants	Hairy-neck plants	
		Number	*Number*	*Percent*	*Number*	*Number*	*Percent*
Selection K × Fultz	1925	23	6	20.7	17	3	15.0
Do	1926	46	8	14.8	54	4	6.9
Total or percent		69	14	16.9	71	7	9.0
Selection C × Purplestraw	1926	34	6	15.0	46	3	6.1
Nittany × Selection C	1929	18	5	21.7	6	0	0
Selection C × Purplestraw	1930	93	11	10.6	92	11	10.7
Total or percent		145	22	13.2	144	14	8.9

Theoretically, there should be agreement among the F_2 segregation, the F_3 family behavior (that is, whether homozygous or heterozygous for the neck character), and the results from the back crosses. The latter indicated that approximately 16.9 percent of the functional eggs and 9.0 percent of the male cells of Selection K × Fultz (table 8) carry the hairy-neck factor. Assuming the same gametic frequency (1+5) (1+10) and the same functioning in the selfed F_1 hairy neck × wheat hybrids, the F_2 population should contain 24.2 percent of hairy-neck plants, and approximately 6.3 percent of these should be homozygous in F_3. Actually, 32 percent of the F_2 plants were hairy (table 3), and 10.8 percent of the F_3 lines were homozygous (table 4).

In Selection C × wheat slightly more than 13 percent of the egg cells and about 9 percent of the male cells carried the hairy-neck character. On this basis the F_2 population from the selfed F_1 hybrids should be approximately 21.0 percent hairy neck, and 5.7 percent of these should be homozygous. The percentage of the hairy-neck plants actually observed in the F_2 generation of the same crosses (Purplestraw and Nittany) was 25.3 (table 3), and 2.4 percent of these bred true (table 4).

The agreement between the data of the different experiments is perhaps as close as should be expected, considering the small populations obtained from the back crosses and the apparent irregularity in genetic expression due to environment.

DIFFERENTIAL FUNCTIONING OF POLLEN CELLS

The low percentage of functional gametes carrying the hairy-neck factor, as shown in the reciprocal back crosses of the F_1 hybrids of hairy-neck selections × wheat with wheat, would indicate elimination of the hairy-neck character at meiosis or at fertilization. The high percentage of fertility in the F_1 hybrids of hairy-neck selections × wheat favors the assumption that functional female gametes carrying the hairy-neck factor are not formed in the expected frequency. The apparent differential functioning of the male gamete of the F_1 hybrids carrying the hairy-neck and smooth-neck characters (table 8) may, however, be due to a growth differential between the two types rather than to nonformation of pollen cells carrying the hairy-neck factor. Experiments were therefore made with mixtures of pollen of Selection C and pollen of three varieties of common wheat, namely, Nittany, Dixie, and Red Rock. Heads of the wheat or of Selection C were emasculated and at the proper time were pollinated with a pollen mixture or first with pollen of Selection C and then with pollen of the wheat variety; in the latter case the interval between the two pollinations averaged about 2 minutes. The pollen mixture was composed of the contents of the same number of anthers of Selection C and of the wheat variety. The anthers of Selection C are larger than those of the wheat varieties used.

When wheat was the female, the progenies were grown and classified as smooth neck or hairy neck, the results showing which pollen grain functioned. When Selection C was the female, glume color or awn contrast of the following progenies showed when the wheat pollen grain functioned, except in Dixie, when the plants were carried to the F_2 generation to identify them. Results of the pollinations are shown in table 9.

TABLE 9.—*Comparative functioning of pollen of hairy-neck selection C and wheat varieties in pollen-mixture and double-pollination experiments*

Female parent	Year	Pollen source	Plants of indicated type resulting from pollination			Flowers fertilized by pollen carrying hairy neck
			Wheat	Selection C	Hybrid	
			Number	*Number*	*Number*	*Percent*
Nittany	1928	Mixture Nittany and Selection C	10		1	
Dixie	1928	Mixture Dixie and Selection C	11		0	
Red Rock	1929	Mixture Red Rock and Selection C	17		2	
Nittany	1928	Selection C and Nittany	11		3	
Dixie	1928	Selection C and Dixie	12		1	
Red Rock	1929	Selection C and Red Rock	42		5	
Total			103		12	10.4
Selection C	1928	Mixture Dixie and Selection C		2	22	
Do	1928	Selection C and Nittany		2	14	
Do	1929	Selection C and Dixie		0	7	
Do	1929	Selection C and Red Rock		1	8	
Total				5	51	8.9

One hundred and fifteen plants resulted from pollinating the common wheat varieties with pollen from the two sources. Only 12, or 10.4 percent, were hairy-neck hybrids, the remainder being selfs. When the wheats were pollinated with the mixture the percentage of hybrids was 7.3, and when pollinated first with pollen of Selection C and then selfed the percentage of hairy-neck hybrids increased to 12.2, possibly indicating an effect due to rate of pollen germination or of pollen-tube growth.

Fifty-six plants were secured in the experiments in which Selection C was the female. Fifty-one, or 91 percent, proved to be hybrids and only 5, or 9 percent, were selfs. Approximately the same number of flowers of wheat and of Selection C were pollinated in these experiments, and the fewer seeds and plants obtained indicates again the sterility of Selection C as compared with that of wheat. These results suggest that the pollen cells of Selection C which carry the hairy-neck factor are less viable or that the pollen tube grows more slowly than that of normal wheat. Poor functioning of pollen cells carrying the hairy-neck factor appears at least as probable as nonformation at meiosis in the F_1 hybrid. This is further supported by the agreement between the results from back-crossing the F_1 of Selection C $\times$ wheat with wheat (table 8) and the results from pollinating wheat and Selection C with the pollen mixture. Wheat fertilized with pollen from the F_1 hybrid (Selection C $\times$ wheat) produced 8.9 percent of hairy-neck plants, whereas wheat fertilized with a mixture of pollen from Selection C and wheat produced 10.4 percent of hairy-neck plants; and Selection C fertilized by a mixture of pollen from Selection C and wheat produced 8.9 percent of selfed hairy-neck plants (table 9).

DISCUSSION

The genetic behavior of the hairy-neck wheatlike selections isolated from wheat-rye hybrids shows that the addition of the rye character results in an unbalanced type. Hairy-neck is a tangible rye character transposed to types that are apparently otherwise *Triticum vulgare*. A preliminary cytological examination of one of the hairy-neck plants

made by Florell [8] showed 44 chromosomes in the root tips as compared to 42 for *T. vulgare*. Inasmuch as the hairy-neck plants are not constant, their chromosomal constitution seems to be better represented by the quantitative expression $2n+2$ rather than $2n$, indicating in this case no homologue in the wheat complement for the rye chromosome. Blakeslee [9] uses the formula $2n+2$ for one of his Globe mutants in *Datura* where the unbalance was of a simple tetrasomic type.

To explain the genetic behavior of the hairy-neck character it may be assumed that the $2n+2$ hairy-neck plants normally produce $n+1$ gametes but that occasionally in male and female gametogenesis the rye chromosome is lost, giving a gamete of n constitution. The fertilization of $n+1\times n$ gametes results in a zygote similar in later behavior to the cross hairy-neck selection × wheat, whereas the mating of $n\times n$ gives a zygote which produces a plant indistinguishable from *Triticum vulgare*.

The chromosome number of the F_1 hybrid hairy-neck selection × *Triticum vulgare*, and also of the variant hairy type, would be $2n+1$ and the plants would be of the hairy-neck type as the character is dominant over the smooth neck. In gametogenesis and fertilization, irregularities in the functioning of $n+1$ and n gametes apparently occur, as the F_2 segregation often shows the hairy character as recessive, and results from the back crosses indicate that from 13 to 17 percent of the functional egg cells and approximately 9 percent of the functional pollen grains carry the hairy character. Furthermore, F_3 lines homozygous for hairy neck do not appear in the expected frequency even for a recessive character. Reduced height and tillering and varying degrees of sterility in the plants with hairy neck as compared to those with smooth neck, in addition to the genetic irregularities, support the belief that there is incompatibility between the wheat and rye complexes and that the reaction is unfavorable both to the normal productiveness of the plant and to its constancy in breeding. Whether the addition or substitution of other rye chromosomes in the wheat complement would react similarly is questionable. Wheat-rye hybrids carrying all the chromosomes in both wheat and rye, $2n=56$, have been produced,[10] but the economic value of such plants has not seemed particularly promising in the United States. Wheat breeders in general are interested in obtaining a definitely *T. vulgare* type with certain desired rye characters rather than a type intermediate between the two genera.

SUMMARY AND CONCLUSIONS

Complete genetic balance has not been obtained in three hairy-neck selections of wheat × rye crosses designated as Selection C, Selection K, and Selection H. In spite of continuous selfing, approximately 1 percent of the plants of Selection C had smooth necks and bred true and about 6 percent had hairy necks and bred in the same manner as the F_1 hybrids.

The observed proportion of smooth-neck plants may be explained by assuming a simultaneous loss of the hairy-neck factor in 10 per-

[8] Letter addressed to J. W. Taylor by V. H. Florell, Feb. 28, 1931.

[9] BLAKESLEE, A. F. VARIATIONS IN DATURA DUE TO CHROMOSOME NUMBER. Amer. Nat. 56: 16-31, illus. 1922.

[10] LEVITSKY, G. A., and BENETZKAIA, G. K. CYTOLOGICAL INVESTIGATIONS OF CONSTANT INTERMEDIATE RYE-WHEAT HYBRIDS. (PRELIMINARY COMMUNICATION.) U.S.S.R. Cong. Genet., Plant and Animal Breeding, Proc. 2: 345-352, illus. 1930. [In Russian. English Summary, pp. 350-352.]

cent of the pollen cells and egg cells, but the observed proportion of hybrid hairy-neck plants has been only about one third of the number to be expected on the basis of this explanation. It seems necessary to assume also differential functioning or vigor of the two types of gametes or of the zygotes, or possibly loss of the hairy-neck character in somatic mitosis.

In crosses between the three selections and several varieties of wheat the hairy-neck character appeared to be dominant, but in later generations it behaved as a recessive or in an irregular manner.

There appeared to be no linkage of the hairy-neck character with glume color, with condition of glumes in regard to pubescence, or with condition of heads in regard to awns.

In studies of sterility it was found that Selection C, Selection H, and Selection K were materially less fertile than wheat, but that the F_1 hybrids were approximately as fertile as wheat. There was no observable inverse relation between degree of hairiness and sterility, as might be expected; Selection H, which had more hair on the necks than the others, was the most fertile.

In a comparison of the germination of segregating hairy-neck lines, homozygous hairy-neck lines, and homozygous smooth-neck lines, no differences were observed.

In study of the height of plants and of vigor as measured by tillering, it was found that in crosses between the three selections and wheat the smooth-neck segregates were invariably taller than the hairy-neck segregates from the same cross. It was also found that heterozygous hairy-neck segregates were taller than homozygous hairy-neck segregates. In all cases smooth-neck plants from these crosses tillered more than comparable hairy-neck plants.

The F_1 hybrids were reciprocally back-crossed with wheat. In all crosses but one, a larger percentage of hairy-neck plants was produced when the F_1 hybrid was used as a female parent. In the one exception there was practically no difference. There was good agreement among the data secured by back-crossing, the F_2 segregation, and the breeding behavior of the F_3 lines.

A study of differential functioning of pollen grains was made by using mixtures of pollen of Selection C and one of three varieties of wheat. The florets were emasculated and either pollinated with a mixture of pollen or pollinated first with pollen from Selection C and about 2 minutes later with pollen from wheat. The results indicated that the pollen cells of Selection C are less viable or that the pollen tube grows more slowly than in wheat. There was apparently no discrimination on the part of the egg toward either type of gamete.

Since the hairy-neck plants are irregular in their breeding behavior, it seems logical to represent their chromosomal constitution by the expression $2n+2$ rather than by $2n$, indicating no homologue in wheat for the rye chromosome carrying the hairy-neck factor. It may then be assumed that the hairy-neck plants produce $n+1$ gametes and that occasionally the rye chromosome is lost, giving a gamete of n consitution. The union of $n+1$ and n gametes results in a zygote similar to that produced by a cross of a hairy-neck selection $\times$ wheat, and the union of n gametes produces a plant which cannot be distinguished from wheat.