"HAIRY NECK" WHEAT SEGREGATES FROM WHEAT-RYE HYBRIDS

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Pollen from rye was successfully used to fertilize wheat flowers as early as 1875 by Wilson (14) in Scotland. Subsequently many plant breeders, both in Europe and America, have made this cross and produced F₁ plants. The natural wheat-rye hybrid has been observed frequently in wheat plats, particularly at the Arlington Experiment Farm of the United States Department of Agriculture, Rosslyn, Va. (8) (see Pl. 1), and at Saratov, Russia (9). However, despite the many F₁ plants produced as the result of these artificial or natural cross-pollinations, few studies on the inheritance of specific morphological characters for other than the F₁ generation have been made and very few fixed segregates having any resemblance to rye have been reported. The plants described in this paper are believed, therefore, to be of peculiar interest in that they are like wheat, except for a single undoubted rye character, and in some cases have produced progeny all of which were like themselves.

SELF-STERILITY IN WHEAT-RYE HYBRIDS

The cross between wheat and rye is intergeneric and the F₁ hybrid is either entirely sterile or only slightly fertile. As shown by Leighty (8), several experimenters have reported a small percentage of fertility in this generation. One natural hybrid found by Leighty had a fertility of 5 per cent, which is apparently unusually high. When the F₁ shows fertility and no precautions have been taken to prevent natural backcrossing, there is always the probability that the seeds present are due to the effect of wind-borne pollen of wheat or rye. The writers have no evidence that viable pollen is ever formed by the F₁ plants, and, furthermore, they have never observed opening of the anther sacs. Jesenko (4) found the F₁ wheat-rye hybrid self-sterile but slightly fertile with wheat pollen and very rarely so with pollen of rye. Investigations by the writers indicate that fertility in the F₁ nearly always is due to backcrossing with wheat pollen.

At Arlington Experiment Farm, during the crop seasons of 1922 and 1923, over 8,000 flowers of natural F₁ wheat-rye hybrids growing in the wheat plats were bagged with glassine bags before blooming and approximately 16,000 flowers were unprotected. The results, given in Table I, indicate that the F₁ was self-sterile, but slightly fertile when open-pollinated. Therefore, unless the pollination of the F₁ wheat-rye hybrid is controlled the source of pollen will be in doubt and inheritance can not be determined with accuracy.

1 Received for publication April 1, 1924.
2 Reference is made by number (italic) to "Literature cited," p. 575-576.
TABLE I.—Number of heads and flowers, bagged and not bagged, on F₁ wheat-rye hybrid plants growing in wheat plats and number and percentage of seed set on these heads

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of heads Bagged</th>
<th>Number of flowers Bagged</th>
<th>Number and percentage of seed set on heads Bagged</th>
<th>Number of heads Not bagged</th>
<th>Number of flowers Not bagged</th>
<th>Number and percentage of seed set on heads Not bagged</th>
</tr>
</thead>
<tbody>
<tr>
<td>1922</td>
<td>142</td>
<td>6,972</td>
<td>11,791</td>
<td>0</td>
<td>32</td>
<td>.65</td>
</tr>
<tr>
<td>1923</td>
<td>34</td>
<td>1,374</td>
<td>4,772</td>
<td>a1</td>
<td>0</td>
<td>.67</td>
</tr>
<tr>
<td>Total</td>
<td>176</td>
<td>8,346</td>
<td>16,563</td>
<td>1</td>
<td>109</td>
<td>.66</td>
</tr>
</tbody>
</table>

* The single seed obtained under bagged conditions is likely due to late or faulty bagging.

In this connection it should be explained that the rye varieties or selections are grown at the Arlington Experiment Farm in twentieth-acre plats, separated by several wheat plats in such a manner that the rye varieties are approximately 90 feet from one another. This tends to reduce somewhat the amount of natural crossing between the rye varieties, but furnishes abundant opportunities for natural crossing between the wheat and rye. Many natural hybrids between these have been found on this farm since 1914, the year in which the first one was discovered (6).

In 1918, 40 seeds were obtained from 19 natural F₁ wheat-rye hybrids found in the wheat plats at Arlington (8). The pollination of these plants was uncontrolled, and it is likely that the F₂ generation plants were natural sesqui-hybrids. The F₂ and F₃ of the wheat-rye hybrids were grown in the greenhouse, where natural crossing with wheat was again possible, though not to the degree existing under field conditions. The later generations were matured in the field rod-row nursery in order to test the yielding ability of the selections. The generation grown in 1922 consisted of 77 rod-rows, or approximately 9,400 plants. This generation was made up of about 63 strains, descended from 24 F₃ plants. These strains, in general, were fully as fertile in the F₅ generation as wheat grown under the same conditions. High fertility in these wheat-rye hybrids was first observed in certain plants of the F₃ generation.

The head type of the F₅ generation plants, grown in the 77 rod-rows, was for the most part identical with that of wheat, and only rarely was a plant found which differed from wheat to a degree that approached the F₁. The majority of the plants could not be distinguished from common wheat. One undoubted rye character, however, was observed on eight plants which in other respects could be called wheat. This was the pubescent peduncle commonly associated with rye, but apparently unknown in wheat (Pl. 2).

THE "HAIRY-NECK" CHARACTER

The peduncle is the upper portion of the stem (culm) and in the cereals is usually considered as being the uppermost internode at the apical node of which the head or spike is attached. The portion of the peduncle just below the head is often called the "neck," and when this is pubescent or covered with hairs, is here referred to as a "hairy neck."

The peduncle of rye is more slender than that of wheat, and its upper portion, the neck, for a distance of a fraction of an inch to three or more inches below the head, is usually covered with short hairs readily discernible to the naked eye. The lower segments of the rachis are also pubescent, but only the neck character is here considered. In some cases the hairiness, located around the apical node,
May 10, 1924

"Hairy Neck" Wheat Segregates from Hybrids

is limited to a few hairs which are difficult to distinguish without magnification. Rye plants with glabrous peduncles are sometimes found. The percentage of such plants is usually very small, but there apparently are varietal differences in regard to this factor despite the fact that the rye plant is almost entirely cross-pollinated. The necks of four typical rye heads are shown in Plate 2.

In Table II are given the data obtained on eight varieties of winter rye for the crop year 1922–23, in regard to the hairiness of the neck as seen by the naked eye. In five of the eight varieties, less than one per cent of glabrous-necked culms were found, while in von Rümker No. 2 there were 8 per cent. The total for all varieties was 1.9 per cent glabrous-necked culms. Gaines and Stevenson (3) report 66 per cent hairy-necked plants among 41 plants of Rosen rye examined at Pullman, Wash.

**TABLE II.—Number and per cent of glabrous-necked culms found in eight varieties of winter rye at Arlington Experiment Farm in 1923**

<table>
<thead>
<tr>
<th>Variety</th>
<th>Number of culms examined</th>
<th>Glabrous-necked culms</th>
<th>Variety</th>
<th>Number of culms examined</th>
<th>Glabrous-necked culms</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>Percent</td>
<td>Number</td>
<td>Percent</td>
<td>Number</td>
</tr>
<tr>
<td>Von Rümker No. 2</td>
<td>500</td>
<td>40</td>
<td>8.0</td>
<td></td>
<td>Winter</td>
</tr>
<tr>
<td>St. Johns</td>
<td>484</td>
<td>7</td>
<td>1.4</td>
<td></td>
<td>Abruzzes</td>
</tr>
<tr>
<td>Rosen</td>
<td>1,363</td>
<td>45</td>
<td>3.3</td>
<td></td>
<td>Von Rümker No. 1</td>
</tr>
<tr>
<td>Virginia</td>
<td>490</td>
<td>3</td>
<td>0.6</td>
<td></td>
<td>Total</td>
</tr>
<tr>
<td>Rimpau</td>
<td>480</td>
<td>4</td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mexican</td>
<td>1,289</td>
<td>16</td>
<td>1.2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The F₁ wheat-rye hybrid is approximately intermediate between the two parents in such characters as shape and density of head, number of spikelets, width and other characters of the empty glumes, and in general appearance (Pl. 1). The hairy-neck character of rye, however, is usually expressed in the F₁ and apparently is a dominant character in this generation. About 300 first generation wheat-rye hybrid plants, nearly all natural hybrids, growing at the Arlington Experiment Farm, have been examined with reference to this character. Approximately 80 per cent of these have had the hairy neck in the varying degrees as found in rye. The glabrous-necked plants in the F₁ may be due to the gametic constitution of the rye parents in these cases in respect to this character.

**INVESTIGATIONS ON HAIRY NECK**

Plants resembling wheat in most characters, but having the hairy neck, were observed in the F₂ and subsequent generations arising from the natural hybrids found in 1918. Investigations on this character were begun in 1920, when a cross was made between Purplestraw wheat and a wheat-like F₃ segregate of a wheat-rye hybrid. The pollen parent of this hybrid, the F₃ segregate, apparently carried the factor for hairy neck in heterozygous condition, for, from the 8 kernels resulting from this cross, 7 glabrous-necked plants were produced and only 1 with hairy neck. The progeny of this hairy-necked plant in 1922 consisted of 36 glabrous-necked plants and 2 with hairy necks. Data on the progeny of these 2 hairy-necked plants obtained in 1923, are given in Table III (A and B). In addition to these 2 plants, 8 other plants having the hairy neck were selected in 1922 from the F₂ progeny of the natural wheat-rye hybrids found in 1918. Data on the plants produced in 1923 from the seed of these 8 plants are given in Table III (C to K), and 3 of the heads, together with a head of Fulcaster wheat for comparison, are shown in Plate 3.
TABLE III.—Total number of plants and numbers with hairy neck and glabrous neck in the progeny of each of 10 wheat-like plants with hairy necks selected in the progeny of wheat-rye hybrids, with data on certain head characters

<table>
<thead>
<tr>
<th>Selection number and head characters</th>
<th>Number of progeny plants</th>
<th>Head characters of progeny</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>Hairy-necked</td>
</tr>
<tr>
<td>Awnless, white-chaffed:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>92</td>
<td>13</td>
</tr>
<tr>
<td>B</td>
<td>100</td>
<td>16</td>
</tr>
<tr>
<td>C</td>
<td>40</td>
<td>100</td>
</tr>
<tr>
<td>D</td>
<td>28</td>
<td>9</td>
</tr>
<tr>
<td>E</td>
<td>-66</td>
<td>5</td>
</tr>
<tr>
<td>F</td>
<td>59</td>
<td>13</td>
</tr>
<tr>
<td>Awned, white-chaffed:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>26</td>
<td>13</td>
</tr>
<tr>
<td>H</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>I</td>
<td>31</td>
<td>22</td>
</tr>
<tr>
<td>J</td>
<td>98</td>
<td>98</td>
</tr>
</tbody>
</table>

(a) All plants with the same head characters as the parent selection.
(b) One semiawned plant with red chaff included, all others with the same head characters as the parent selection.
(c) Eighty-four bearded, white-chaffed plants, 14 semiawned plants, all white-chaffed.

All 10 of the plants selected in 1922 had been fertilized naturally, no attempt being made to control pollination by bagging or isolation. These plants were fully fertile, with the exception of selection K, in which the fertility was about 75 per cent. The seed of these plants germinated well and about 75 per cent of the kernels produced plants the next year, which was fully equal to the performance of several pure lines of wheat sown in the same nursery.

The pubescence on the peduncles of the several selections made in 1922 varied somewhat in amount and extent. Several of the necks are shown in Plate 4, together with the necks of wheat and rye. The pubescence on selection I is very heavy, the hairs extending down the neck for 5 or more inches below the head, which is farther than has been observed on any rye plant examined. Selection K has a sparse pubescence, extending down the neck not more than an inch. The pubescence in the progenies of different selections in some cases was of much the same type as that of the parental selection, while in other cases different members of the progeny of a selected parent varied considerably among themselves as to pubescence.

In the progenies of the 10 selections, as shown in Table III, there were in all 247 plants with hairy necks and 311 with glabrous necks. Only 3 of these 10 selections, C, H, and K, produced plants all of which were hairy-necked. It is probable that these progenies are homozygous with respect to this character, but this is not regarded as a certainty. The expression of the character in later generations must be observed before it can be concluded that strains entirely homozygous in respect to the hairy-neck character have been established.

On the matter of the fixation of the hairy-neck character, Carman (1) who conducted some of the earliest and most extensive experiments on wheat-rye hybrids, reports as follows:

The Rural New Yorker No. 6 is one of the rye-wheat hybrids, though all appearance of rye has disappeared except that the culms just under the heads are now and again downy as in rye. This downiness of the stem is variable. We have tried by selection for many years to fix it without any approach to success. Of all our rye-wheat hybrids, the downy culm is permanent in but one, and that resembles rye in several other respects.

The progenies of the other 7 selections (A, B, D, E, F, G, and I) consisted of both hairy-necked and glabrous-necked plants, there being a total of 91 plants with hairy necks and 311 with glabrous necks, or very nearly a 1 to 3 ratio.
May 10, 1924  "Hairy Neck" Wheat Segregates from Hybrids

This is the ratio that would be expected if the hairy-neck character is recessive. But in the different progenies the ratios of hairy-necked to glabrous-necked plants varied from 1 to 12.2 in selection E to 2.4 to 1 in selection I. Furthermore, all of the parent plants had hairy necks. Therefore, the character does not appear to be recessive.

The hairy-neck character, however, has not been consistently dominant, as is evident from data given above. Nevertheless, at least a high degree of dominance occurs in the F1. Additional data on the F2 generation of wheat-rye hybrids also are at hand. One lot of such plants grown by the writers in 1923 consisted of 21 with hairy necks and 8 with glabrous necks. These were descended from 24 natural hybrids, all with hairy necks, and all open-fertilized. Gaines and Stevenson (3) report that in the F2 they obtained 11 plants with hairy necks and 4 with glabrous necks.

POSSIBILITY OF NATURAL CROSSING

It is known that natural crossing occurs to some extent in wheat-rye hybrids. The data presented in Table I indicate that fertility in the F1 is dependent on pollen from outside sources and not on self-pollination. The plants used in this study of the hairy-neck character were open-fertilized throughout the experiment, as were also all parental plants in preceding generations. In 1923, however, heads to be used in further studies were selfed by bagging. In this connection it should be noted that the percentage of fertility of 21 bagged (selfed) heads, excepting 2 in which the fertility for some reason was low, was 77 per cent, while the percentage of fertility of 21 unbagged (open-fertilized) heads, was 79 per cent. Some of the selected heads, both selfed and open-fertilized, showed higher fertility than Purplestraw wheat, which varied from 80 to 85 per cent, but others were somewhat less fertile.

The progenies of the selections listed in Table III do not disclose a large amount of natural crossing. All plants in 5 of the 10 progenies were identical with their respective parents in head characters. Four of the progenies each contained one individual that appeared from its head characters to be due to a natural cross on the parent selection, the off-type plant in each case differing from the parental selection in degree of awn development and in glume color.

Considerable natural crossing was evident in only one progeny (K), which consisted of 84 awned and 14 semiawned plants. These plants lacking full development of awns, in the progeny of an awned plant, indicate natural crossing with pollen from an awnless plant, inasmuch as the factor for presence of awns in wheat normally is incompletely recessive to the factor for their absence, which results in a semiawned plant in the F1. In spite of this evidence of natural crossing all plants in selection K were hairy-necked. There is perhaps a slight possibility that the different head characters appearing in this progeny, likewise also in the other cases noted, are not evidence of natural crossing but indicate some unusual factorial composition of the gametes, resulting in abnormal segregation.

In addition to the differences in respect to awns, the progeny of selection K, though consisting entirely of hairy-necked individuals, also differed somewhat in head type, as is shown in Plate 5. All heads had white or yellow glumes, but one type had a lax, fusiform spike, while that of the other was more dense and oblong in shape. The width and shape of the shoulder of the outer glume, as well as the length of the beak, differed greatly, as may be seen from the figure.

In Plate 2 are shown the kernels obtained from one head each of Abruzzes rye, Fulcaster wheat, and the fusiform and oblong types of head present in selection K. Resemblance to rye may be seen in the seeds from the fusiform head. The
kernels are narrower, blunter at the base, and have longer and more sharply pointed germs than the kernels from the oblong head. The longer, narrower glume of the fusiform head no doubt influences the shape of the grain, but whether or not the glume character can be attributed to the F₁ rye parent is open to question. According to Fruwirth (2, p. 183–184), a segregate somewhat similar to this fusiform type resulted from a wheat-rye hybrid made by Rimpau in 1888. It was largely wheat-like, but in comparison to wheat the head and glumes were longer, the latter closely pressed together, and the keel ciliated as in rye. This strain was grown for many years in an experimental way in Europe and remained fully constant in all respects, including a partial sterility exhibited by it.

DISCUSSION AND SUMMARY

It is evident that the hairy neck found in wheat-like segregates of wheat-rye hybrids is a heritable character, but the data at hand are not sufficient to permit definite conclusions regarding the number of factors involved or the manner in which these factors are transmitted. Considerable irregularity in segregation is apparent and both dominant and recessive tendencies are observed. The reason for this is unknown, but it is suspected that it is related to probable irregularities in chromosome behavior.

According to Sakamura (11), Triticum vulgare has 21 and Secale cereale 7 haploid chromosomes. These numbers have been confirmed by Sax (12). The number of chromosomes in the F₁ of the hybrid between these species has not been determined. Nakao (10), who made cytological studies of the F₁ of a wheat-rye hybrid, states that “the chromosome number is not definite (17–23), being almost always more than the expected number, 16.” From our present knowledge of chromosome numbers in these species as given by Sakamura (11) and Sax (12), we would expect 28 chromosomes in the F₁, 21 from the Triticum vulgare parent, and 7 from the Secale cereale. This would be in accord with the observation of Kihara (3), who found 35 somatic chromosomes in the F₁ of hybrids between different members of the “Emmer group” of wheat, which contain 14 gametic chromosomes, and members of the “Vulgare group” of wheat, which contain 21 gametic chromosomes. Sax (12) also observed 35 chromosomes in hybrids between these groups, while in an F₁ hybrid between T. monococcum with 7 gametic chromosomes and T. turgidum with 14, the F₁ had 21 somatic chromosomes. In the F₁ hybrid between the “Emmer” and “Vulgare” groups, according to both Kihara and Sax, 14 pairs of chromosomes and 7 univalent chromosomes are found in the pollen mother cell. The 14 pairs, as stated by Sax, “divide as usual in meiosis while the 7 univalents lag behind but ultimately divide equationally in the first division, and pass at random, without dividing, to either pole in the homoeotypic division.” As a result of these abnormalities, Sax estimates that 20 per cent of the pollen produced is obviously imperfect and a large percentage is nonfunctional. Considerable sterility is found in these hybrids between the groups of wheat. If such phenomena should occur in the wheat-rye hybrid there would be 7 bivalent and 14 univalent chromosomes in the F₁ generation. With the higher number of univalents and the increased ratio of these to bivalents, abnormalities in chromosome behavior would be expected to occur in even greater degree than in the hybrids between different groups of wheat. Furthermore, with the gametes effecting the hybrid having come from plants belonging to different genera, incompatibility between the chromosomes contributed by the respective parents could hardly fail to exist. The results of Nakao (10) confirm this expecta-

1 Nakao states: “In wheat, as described by Overton and Koernicke, and in rye, the reduced number of chromosomes is 8.”
tion. In his studies on the nuclear divisions of the pollen mother cells of the wheat-rye hybrid he found degenerative phenomena in the pollen mother cell and in the pollen. "The degenerating phenomena of the pollen cells are observed at every stage of their development, e.g., in synopsis, spireme, the first division, the second division, etc." Jesenko (4) in studies of the pollen mother cell of the wheat-rye hybrid also found abnormalities which would seldom permit the formation of fertile pollen. These cells seldom divided into 4 parts, as is natural in wheat and rye, but frequently divided into 3, 5, 6, or even more different parts.

Pollen grains are formed in the F1 wheat-rye hybrid, but nearly all of them are shrunken and poorly developed, and lack the usual cell contents. A few are found now and then, however, that are better developed and that may be capable of growth. But anthers filled with such pollen have never been found, and, probably on account of the resulting lack of internal pressure, no anther has been observed to dehisce. F1 plants isolated or bagged have always been sterile. Pollinations made by artificially rupturing the anthers also have not been successful. Jesenko pollinated over 3,000 hybrid flowers with pollen forced out of the anthers but no flower set seed. The writers have made several hundred such pollinations with like result.

The F1 wheat-rye hybrid appears to be self-sterile, but seeds sometimes are set on such plants when open pollinated. In 1922, at the Arlington Experiment Farm, 11,791 wind-pollinated flowers of F1 wheat-rye hybrids growing in the wheat plats produced 6.5 seeds per thousand, and in 1923, under similar conditions, 4,772 hybrid flowers produced 6.7 seeds per thousand. The results for the two years agree so closely that it appears that heredity rather than environment is the factor determining seed formation. Leighty and Hutcheson (7) found, in 1919, that of the wheat flowers emasculated and exposed in the field at Arlington, 83.3 per cent set seed, a high seed formation for wheat heads. This indicates that an abundance of wheat pollen was disseminated by the wind to effect fertilization of exposed stigmas. It is well known also that rye pollen is widely disseminated by the wind. The flowers of the wheat-rye hybrid open at an average date intermediate between the average for wheat and rye, and, as is usual with small grain plants when fertilization has not occurred, remain open for a week or longer. Since the natural wheat-rye hybrids at Arlington grew in close proximity to both wheat and rye plants, there is little doubt that all their flowers were pollinated at some time or other with wind-borne pollen of both wheat and rye. The flowers thus pollinated produced on the average about 6.6 seeds per thousand. Jesenko (4) obtained 3 seeds per thousand pollinations when he backcrossed his F1 wheat-rye hybrid with wheat pollen (and one seed from almost 5,000 pollinations with rye). The difference in results obtained by the writers and by Jesenko probably indicates the greater effectiveness of natural pollination, and is in line with the results usually obtained in artificial croses of wheat.

Although the F1 wheat-rye hybrid has produced no seed when bagged, but when open pollinated has shown 0.66 per cent of fertility, it cannot be definitely concluded that the female gamete is more fertile than the male. No cytological studies of the egg mother cell of the F1 wheat-rye hybrid have been made and nothing is known regarding the phenomena connected with development of the female gamete. Self-sterility, when a head is bagged, may be due to lack of development of sufficient pollen in the anther to cause dehiscence. Following artificial rupture of the anthers and self pollination, it may be due to the same causes that are responsible for the usually nearly complete self-sterility in rye itself. It is evident, however, that the stigmas of the F1 are brought into contact with viable pollen of wheat and rye more frequently than the pollen of the
F₁ is brought into contact with stigmas of any kind, and especially with ovules capable of being fertilized. Thus, the apparent greater fertility of the female gamete may be due merely to chance.

With 7 bivalent and 14 univalent chromosomes present in the F₁, numerous recombinations at the time of gamete formation would be theoretically possible. It is probable that the gametes formed would contain 7 bivalents in every case and that nearly all of the gametes would contain, in addition, one or more of the univalents. Assuming random assortment, one gamete out of 16,384, on the average, would be expected to contain no univalent, and an equal number would contain all 14 univalents.

There is some basis for assuming that successful backcrosses on the F₁ wheat-rye hybrid with wheat and rye pollen are related in some way to the number of univalents present in the hybrid gamete, and that with a high number of univalents a successful backcross with wheat can result, while with none or possibly one univalent the rye backcross is possible. If it is assumed that a gamete with 12, 13, or 14 univalents is required for a successful backcross with wheat pollen the theory would explain the results obtained. The 12, 13, or 14 univalents present in the gamete would appear to counteract any incompatibility that may exist between wheat and rye chromosomes to a sufficient degree to allow the setting of seed.

Sakamura (11) found 42 somatic chromosomes in a fertile strain descended from a backcrossed wheat-rye hybrid. Kihara (5) confirmed this number in the fifth generation of this same lot of fertile hybrids. Two plants resulting from seed produced by an almost sterile plant in this same lot of wheat-rye hybrid descendants contained 38 and 42 somatic chromosomes, respectively.

Jesenko (4) observed a self-fertile plant with dense hairiness on the sheaths of the lower leaves in the progeny of an F₁ wheat-rye hybrid backcrossed with wheat. This character was not observed in either the wheat or rye parent. In the F₂ generation of this hairy-sheathed plant there were 31 hairy-sheathed individuals and 23 glabrous-sheathed, or approximately a 9 : 7 ratio. On the assumption that 2 factors are concerned in the inheritance, there should be 2 equal groups in the F₂, segregating into 3 : 1 and 9 : 7 ratios, or a total of 3 hairy plants to 2 glabrous plants. The actual ratio obtained by Jesenko was 3 : 1.96. This is apparently an example of simple Mendelian inheritance in wheat-rye hybrids.

The unusual ratios obtained on the segregation for the hairy-neck character can not be explained satisfactorily, as they are based upon too few plants, and also upon plants in the ancestry of which natural crossing has occurred at least to a small extent. Further investigations may show that we are observing plants in which an excess of recessive factors, accumulated in the gametes through random assortment of wheat and rye chromosomes, results at times in a reversal of dominance, and at times in unusual ratios in inheritance. If this is the case it is possible that the three selections showing all hairy-necked individuals in their progeny are not fixed for this character, and that it may be impossible of fixation.

The F₂ and later generations of wheat-rye hybrids show greater fertility but less rye resemblance than the F₁. As the F₂ is usually a sesqui-hybrid with the parentage (T. vulgare ♀ × S. cereale ♂) ♀ × T. vulgare ♂ (21 haploid chromosomes X 7 haploid chromosomes) X 21 haploid chromosomes, the rapid disappearance of the rye characters in generations later than the F₁ appears explainable. In the F₁ generation two complete sets of chromosomes are present, one from the wheat parent, the other from the rye. The possibility of obtaining, in the F₁, an egg cell containing only 7 rye chromosomes or 21 wheat chromosomes, is extremely
small, but if such occurred and fertilization were effected with a pollen grain from wheat or rye, respectively, the F₁ type would be expected in the following generation. This has been seldom, if ever, realized. Individuals with certain rye characters and others showing little rye influence morphologically but exhibiting a high degree of sterility are to be found, however, in all generations so far grown, though the number of such individuals diminishes annually. The increasing resemblance to wheat and the increasing fertility is supposed to be accompanied by progressive change in the chromosome number and constitution in the direction of the wheat type. This would be comparable to the phenomena observed by Sax (13) in hybrids between wheat groups with different chromosome numbers.

The hairy-neck character dealt with in this paper is an example of a definite rye character present in individuals of the F₆ generation which may be traced to the original rye parent, the parent with the lesser number of chromosomes. In other respects the selections possessing the hairy necks appear similar to wheat, and exhibit very little sterility. This is of interest and possibly of importance, inasmuch as the result obtained in interspecific wheat crosses, made with the aim of combining desirable characters of two species, have been disappointing for the most part, as the segregates reverted to the parental types, seldom showing recombinations of characters of both parents. The previously reported segregates of wheat-rye hybrids nearly always reverted rapidly to wheat, but it appears from the results reported above that it is possible to obtain plants combining certain characters of the wheat and rye parents.

**LITERATURE CITED**

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*Once each in over 2 million gametes.*
(9) Meister, G. K.

(10) Nakao, M.

(11) Sakamura, T.

(12) Sax, K.

(13) ———

(14) Wilson, A. S.
PLATE 1

Heads of Purplestraw wheat (A), rye (D) and two natural F₁ wheat-rye hybrids, one with pubescent or hairy neck (B), and one glabrous neck (C). (Natural size.)
"Hairy Neck" Wheat Segregates from Wheat-Rye Hybrids

PLATE I

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"Hairy Neck" Wheat Segregates from Wheat-Rye Hybrids

PLATE 2

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PLATE 2

Necks (upper portions of peduncles) of rye culms: A, glabrous; B, sparsely pubescent; C and D, densely pubescent. (X3) Kernels of rye, wheat, and of two different types of head in the progeny of selection K (see Pl. 5). E, Abruzzes rye; F, Fulcaster wheat; G, fusiform head type (3) in selection K; H, oblong head type (4) in selection K. (Natural size.)
PLATE 3

Heads of wheat and 3 wheat-like selections with hairy necks from the $F_5$ progeny of natural wheat-rye hybrids: 1, selection K; 2, selection H; 3, Fulcaster wheat; 4, selection C. (Natural size.)
"Hairy Neck" Wheat Segregates from Wheat-Rye Hybrids
"Hairy Neck" Wheat Segregates from Wheat-Rye Hybrids

PLATE 4

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PLATE 4

Necks (upper portions of the peduncles) of the culms of wheat, rye, and selections from wheat-rye hybrids: 1, wheat; 2, selection K; 3, probable natural hybrid in progeny of selection 1; 6, selection D; 7, selection F; 8, selection C; 9, rye. (Natural size.)
Head types present in the F₆ generation of wheat-rye hybrid plants with hairy necks: 1 and 2, probable natural hybrids found in progeny of selections I and K, respectively; 3 and 4, two types of heads in the progeny of selection K. Head No. 3 produced the rye-like kernels (G); and head No. 4 the wheat kernels (H) shown in Plate 2. (Natural size.)
"Hairy Neck" Wheat Segregates from Wheat-Rye Hybrids

PLATE 5