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University of Minnesota
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Studies of Self-Fertilization in Rye

By H. E. Brewbaker
Division of Farm Management, Agronomy, and Plant Genetics

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H. E. Brewbaker[2]

INTRODUCTION

Cultivated rye, *Secale cereale* L., is considered by Schulz (26) to have descended from *Secale anatolicum* Boissier, which is found at the present time growing wild in Syria, Armenia, Persia, Afghanistan, Turkestan, Sungari, and the Kirghiz Steppe. It is supposed to have come into cultivation in Turkestan. Engler-Gilg (4) considers *S. cereale* to have originated from *S. montanum,* a wild species growing in Southern Europe and the adjoining part of Asia, and to have been grown first as a cultivated plant in the Bronze Period. Vavilov (31, 32) believes the morphological or physiological similarity between *S. montanum* and *S. cereale* insufficient evidence to prove that the one originated from the other. *S. cereale* is found as a weed widely distributed among wheat and barley plantings throughout the southwest of Asia, where rye has never been grown as a cultivated crop. This rye-weed appears to be indigenous in this section of Asia. Vavilov believes that seed of this rye-weed was intentionally sown with wheat and barley and that when the value of the rye became fully appreciated it was sown as a separate crop.

Rye is now one of the world's great cereal crops. The total production of rye[3] for the three-year period, 1922-24, averaged slightly more than one billion bushels per year. This was a little less than the production of barley, about one-third that of wheat, and a little more than one-fourth that of oats. The United States during this time produced about 7.5 per cent of the total world production, or an average of more than 76 million bushels per year. Minnesota raises approximately one-fifth of the rye grown in the United States. In 1924 about 4.5 per cent of the crop land in this state was planted to rye. Rye does not usually outyield a hardy winter wheat, but on dry land and poor soils, or in seasons when black stem rust is a limiting factor in wheat production, it generally yields more than spring wheat. Rye is especially valuable throughout the Corn Belt for late autumn and early spring pasture, as a green manure crop, and as a companion crop with alfalfa and clover. Whether or not rye will become of increasing importance in the United States depends somewhat upon the development of high-yielding commercial varieties.

[1] A thesis submitted to the faculty of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy. 1926.

[2] Grateful acknowledgment is made to Dr. H. K. Hayes, under whose direction the studies were made; to Dr. E. C. Stakman and Dr. M. N. Levine for help in connection with the rust reaction phase of the problem; and to Mr. Lee Alexander for general assistance.

[3] See Yearbook of the U. S. Dept. of Agr. for 1924.

Improvement in rye has been accomplished largely through mass selection and, to a lesser extent, by individual plant selection. The necessity of controlling the male as well as the female parentage in breeding heterozygous plant material is appreciated now as it has not been in the past.

The purpose of this investigation was to study the effects of self-fertilization in rye and the possibility of the use of inbred lines as foundation material for further improvement.

MODE OF RYE POLLINATION

In initiating a breeding attack on any crop it is of fundamental importance to know the natural mode of reproduction and the extent to which self-pollination or cross-pollination takes place. The rye flower is especially well adapted for cross-pollination (see Plate I). According to Hildebrand,[4] the anthers project between the partly closed glumes until their bases emerge. They then tip over and dehisce, spilling the pollen outside the flower. Fruwirth (7), on the other hand, states that the filament lengthens rapidly and forces the anther out of the flower; and that dehiscence begins before the anther has tipped over. Thus a small amount of pollen may fall on the stigma of the same flower while the larger part is carried away.

Observations on anthesis were made by the writer on several plants which were grown in the field, transplanted into flats, and brought into the laboratory. Florets located slightly above the center of the head are usually the first to open, flowering proceeding in both directions. Opening of the floret starts slowly and gradually increases in rapidity until the anthers finally emerge and dehiscence has taken place, the whole process requiring about an hour. Dehiscence was found to take place rarely before the anthers were extruded and tipped over, and in some of these exceptional cases the anther was found to catch temporarily on the awn of a lower floret. Self-pollination is made improbable by the late dehiscence of the anthers, and the large feathery stigma (Plate I a, b, c) offers splendid opportunity to catch foreign pollen carried by the wind. After artificial pollination with pollen from another plant, the floret closed completely in 45 minutes. If cross-pollination was not effected the floret stayed open much longer. Heribert-Nilsson (14) found the stigma receptive 14 days after blossoming. The writer found the unfertilized florets to remain open as long as 19 days in the greenhouse. The florets finally close whether or not fertilization is accomplished. It is concluded from these observations that natural cross-pollination is greatly favored, but that self-pollination is not prevented.

[4] See Knuth's Handbook of Flower Pollination, Vol. III, pp. 531-32.

Heribert-Nilsson (16), in a test of vicinism, or natural crossing between plants, used a wax-free strain as the "indicator." The wax-free character is a simple Mendelian recessive, hence any natural crossing between wax-free and normal plants when the normal is the pollen parent, will be apparent in the F_1 generation. A single indicator plant was separated from a plot of 3500 square meters of normal rye, with the following results:

Separated	by	50	meters	— 54.5%	natural	crossing
"	"	250	"	— 46.3%	"	"
"	"	350	"	— 29.7%	"	"
"	"	400	"	— 19.0%	"	"

Single indicator plants separated by 50 meters from a small plot of 10 square meters of normal rye were cross-pollinated by normal rye to the extent of 10 per cent.

While the vicinism experiment of Heribert-Nilsson was not designed to determine the degree of natural crossing which takes place within a variety, the results obtained, when considered in relation to the flower structure and anthesis, and the high degree of self-sterility in rye, justify the conclusion that rye is to a very large extent naturally cross-pollinated.

SOURCE AND HISTORY OF MATERIAL USED

Minnesota No. 2 rye was used for all the investigations herein reported. This variety was developed from the well known Swedish variety, the original stock having been obtained in 1895 from John Brogard, at Henning, Minn. Plants which survived the winters of 1896-97 and 1897-98 were used as foundation stock. In 1897, 120 seeds were planted in the nursery, from which 16 plants were harvested in 1898. These few plants were the original source of the variety now known as Minnesota No. 2, which excels in winterhardiness (see Boss, 1).

In 1916, a selection experiment was planned by Dr. H. K. Hayes for the purpose of obtaining varieties with more uniform color of grain. Individual plants were selected on the basis of plant vigor in the field and later for grain color and plumpness in the laboratory, and the seed of each selected mother plant was sown in a small isolated plot, using 50 to 75 seed for each plot. These plots were located among the winter wheat nursery plots and were separated from each other by a distance of 50 to 100 feet or more, depending upon the space available and the number of strains to be isolated. Continuous selection has been carried on since 1916.

Fig. 1. Minn. No. 90, a Colorless Strain of Rye Grown in an Isolated Plot
This strain was produced as a result of five years continuous selection in Minn. No. 2 Rye.

While it is not the intention to give a complete report of this selection experiment, certain facts appear of interest in relation to the self-fertilization studies. Indications of approaching homozygosity through inbreeding are apparent, not alone in relative purity for grain color, for which selection was made, but also in relation to the occurrence of increased numbers of certain types of seedling and plant abnormalities in some strains and the comparative freedom from others (see Table I). Minnesota No. 92, a strain having dark green seed, produces many more white seedlings than does normal Minn. No. 2; the same is true to a lesser extent of Minn. No. 91, a light green seeded strain. In contrast to this, Minn. No. 90 (Fig. 1), a colorless seeded strain, appears to be practically free from white seedlings, only one having been found since 1923. During the same time yellow-green seedlings were found quite frequently in Minn. No. 90, while none have been recorded in Minn. No. 92 (see Tables I and VII). The results obtained in relation to purity for grain color corroborate to a considerable extent those of von Rumker (23, 24, 25), who obtained several pure color types as a result of continuous selection for seven or eight years.

TABLE I

Occurrence of Seedling and Plant Abnormalities in the "Selection" Strains, Commercial Minn. No. 2, and a Recombination Variety

Rod Row Test

Nursery stock No.	1923		1924		1925		1926	
	Total	Per cent abnormalities*	Total	Per cent abnormalities*	Total	Per cent abnormalities*	Total	Per cent abnormalities*
1-22-5	1237	None	1647	None	2249	0.2 yg	1650	None
1-22-6	1414	10.4 w	1361	10.2 w	1672	4.6 w 0.06 st	1336	0.8 w 0.2 vw
1-22-8	1373	6.6 w	1404	2.1 w 6.3 yg	1809	0.3 w 5.3 yg		Discarded
1-22-10	1395	1.3 w	1478	None	1622	None	1300	None
1-22-11	1211	2.3 w	1406	None	1921	0.05 cyl 4.7 w	1300	None
1-22-12	1236	1.6 w	1885	2.0 w 1.3 yg	2358	1.5 w 1.1 yg	1600	0.6 w
1-22-13	1336	1.0 w	3542	1.0 w 0.8 yg	2765	0.8 w	1780	0.6 w
1-22-14	1468	2.0 w	2422	1.5 w 0.3 vw 0.1 st 0.4 yg	2136	1.0 w 0.1 yg 1.7 vw	1500	0.7 w 0.4 vw
Minn. No. 90	1/40 A.	Trace yg	3701	0.03 w 0.03 vw 0.3 yg	1911	0.4 yg	1400	None
Minn. No. 91	3126	1.2 w	3582	0.8 w 0.2 yg	1590	0.8 w	1170	0.4 w
Minn. No. 92	3523	2.7 w	4120	2.6 w	1737	1.1 w	1455	1.0 w
Minn. No. 2	2511	0.04 w	2112	0.05 w 0.05 vw	2527	None	1700	None
Recomb. AA of 8 selfed strains	....	.....	....	....	642	None	1600	None

* w = white seedlings.
cyl = seedlings with a cylindrical first leaf.
yg = yellow-green seedlings. (The type of plant produced by these seedlings was not determined in each case.)
st = striped seedlings.
vw = virescent white seedling and plant.

A reduction in yielding ability has been obtained for most of the selection strains, as determined by rod-row studies; a few strains, on the other hand, appear very promising in this respect in relation to normal Minn. No. 2.

The studies of self-fertilization were begun in 1920, the selfings that year being made in the above mentioned selection strains.

INBREEDING THROUGH SELF-FERTILIZATION

The use of artificial self-pollination in cross-fertilized crops as a means of reducing heterozygous material to pure lines is a relatively new method. It is being applied extensively in corn breeding work in the United States and Canada, and to a lesser extent with timothy, sunflowers, red clover, and many other crops that are naturally cross-pollinated, as well as for certain clonally propagated crops such as potatoes. Its successful application to any particular crop depends to a considerable extent upon the ability of individual plants to set sufficient seed under artificially self-pollinated conditions to carry the strains year after year. Corn is nearly, if not entirely, self-fertile. Red clover and sunflowers were formerly considered to be completely self-sterile, but Fergus (6) obtained considerable seed setting in self-pollinated red clover; and McRostie (20) and Hamilton (9) have shown that artificial self-pollination is a practical means of isolating pure breeding strains of sunflowers. That selfed strains of timothy differ in their ability to produce selfed seed, some appearing highly self-fertile and others largely self-sterile, has been determined by Hayes and Clarke (13). It has long been recognized that a high degree of self-sterility is characteristic of rye.

The extent to which vigor and yielding ability are reduced as a result of self-fertilization is of great importance. Formerly it was believed that continued self-fertilization in cross-fertilized crops would lead to a continuous reduction in vigor. It has been shown in recent years, particularly for corn, that such is not the case, but that after homozygosity is reached there is no further reduction in vigor.

EARLY STUDIES OF SELF-FERTILIZATION IN RYE

Most of the early work with self-fertilization in rye was done by German and Swedish plant breeders. Rimpau (Ulrich 30) was the first to attempt a solution of the question concerning the self-fertility of this plant. By the use of parchment bags he obtained an average seed setting of 1.1 per cent for spikes bagged singly, and 1.7 per cent for two spikes of the same plant bagged together; and with glass tubes 0.9 per cent and 4.4 per cent, respectively, for the same methods. He concludes that self-sterility is not absolute in rye, but that self-fertility is very limited.

Ulrich studied the comparative self-fertility of three varieties of rye, Petkuser, Probsteier, and Schlanstedter. Parchment bags were used to cover the spikes. The results are summarized in Table II.

TABLE II

Comparison of Percentage Seed Setting by Self-Fertilization, Using Parchment Bags as an Isolation Agent

Variety	Single spike selfed	Two or more spikes bagged together		Normal polli-nation
		Single plant	Different plants	
Petkuser	1.30	2.52	28.29	80.0
Probsteier	2.33	4.98	25.12	59.0
Schlanstedter	5.02	7.31	38.32	78.0

In another experiment, using two varieties of rye, Schlanstedter and Zwätzener, glass test tubes and parchment bags were compared as isolation agents. When the bags were used, one was shoved inside the other as a better protection against stormy weather. The results obtained are presented in Table III.

TABLE III

Comparison of Percentage Seed Setting by Self-Fertilization for Schlanstedter Rye and Zwatzener Rye, Using Both Parchment Bags and Glass Tubes as Isolation Agents

Variety	Isola-tion agent	Year	Single spike selfed	Two or more spikes bagged together		Normal polli-nation
				Single plant	Different plants	
Schlanstedter	P.B.	1877	1.10	1.90	23.40	77.30
Schlanstedter	G.T.	1881	0.90	4.40	26.20	
Schlanstedter	P.B.	1900	5.02	7.21	38.32	78.00
Zwätzener	P.B.	1900	8.26	7.79	....	82.53
Zwätzener	G.T.	1900	0.96	0.60	22.92	82.53

Ulrich concluded from these and other experiments that there are individual differences within a race, both fully sterile and strongly self-fertile individuals being found.

Obermayer (22) performed two small experiments with rye, in one of which he removed all but the central florets and artificially selfed those, and in the other he used the ordinary method of bagging a single spike. An average percentage seed setting of 3.2 was obtained by the first method for 7 hand-pollinated spikes and 8.8 per cent by the latter method for 8 spikes bagged. In another experiment, in 1911-12, plants were enclosed in large isolation cages, but no seeds were obtained. He concludes that varieties and plants within a variety differ in self-fertility.

The work of N. Heribert-Nilsson (14, 15, 16) is the most extensive of its kind reported. He found that linen as employed by Giltay is not a sure isolation agent, as it has too large a mesh; that parchment bags are ideal if they can be protected from wind and rain; and that glass test tubes are not so good as parchment bags because they constitute a hindrance to transpiration but that they will serve the purpose where parchment can not be used. Heribert-Nilsson used three principal methods of isolation, namely, (1) glass test tubes; (2) isolation by space, i.e., single plants were separated 50 meters apart in wheat fields; and (3) parchment bags. As an average of 356 plants isolated, he found the seed se'ting to be about 1, 7, and 4 per cent, respectively, for the three methods. Seed setting for most plants ranged from 0 to 5 per cent with one or two in every 100 plants showing a high degree of self-fertility. Most of these highly self-fertile plants produced very poor seed, and in a mixed stock would tend to be eliminated. In 1921, strains were being carried that had been continuously inbred by self-fertilization for nine generations. There was, in general, a decrease in vigor due to inbreeding, but since the fifth generation there has been no further decrease in vigor. A few strains which had been selfed for several generations continued vigorous and yielded more than the normal variety. When the better inbred lines were again crossed, it was possible to obtain increased vigor, and new varieties were produced which showed improvement over the old. The variety "Stormrag," a rather short, stiff-strawed variety with compact spikes, was produced by crossing inbred strains of Petkuser.

STUDIES OF SEED SETTING WITHIN A SINGLE FLORET AND BETWEEN NEARBY FLORETS ON THE SAME HEAD

Rimpau, in 1876 (Ulrich, 30) wrapped thread about each of four spikes of rye with complete barrenness as a result. Ulrich covered spikes of rye with cotton wadding tied with raffia. He did not obtain any selfed seeds and he concludes, as did Rimpau, that "the rye flower is self-sterile," but he believed also that "self-fertilization within a spikelet is possible." Fruwirth (7) reached a similar conclusion regarding the lack of fertility within a single flower.

Heribert-Nilsson (14) considered these experiments untrustworthy, for he says "flowers which can not open form no seeds," but he did not substantiate his criticism with experimental data.

An investigation was undertaken by the writer in 1922 for the purpose of bringing more evidence to bear upon the question of single floret and single spikelet fertility. All the spikelets but one were removed from some of the spikes, while a single floret was left on others. Some of the single florets were artificially self-pollinated. A floret was chosen which showed signs of immediate anthesis and all others were removed from the spike. The anthers were then removed with forceps and the stigma was dusted well with pollen, assuring self-pollination. After each pollination the forceps and scissors were dipped in alcohol, and all spikes manipulated were covered with glassine bags. From the 64 single florets which were hand-pollinated, 3 seeds were obtained (Table IV). This indicated the probability that a single floret was sometimes self-fertile, altho it was recognized that accidental cross-pollination may have occurred.

TABLE IV

RESULTS OBTAINED IN A DETERMINATION OF SEED SETTING WITHIN A SINGLE FLORET AND A SINGLE SPIKELET

Variety	Type of manipulation	Single floret		Single spikelet		
		No. of heads bagged	No. of seeds	No. of heads bagged	No. with one floret fertile	No. with both florets fertile
Results obtained in 1922						
Minn. No. 2	Bagged, untreated	35	0	34	7	4
Minn. No. 2	Selfed by hand..........	64	3	..	..	..
Minn. No. 2	One floret selfed by hand, other floret untreated..	..	..	12	0	3
Prolific Spring	Bagged, untreated	41	0	18	0	0
Results obtained in 1923						
Minn. No. 92	Bagged, untreated	35	0	34	4	0
Minn. No. 92	Not bagged, check........	12	11	13	6	1
Minn. No. 91	Bagged, untreated	24	0	13	1	0
Minn. No. 91	Not bagged, check........	12	2	5	0	1
Minn. No. 92	One floret emasculated....	..	..	6	0	0
Minn. No. 91	One floret emasculated....	..	..	19	1*	0
Minn. No. 91	One floret emasculated, not bagged, check	..	..	7	1* 2†	4

* Floret emasculated.
† Floret not emasculated.

In 1923 further results were obtained (Table IV). In some of the single spikelets, one floret was emasculated while the other was left intact. On 26 spikelets so treated 4 seeds were obtained, 2 in emasculated florets, and 2 in florets in which the anthers were left.

A slightly different method was used for part of the studies in 1923 and all of the studies in 1924 and 1925. All spikelets were removed from the head except two, the one located just above the other. Sometimes one or two spikelets were removed between the two. The central floret was plucked from the remaining spikelets. The left- and right-hand florets of the upper spikelets were designated as "a" and "b," and those of the lower spikelet as "c" and "d," respectively. The "b," "c," and "d" florets were emasculated when the anthers were still green but "a" retained its anthers. The data obtained by this method in 1923-25 are presented in Table V. In a total of 392 spikes treated in this way and bagged, 31 seeds were produced in the "a" florets, 26 in the "b" florets, and 34 in the "c" and "d" florets of the lower spikelet. In 1924 the awns were clipped close to the lemma on several of the manipulated spikes. On several spikes the bags were rolled somewhat tightly about the head. Neither of these treatments seemed to influence the degree of seed setting. Under the conditions of this experiment there appears to be no physiological difference in fertilization within a single floret or between different florets on the same head. The fact that seed setting was very limited when pollination was done artificially shows that the apparent self-sterility is not a result of lack of pollination but is probably largely genetic in nature. The difference in seed setting between the lower and the upper spikelets is believed to be due to a difference in pollination, since it is probable that the bag would induce a greater degree of self-pollination than is obtained under open-pollinated conditions.

TABLE V

RESULTS OBTAINED IN AN EXPERIMENT TO DETERMINE WHETHER POLLEN FROM AN INDIVIDUAL FLORET WOULD FERTILIZE THAT FLORET AS READILY AS OTHER FLORETS IN THE SAME SPIKE

Variety	No. of heads bagged	Total No. of florets	Total No. of seed			Per cent of seed setting			Mean per cent seed setting
			a floret	b floret	c & d florets	a floret	b floret	c & d florets	
Results obtained in 1923									
Minn. No. 92......	8	32	0	0	1	0	0	6.3	3.1
Minn. No. 91......	40	160	1	0	0	2.5	0	0	0.6
Results obtained in 1924									
Minn. No. 90......	49	196	3	2	1	6.1	4.1	1.0	3.1
Minn. No. 90......	48	192	4	3	1	8.3	6.3	1.0	4.2*
Minn. No. 92......	56	224	0	3	1	0	5.4	0.9	1.8
Minn. No. 92......	29	116	1	3	7	3.4	10.3	12.1	9.5*
Results obtained in 1925									
Minn. No. 92......	71	284	8	6	8	11.3	8.5	5.6	7.7
Minn. No. 92......	43	172	5	5	11	11.6	11.6	12.8	12.2*
Minn. No. 91......	20	80	2	0	0	10.0	0	0	2.5
Cult. R63†	11	44	2	1	0	18.2	9.1	0	6.8
Cult. R99†	7	28	0	0	0	0	0	0	0
Cult. R105†	2	8	1	1	1	50.0	50.0	25.0	37.5
Cult. R87†	8	32	4	2	3	50.0	25.0	18.8	28.1
Total.........	392	1568	31	26	34				
Mean per cent seed setting			7.9	6.6	4.3				

* Bags were found to be slightly damaged at harvest.

† Highly self-fertile strain.

To determine if flowers that were prevented from opening would set seed, several spikes of Minturki winter wheat and Velvet barley were wrapped tightly, some with cloth tape and others with strings. A very good seed setting was obtained under these conditions, altho it was not normal (see Table VI).

TABLE VI

RESULTS OF A STUDY OF WRAPPING MINTURKI WINTER WHEAT AND VELVET BARLEY SPIKES TO DETERMINE WHETHER OPENING OF THE FLOWER IS ESSENTIAL FOR SEED PRODUCTION

Head No.	Wrapping material used	No. of florets wrapped	No. of seed set	No. of florets unwrapped	No. of seed set
Results with Wheat					
1	Cloth tape	20	11	12	12
2	do	14	7	16	15
3	do	26	21	..	..
4	String	30	17	..	..
5	do	34	23	..	..
*Results with Barley**					
1	Cloth tape	20	19	10	6
2	do	20	0	10	0
3	do	20	20	..	..
4	do	22	15	6	3
5	String	26	6	12	12
6	do	10	0	14	2

* Only lateral florets were counted.

In consideration of the fact that in the barley variety used in this experiment the anthers may often be found dried up at the end of the mature kernel, and that, furthermore, fertilization commonly takes place before the spike is out of the leaf sheath, it appears probable that opening of the floret does not necessarily accompany the flowering stage.

METHOD USED AND RESULTS OBTAINED FROM SELF-FERTILIZATION IN MINN. NO. 2 RYE

The first selfings were made in 1920 but the data for that year were not extensive and have not been included in the material herein presented.

Good quality glassine bags were used almost entirely previous to 1925. These bags were very light in weight and consequently it was not necessary to tie the bagged plants to stakes. As a protection against storms, which are very common at this time of year, a muslin cage (Fig. 2) was placed around the selfing plot just previous to flowering time. In spite of this, heavy storms occasionally caused considerable damage to the glassine bags. Extreme care was taken at these times, as long as flowering continued, either to replace torn bags with new ones, if the work was done immediately following the storm before any pollen was in the air, or to discard the spikes when there was danger of off-pollination. Obviously, in very unfavorable years, particularly when as many as three severe storms came within the flowering period in a single year, it is possible that, with the closest inspection, some slightly damaged bags may have escaped attention. In 1925 a vegetable parchment bag which was glued with a casein waterproof glue was used for rye pollination. After having gone through several storms every bag was perfect at harvest time. These bags were much larger and heavier than the glassine bags and the bagged plants were tied to stakes (Fig. 3). In previous years usually only one or two spikes were enclosed in a single bag, while in 1925 as many as 10 to 12 spikes on one plant were bagged together, with very satisfactory results.

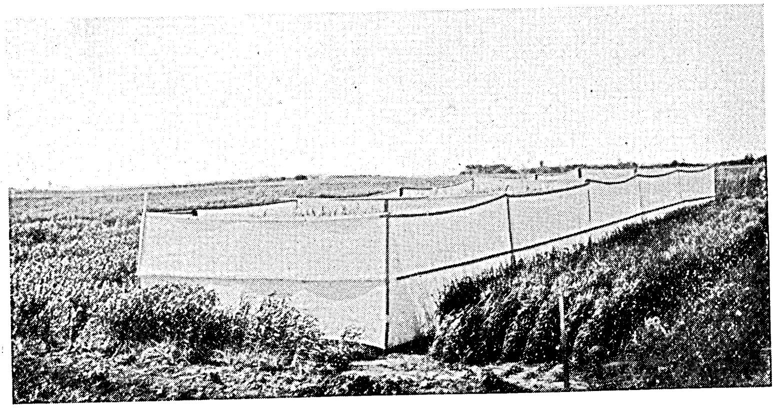

Fig. 2. Plot in Which the Artificial Self-Pollination Studies Were Made in 1922
Glassine Bags Were Used in These Studies
Upper, Selfing plot enclosed in a muslin cage as protection against strong winds.
Lower, Selfing plot with heads bagged before muslin was put up.

Occurrence of abnormalities.—Chlorophyll deficiencies appear to be one of the most common types of abnormalities observed in many crops. White seedlings have been found in many selfed strains of rye. Similar characters have been reported in corn by Lindstrom (18, 19), Hutchison (17), Hayes and Brewbaker (12), and others; in timothy by Hayes and Barker (11); in red clover by Fergus (6); in sorghum by Conner and Karper (2); and in barley by Hallquist (8).

Many other types of chlorophyll deficiencies characteristic of seedlings and plants have been observed by these and other investigators, particularly in connection with inbreeding studies in heterozygous plant material. Practically all chlorophyll deficiencies reported appear to be recessive, and plants exhibiting those characters are either lethal or at least much less vigorous than the normal green plants. White seedlings and other lethal or semi-lethal types tend to be eliminated from heterozygous cross-pollinated stock. This fact has been well demonstrated in an investigation reported by Heribert-Nilsson (15) in which a cross was made between a wax-free recessive character and normal plants and the progeny carried as a bulk in an isolated plot for six generations. Each year the wax-free plants were removed before flowering. As a result the relative proportion of gametes and plants of the normal and wax-free types, in each generation beginning with F_2, could be determined from the following formulas:

$$n:1 = \text{gametic ratio}$$

$$n^2-1:1 = \text{phenotypic ratio}$$

when n = filial generation following the cross, while the first and last terms of the ratio represent normal and wax-free gametes and plants, respectively. Thus, in the F_6 generation the gametic ratio of any pair of factors would be 6:1 and the pheno-typic ratio 35:1. The results obtained by Heribert-Nilsson agree very well with the expectation on this basis.

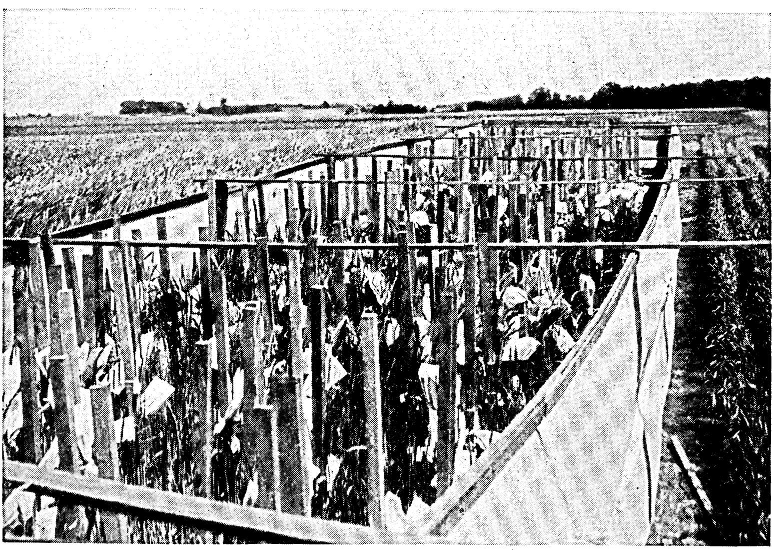

Fig. 3. Encaged Selfing Plot in 1925

Vegetable parchment bags were used as isolation agents and the plants were tied to stakes for protection from storms. As many as 10 or 12 spikes on one plant were frequently enclosed in a single bag.

The theoretically expected percentage of abnormal types may be obtained likewise by the use of a formula presented by Emerson (5) as follows:

$$F_n = \frac{100}{(n-1)^2 + 2(n-1) + 1} = \text{per cent of abnormal plants in } F_n \text{ generation.}$$

This formula reduced to its lowest terms becomes $F_n = \frac{100}{n^2}$

A survey of the rye varieties included in the varietal test at University Farm in the fall of 1924 revealed the fact that white seedlings were segregating out from each of the varieties except Minnesota No. 90, one of the selection strains previously referred to; while other chlorophyll deficient types were of less frequent occurrence in most of the strains (see Table VII). The data for the occurrence of similar abnormalities in the selection strains have been summarized in Table I. Elimination of these and other seedling and plant abnormalities appears to be an important feature in rye breeding, and while individual plant selection with progeny isolation will accomplish this purpose more rapidly than mass selection, neither method can be considered very efficient for this purpose.

TABLE VII

OCCURRENCE OF SEEDLING ABNORMALITIES IN COMMERCIAL RYE VARIETIES
One-Fortieth Acre Plots, 1924

Variety	Total seedlings	Seedling abnormalities*			
		w	vw	yg	st
Petkuser	23,200	5	2	..	..
Midsommerog	36,170	6	6	..	..
Colorless, Minn. No. 90	30,400	..	..	46	1
Medium Green, Minn. No. 91	17,440	120	1	20	..
Dark Green, Minn. No. 92	31,680	236	..	..	..
Swedish, Minn. No. 2	34,400	3	1	1	..
Rosen	21,120	2	..	1	..
Dakold	23,200	13	..	1	..

* w = white. yg = yellow-green.
vw = virescent white. st = striped.

Through the isolation of self-fertilized lines, recessive abnormalities can be quickly eliminated. There has been no particular selection for freedom from abnormalities in any of the selfed strains. The progenies each year were not large, consisting of perhaps 12 to 15 plants on the average and varying from 1 to 30 plants, depending upon the selfed seed available for planting. It is to be expected that small progenies may apparently be normal under those conditions, but still carry the recessive factor for some abnormality in the heterozygous condition. Of 31 strains which have been continuously self-fertilized since 1922, 8 appeared to be free from chlorophyll deficiencies throughout the four years. Twelve other strains which segregated in 1922 appeared normal for both 1924 and 1925. The apparent complete freedom of some strains and the reduction of segregating strains to purity for normal plants are indications of the effects of self-fertilization.

A chlorophyll-deficient seedling and plant character which has been fairly common in occurrence in the inbred strains has been designated as "yellow-green stripe." There appears to be considerable variation in the character from almost pure yellow plants striped with green to almost pure green plants striped with yellow. The parental strains studied in 1922 and 1923 segregated for 65 normals and 20 yellow-green stripes. Crosses were made in 1923, and the F_1 in 1924 was backcrossed to yellow-green stripe with the following results:

Backcross culture numbers	Normal	yg stripe
R 94 b × R 35 yg stripe	10	7
R 94 × do do	17	14
R 94 c × do do	33	34
R 95 b × do do	25	21
Observed total	85	78
Calculated (1:1 ratio)	81.5	81.5
P. E.	3.73	

From these results it appears that the yellow-green stripe character is a simple recessive to normal green.

What appeared to be a "yellow-green stripe" bud variation was observed on a plant obtained in one of the selfed lines. This plant had 17 normal green culms and only 1 striped culm, the latter being very much reduced in vigor. The spike on this single culm was bagged but no seeds were obtained.

Another chlorophyll deficient type observable in both seedlings and plants has been called "golden-green blend." In contrast to the yellow-green stripe, it has a much deeper yellowish color, is very uniform in its expression, and while there is a tendency to striping, the stripes of green and yellow are blended together. It is less vigorous than normal plants, and it appears to be much less common in occurrence than the yellow-green stripe. In 1923 a cross was made of a golden-green blend plant in selection culture 901 with a normal green plant in a pure green selfed strain, and in 1924 the F_1 was backcrossed to a golden-green blend plant. Only 21 seeds were obtained, and the resulting progeny consisted of 10 normal and 11 golden-green blend plants. While these data are very limited, they indicate that this character is probably inherited as a simple recessive.

Virescent-white seedlings, somewhat similar to those reported in maize (Lindstrom, 18), have been found about as frequently as golden-green blend plants. They appear to be fairly vigorous, altho not approaching the normal condition in this respect. A virescent plant in the 1923 selection culture No. 1501 was crossed with a normal green plant. In the F_2 generation from this cross there were 107 normal to 35 virescent-white seedlings. This closely approaches a 3:1 ratio, and it may be concluded that the character behaves as a simple recessive to normal green.

Another seedling abnormality, called "cylindrical" because of the cylinder or tube-like nature of the first leaf, has been obtained in two cultures. It is of considerable interest because of its similarity to a character now being studied in maize.

Fig. 4. Stubble of Brittle Plants as Commonly Broken Off by the Wind

So-called "brittle" plants have been observed in a number of selfed lines. Such plants may often be recognized in the field (Fig. 4), particularly after a storm, by the broken stubble where the culm has broken off completely. A chemical analysis as well as a histological and microchemical examination (Davison, Brewbaker, and Thompson, 3), shows that these brittle plants have a much thinner cell wall, a lower crude fiber, a higher pentosan content, and considerably less lignin than the normal plants. Because of the very weak, brittle nature of the straw, it is difficult to obtain selfed seed by bagging. A hand-pollinated cross of two brittle plants gave 42 brittle plants in 1925. The character was observed in 16 selfed lines during 1922, 1924, and 1925; and in these lines there were 158 normal to 56 brittle plants. The ratio expected on the basis of a single factor difference would be 183 normal to 61 brittle, the difference being well within the range of probability.

Other abnormalities, among which might be mentioned crinkled awns and pollen sterility, have been observed in the inbred strains. Pollen sterility was found in one strain segregating with plants which were apparently self-fertile to a fairly high degree. In a total of 35 plants obtained, 19 had defective pollen and did not set seed when bagged, 9 gave less than 8 per cent seed-setting, and 7 set seed in from 14.7 to 34.5 per cent of the florets.

Seed-setting ability in relation to self-fertilization.—A high degree of self-sterility has been characteristic of the majority of the inbred plants. Individual plants giving a high percentage of seed setting have been obtained each year and certain strains appear to be more or less uniform for this character, altho the greater part of the data obtained show much variability from year to year. The average percentage of seed setting obtained for the selfed strains during the years 1921 to 1925 is presented in a summary table (Table XIII, Appendix). A study of this table reveals many cases of apparently highly self-fertile individual plants having produced strains of low average fertility, and vice versa. A more detailed study of three lines selfed for five successive generations and having a common origin in 1920 is given in Table VIII. The first strain appears to be pure for relatively high self-fertility in 1924 and 1925; the second strain is segregating; and the third strain seems to be pure for fairly low self-fertility, altho the progenitor of this line in 1921 gave the highest percentage seed setting of any plant in the strain.

Throughout the course of these investigations there has been a rather consistent selection of plants which set the highest percentage of seeds, other things being equal. The effects of this selection are well brought out in Table IX, which summarizes the percentage seed setting in 1925 for strains that have been selfed the same number of years. There is a gradual increase in mean percentage seed setting from 3.1 for lines selfed one year to 14.1 for lines selfed 4 years, then dropping back to 7.7 for 5-year selfed lines. This is a further indication that the character of self-fertility is a heritable one.

TABLE VIII

PEDIGREE OF THREE SELF-FERTILIZED LINES HAVING A COMMON ORIGIN IN 1920, WITH PERCENTAGE SEED SETTING FOR THE PLANTS OBTAINED EACH YEAR

1921		1922		1923		1924		1925	
Plant No.*	Percentage seed setting	Plant No.	Percentage seed setting	Plant No.	Percentage seed setting	Plant No.	Percentage seed setting	Plant No.	Percentage seed setting
5—12	1.7	1—3	35.1	3—5	51.1	32—3	50.9	69—1	19.9
—18	1.6	—1	67.6	—1	0	—1	50.7	—2	41.3
—22	1.6			—4	4.3	—2	40.5		
—25	1.3			—6	0	—4	10.4		
—30	2.9			—7	0	—5	23.8		
—35	3.3								
—42	5.9								
—43a	1.5								
—48	1.5								
—39	9.4	2—4	12.5	4—10	7.5	31—4	76.8	67—1	0
—49	9.7	—2	5.0	—1	1.6	—1	0.8	—2	69.0
		—3	1.1	—3	0	—2	64.4	—3	34.0
		—5	0.5	—4	0	—3	0	—4	52.4
		—6	0	—5	0.7	—5	14.3	—5	1.4
		—8	2.8	—7	0	—6	1.0		
		—9	6.3	—8	0	—7	37.5		
		—10	0	—9	0.8	—8	13.0		
				—11	0.8	—9	3.0		
				—12	14.3	—10	0		
						—11	4.2		
—45	19.7	3—11	10.9	6—3	19.5	35—3	2.7	73—1	0.6
		—1	9.4	—1	2.2	—1	10.8	—2	0.3
		—6	0	—2	0.5	—2	4.2	—3	3.4
		—7	0	—4	0	—4	3.4	—4	10.9
		—8	0	—5	0	—5	3.3		
		—9	0	—7	0	—6	0.6		
		—10	0.4	—8	0.4	—7	1.7		
				—9	0.4	—8	6.3		
						—9	2.8		
						—10	0.9		
						—11	7.6		

* The underscored plant numbers are the parents for the succeeding strain. In 1921, seed from nine plants was bulked for planting in the first strain and seed from two plants for the second strain.

TABLE IX

PERCENTAGE SEED-SETTING FOR SELFED LINES IN 1925

No. of years selfed	Classes for percentage seed-setting																		Total	Mean
	2	5	8	11	14	17	20	23	26	29	32	35	38	41	44	47	50	53		
1	21	11	3	1															36	3.1
2	5	2						1											8	4.7
3	7	2	2				1											1	14	9.1
4	4	3	2	1	1	1	1		2	1	2	1							19	14.1
5	2	3	2	3	1			1											12	7.7

While there appears to be no doubt as to the heritability of the characters of high and low self-fertility, the fact remains that there is considerable variability in the degree of fertility in one year as compared with another. A correlation of the percentage seed setting in

1925 of 45 strains which had been selfed 3, 4, or 5 years with the percentage seed setting of the same strains for 1924 gives a correlation coefficient of 0.2044 ± 0.0963. Somewhat similar results were obtained by Heribert-Nilsson (14) in a comparison of two consecutive years' results. The writer studied Heribert-Nilsson's data by computing a correlation coefficient for percentage seed setting of 42 strains in consecutive years. The calculated coefficient was 0.1709 ± 0.1010. Heribert-Nilsson considers the character of high self-fertility to be a simple recessive. In that case highly self-fertile plants should produce uniformly highly self-fertile progenies. As has already been pointed out, such results have not always been obtained in these studies. Part of the variability in the degree of seed setting in certain strains year after year is without doubt due to the small number of plants available for selfing; thus, the mean percentage of seed setting for the strain may not always be a true mean of the genetic variation in this respect. It is true, also, that the degree of seed setting varies considerably with the year, e.g., in 1921 the average percentage fertility for single heads, two heads bagged together, and sibs was 1.7, 2.2, and 14.2; while in 1922 the average results for the same three methods were 10.6, 13.5, and 41.1, respectively. Climatic conditions during the period of flowering may cause fluctuations which prevent the expression of heritable differences.

Furthermore, it is possible that the environmental conditions under the bag may influence the degree of seed setting to a greater extent for some strains than for others. Certain unpublished data which appear pertinent in this connection have been furnished by Dr. H. K. Hayes. The percentage barrenness was determined for covered heads in relation to uncovered heads in Marquis and Mindum wheat and in Emmer. The results obtained are presented in Table X.

TABLE X

COMPARISON OF EFFECT OF COVERING HEADS WITH BAGS UPON DEGREE OF SEED SETTING

Variety	Uncovered		Covered		Difference in mean per cent barrenness for uncovered and covered heads
	No. of plants in trial	Mean per cent barrenness	No. of plants in trial	Mean per cent barrenness	
Marquis	30	16.6	30	31.3	14.7
Mindum	16	14.4	10	46.4	32.0
Emmer	33	3.7	29	47.9	44.2

Covering the heads with a bag increased the mean percentage barrenness 14.7 for Marquis, 32.0 for Mindum, and 44.2 for Emmer. Such a differential effect may account to some extent for the variability in percentage seed setting for the selfed strains of rye in consecutive years.

Resistance to Puccinia graminis secalis.—The seedlings of selfed lines and normal varieties were tested for their reaction to *P. graminis secalis* during the winter of 1922-23. The readings were based upon the scale devised by Stakman and Levine (27) using "0" to "4" classes; "0" standing for complete immunity or non-infection, and "4" standing for complete susceptibility. (Note Figs. 5 and 6.)

Conditions in the greenhouse were not always the most favorable for rust development, hence it seems probable that most, if not all, of the plants classed as "0" should not be considered immune, but merely as having escaped infection. Such a condition is certainly true in the case of certain cultures which on first test gave "0" infection and on second test proved susceptible.

Not a single strain was tested, however, which appeared uniform for resistance. Recent work of Mains (21) indicates that resistance to black stem rust, as well as to leaf rust and mildew, is dominant to susceptibility. The fact that a condition of homozygosity for resistance to black stem rust was not noted in these studies would not be unexpected, since only 39 strains, none of which had been selfed for more than three generations, were tested. Certain it is, however, that individual plants in Minn. No. 2 and in many of the selfed strains proved to be highly resistant.

Uniformity and relative vigor of selfed lines.—The tendency toward homozygosity for rust reaction has already been mentioned. A number of strains are free from striking abnormalities. Evidences of uniformity for other characters have also been observed. The 3-year selfed progeny of plant R14-3 appeared uniform for size and general plant characteristics (Figs. 7 and 8) and the grain was uniformly green in color. A marked reduction in vigor as indicated by plant growth is also noted.

Many of the selfed strains are pure for aleurone color. Lack of color is recessive in inheritance to the presence of green or blue in the aleurone layer (Steglich and Pieper, 28; Treboux, 29). Treboux points out, however, that grains which appear colorless to the eye will sometimes give color in the progeny, and that the presence of a small amount of color in the aleurone layer may be masked by a thick seed coat. This has been noted also in connection with the Minnesota studies.

In general, the vigor and yielding ability of the self-fertilized strains are somewhat reduced, altho a few outstanding long-time selfed strains continue to be vigorous. One such vigorous 3-year selfed strain is shown in Figure 9 in relation to a very weak, altho uniform, sister strain, and a check row of Minn. No. 2.

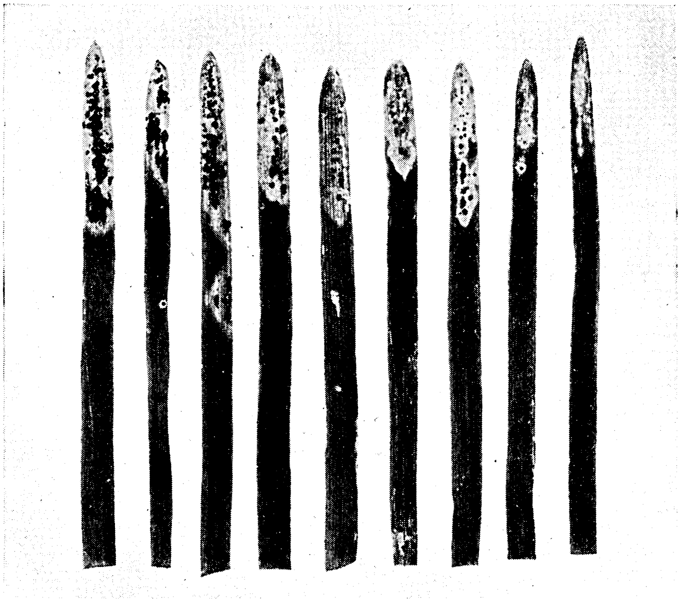

Fig. 5. Types of Reaction of Minn. No. 2 Rye to *P. graminis secalis* Ranging from "4" Infection at Left to "0" Fleck at Right

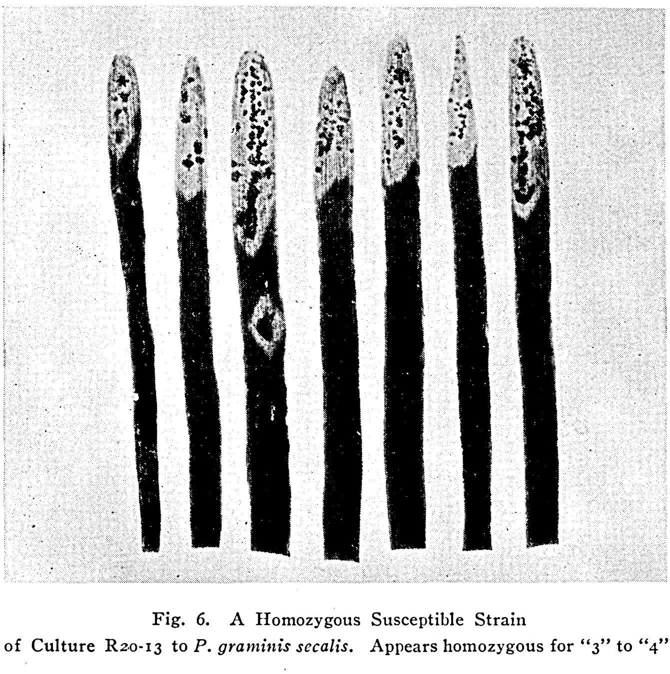

Fig. 6. A Homozygous Susceptible Strain
Reaction of Culture R20-13 to *P. graminis secalis*. Appears homozygous for "3" to "4" Infection.

A preliminary yield test of the selfed strains, when seed was available, has been conducted for three consecutive years, 1923-25. Twenty seeds of each strain were planted in 5-foot rows (see Fig. 9). Replication was not practiced because of the small amount of seed usually available. Normal Minn. No. 2 was planted in every sixth row as a check. The yield and height data are included in Table XIV, Appendix. The average yield, in grams, for the check rows was considered as 100, and the yields of the selfed strains were calculated in percentages of the check. The percentage yields have been grouped

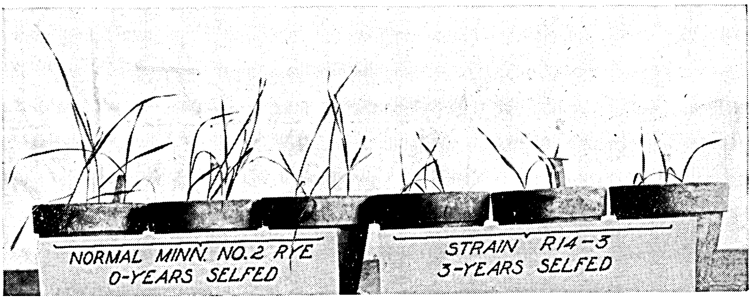

Fig. 7. Relative Vigor of Seedlings of a 3-Year Selfed Line Compared with Minn. No. 2
At left: Normal Minn. No. 2 rye; at right: A strain selfed for three years.

together for the three years and distributed into yield classes in Table XI. There is a gradual reduction in yielding ability for the 1-, 2-, and 3-year selfed strains. The less vigorous strains have been discarded in the third or fourth year of selfing, resulting in a slight average increase in yield in the 4-year over the 3-year selfed lines. The 5-year selfed lines yielded as much on the average as the check rows of Minn. No. 2. In comparison with the results obtained for corn, the reduction in vigor and yielding ability in rye appears to be much less. In this respect the results obtained for rye are similar to those obtained for timothy (13) and for sunflowers (9, 20).

TABLE XI
COMPARISON OF PERCENTAGE YIELDS OF SELFED STRAINS IN RELATION TO THE MEAN OF THE CHECKS

	Percentage yield classes																		No. of tests	Mean per cent
	5	15	25	35	45	55	65	75	85	95	105	115	125	135	145	155	165	175		
Individual checks (1923)						1	1	1	2	2	3	4	2						16	100
Individual checks (1924)							2	1	3		4	2		2					14	100
Individual checks (1925)					2		1			4	2			1	1	1			12	100
1 yr. selfed (1923, 1924, 1925)....				2	1	5	1	4	3	3	1	2		1					23	74.9
2 yr. selfed (1923, 1924, 1925)....	3	2	2	1	1	2	6	4	2	4		2	1						30	63.5
3 yr. selfed (1923, 1924, 1925)....	2	6	5	2	4	2	3	1	4		4		2	1					36	56.2
4 yr. selfed (1923, 1924, 1925)....		3	5	4	3	1	2		2		3		1	1				1	26	59.7
5 yr. selfed (1923, 1924, 1925)....				1	2						1	1			1	2			8	100.5

A correlation study of the percentage yielding ability of thirty-eight 3-, 4-, and 5-year selfed lines for two successive years gives a correlation coefficient of 0.0716 ± 0.1614. As the yield test was necessarily conducted on a very small scale and without replication to overcome the effects of soil heterogeneity, it is evident that under these conditions a correlation coefficient does not well express the inheritance of such a variable character as yielding ability. Certain outstanding cases of uniformly vigorous high-yielding strains in contrast to others which are uniformly reduced in vigor, as, for example, those shown in Figure 9 (cultures 55 and 44, respectively, in Table XIV, Appendix), lead to the conclusion that the character of vigor and yielding ability is very definitely inherited, and that homozygous selfed strains may be obtained which are equal to or even surpass the normal variety in this respect.

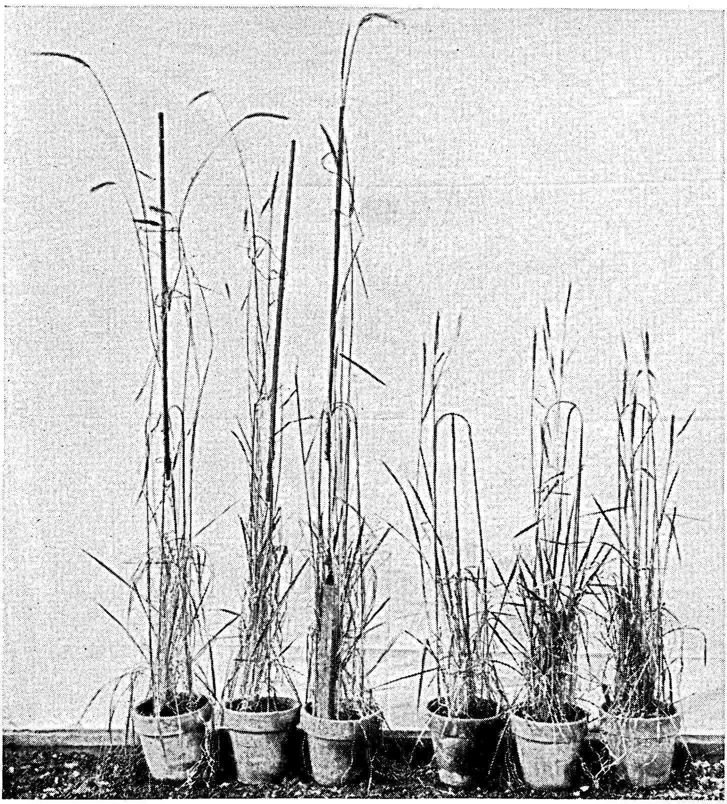

Fig. 8. Comparison of Height of Mature Plants Resulting from Seedlings Shown in Fig. 7
At left: Three pots of normal Minn. No. 2; at right: Three pots of strain R14-3, 3 years selfed. Note uniformity of R14-3.

The 1-year selfed lines appeared to be about equal in height to the normal checks (Table XII), while the 2-, 3-, and 4-year selfed lines showed a gradual reduction as a result of approaching homozygosis due to selfing. A correlation study similar to that made for yield for the same 38 strains gave a coefficient of 0.4450 ± 0.0855, indicating fairly consistent differences in height one year with another.

TABLE XII

COMPARISON OF PERCENTAGE HEIGHT OF SELFED STRAINS IN RELATION TO THE MEAN OF THE CHECKS

	Percentage height classes													No. of tests	Mean pr.cent height
	58	63	68	73	78	83	88	93	98	103	108	113	118		
Individual checks (1923)								2	8	4	2			16	100
Individual checks (1924)								3	4	6	1			14	100
Individual checks (1925)							1	1	8		1		1	12	100
1 yr. selfed (1923, 1924, 1925)							2	2	6	7	2	2	2	23	101.5
2 yr. selfed (1923, 1924, 1925)	1				1	3		5	8	5	2	3	1	29	97.4
3 yr. selfed (1923, 1924, 1925)				2	1	4	5	7	8	4	2			23	92.3
4 yr. selfed (1923, 1924, 1925)		1	1	5	1	3	1	8	6	1				27	87.3
5 yr. selfed (1923, 1924, 1925)			1			2	3		3		1			10	90.2

UTILIZATION OF SELFED STRAINS FOR THE PRODUCTION OF IMPROVED VARIETIES

There are many undesirable recessive abnormalities in commercial varieties of rye. These can be eliminated by selection in self-fertilized lines, and uniform strains can be obtained which are as vigorous as the normal variety, or more so. The problem of how best to utilize these desirable strains in the production of improved varieties remains to be solved. There appear to be two possibilities, (1) a single strain may be increased, or (2) two or more strains may be recombined.

There are certain apparent difficulties in the use of a single strain as a basis for a pure line variety. A selfed strain to be of value in this connection must be highly vigorous, produce well-developed kernels of good quality, and be desirable for such other characters as stiffness of straw, winter-hardiness, resistance to disease, and grain color. Besides, it must be highly self-fertile, for in a pure line sib-fertilization is genetically equivalent to self-fertilization; and assuming fertility and sterility to be heritable qualities, as they appear to be, the same degree of sterility would be expected to result from pollinations *inter se* as from self-pollinations. The possibility of obtaining a homozygous strain which combines all of these desirable characters by selfing individual plants and isolating biotypes within a variety appears to be rather remote. On the other hand, it is reasonable to suppose that all of these desirable characteristics could be combined synthetically by crossing inbred strains, each of which exhibited certain desirable characters which the other lacked, followed by continued self-fertilization and selection for the desirable combinations.

Fig. 9. Comparison Under Field Conditions of Selfed Strains and Minn. No. 2
At left: Minn. No. 2; in center: A vigorous 3-year selfed strain; at right: A weak 3-year selfed strain. The selfed strains are progenies of sister plants. Photo, 1923.

The second method for utilizing selfed strains in the production of improved varieties involves the recombination of two or more lines. The first crosses of two or more lines may be made artificially and random mating allowed for several years in an isolated plot. Very much the same results may be obtained by mixing seed of the strains to be recombined and planting in an isolated plot. In this kind of planting there may be some self-pollination and sib-pollination between plants of the same original inbred strains, but individuals resulting from such pollinations would decrease rapidly in succeeding generations. After several years approximately the same recombined variety will be obtained as if the crosses were made artificially. Hybrid vigor will be expected in the first-generation cross of inbred lines which contain different important growth factors, and some decrease in this vigor will be expected in the second generation. Theoretically, the extent to which this decrease in vigor takes place varies indirectly with the number of strains entering into the recombination, altho the relative vigor of the inbred lines as compared with F_1 crosses is a factor of major importance in this connection. Wright (33) concludes that "a random-bred stock derived from *n* inbred families will have 1/nth less superiority over its inbred ancestry than the first cross or a random-bred stock from which the inbred families might have been derived without selection."

The choice of strains to use in making recombinations is important. Logically, a uniformly vigorous condition is of prime importance; in this respect, however, strains may supplement each other for different growth factors. Results obtained for corn prove conclusively that strains which are much less vigorous than normal may be recombined and improvement in yielding ability over the original variety obtained (see Hayes, 10). The question of whether a high degree of self-fertility is an essential or desirable characteristic of selfed lines which are to be used in recombinations is difficult to answer. If a variety was produced from strains which were highly self-fertile, it is possible that the percentage of seed setting under field conditions would be increased as compared to normal varieties. On the other hand, if this characteristic resulted in considerable self-fertilization or inbreeding, it is possible that a high degree of self-fertility would be undesirable. To one interested particularly in resistance to disease or other specific characters, the isolation of strains homozygous for the characters in question is of major importance. Under any circumstances, it is desirable to determine how each strain chosen combines or "nicks" with other selected strains. The progeny of a few seed obtained from artificial crosses would probably be sufficient to give this information. Strains which in crosses with other strains produced uniformly vigorous, normal progeny would be used for varietal recombinations.

A somewhat less intensive mode of attack may be of value under conditions where a single character such as color of grain, disease resistance, or winter-hardiness appears of prime importance. Extensive self-fertilizations could be made for perhaps one or two generations, the strains which appeared pure for the desired character selected and an immediate recombination of these strains made.

For the purpose of securing some preliminary information, a mixture of seed from 8 lines which had been selfed for 2, 3, or 4 years, was made. The lines were selected on the basis of desirable field appearance, freedom from striking abnormalities, and plumpness of grain. They were selected as the most desirable from about fifty possible strains, it being appreciated that no information had been obtained as to how each strain would "nick" with each other strain. A few seeds from each strain were bulked and planted in an isolated plot in 1924. Seed harvested from this plot was included in the rod-row yield test in 1925, the yield being 170.5 grams in comparison to 205.5 grams for Minn.

No. 2. As previously stated, a certain amount of self-pollination and sib-pollination has undoubtedly taken place in this mixture of strains, and an accurate determination of yielding ability of the new variety can not be made until a complete random mixture is obtained. This new variety is being carried in an isolated plot each year and its yielding ability will be determined. It is of some interest to note that this variety was free from any striking abnormalities in 1925; and that it appeared to have survived the severe winter of 1925-26 as well as commercial Minn. No. 2 and better than several other varieties in the test.

It is concluded from these studies that the utilization of selfed strains as foundation material for the production of crosses or recombinations is probably the most practical means of improvement in rye.

SUMMARY

1. Continuous selection of single plants of Minnesota No. 2 rye, with distance isolation of the progeny lines, for ten years has resulted in the production of several lines which are highly pure for grain color and relatively pure for certain other characters. Certain of these strains are characterized by the presence of many seedling and plant abnormalities. While there is, in general, a reduction in vigor and yield, certain strains appear promising in comparison with Minn. No. 2.

2. Considerable evidence has been obtained which indicates that there is no consistent difference in degree of seed setting as a result of fertilization within a single floret or between two florets on the same head.

3. The characters of high and low self-fertility appear to be heritable. While the expression of these characters appears to be somewhat variable, certain strains have been isolated which are rather uniformly highly self-fertile in contrast to other strains that are able to set only a few seeds under similar conditions. There has been a conscious selection in these studies for rather highly self-fertile plants. The results of this are reflected in the percentage fertility in 1925 for all strains selfed 1, 2, 3, 4, and 5 years, the mean for these strains being 3.1, 4.7, 9.1, 14.1, and 7.7, respectively.

4. The ability to set seed under controlled conditions appears to be influenced considerably by seasonal conditions. Thus, in 1921, the average percentage seed setting for all selfed strains was 1.7, 2.2, and 14.2 as compared to 10.6, 13.5, and 41.1 in 1922 for single heads bagged, two or more heads on the same plant bagged together, and sib-pollinations, respectively.

5. The high degree of self-sterility in rye is not a serious handicap in the selfing work, as by making sufficient isolations, enough seed of

practically all lines, including the more highly self-fertile ones, can be obtained to continue the strains year after year.

6. Seedling and plant abnormalities are of common occurrence in the selfed lines. White seedlings are the most common type of seedling abnormality. Yellow-green stripe, golden-green blend, and virescent-white types may be recognized in both seedling or plant stages. Inheritance studies of these three characters as well as a brittle plant character indicate each to be a simple recessive to the normal condition. Other types of abnormalities—including seedlings having cylindrical first leaves, plants with crinkled awns, and male or pollen sterility—have been observed.

7. In a test of reaction to *Puccinia graminis secalis,* a number of individual plants in the selfed strains, as well as in the Minn. No. 2 commercial variety, appeared to be highly resistant to the disease. Certain strains were uniformly susceptible, but none of the strains appeared uniformly resistant.

8. Approaching homozygosity in the selfed strains is accompanied generally by a marked reduction in vigor, considerable shrivelling and lack of plumpness in the grain, and some reduction in height of plant, altho in each of these respects individual strains are found which are just as desirable as the parental variety, if not more so.

9. Certain strains appear outstanding in vigor and yielding ability, being equal to or better than Minn. No. 2 in this respect. Some selfed strains are shown to be uniformly vigorous year after year, while others are uniformly stunted and weak. Rye is somewhat similar to timothy and sunflowers in this respect, in contrast to the much greater reduction in vigor in corn as a result of inbreeding.

10. The results obtained in this study, in common with those obtained by Heribert-Nilsson in Sweden, justify the conclusion that the method of breeding rye by selection in self-fertilized lines is not only feasible but is the most effective and practical mode of attack as a means of rye improvement.

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APPENDIX

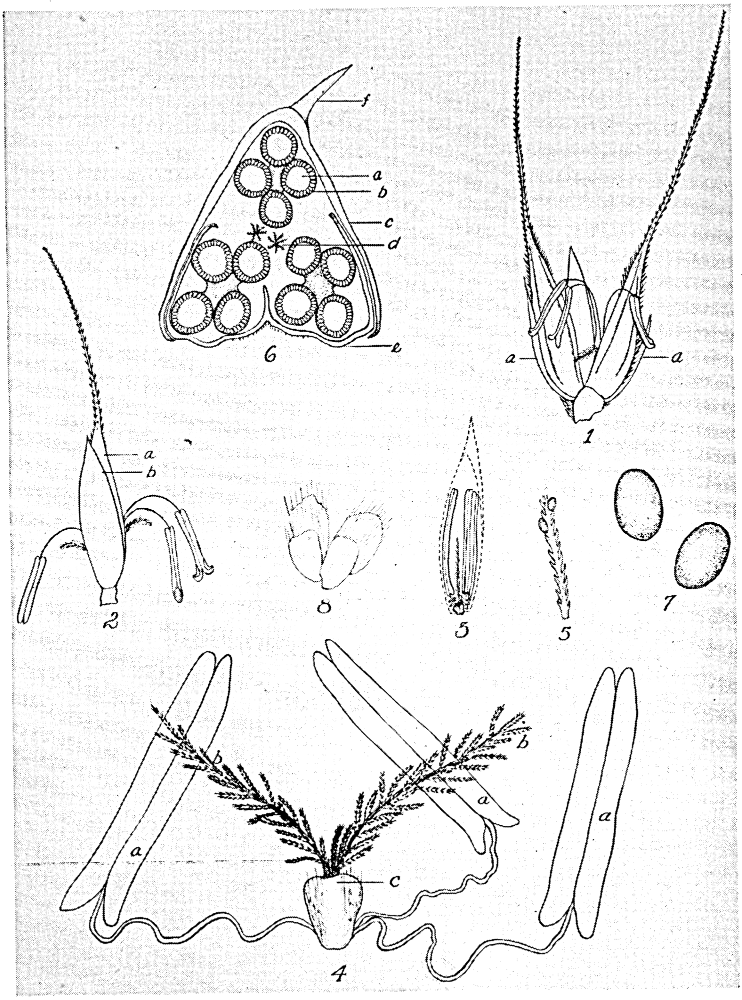

PLATE I

DETAILS OF RYE INFLORESCENCE

1. Spikelet (x 2.0) consisting of two florets, right hand floret is flowering. a= glumes.
2. Single floret (x 2.3). a= lemma; b= palea.
3. Diagram of floret just before flowering (x 2.3).
4. Reproductive organs (x 9). a= anthers; b= two-parted feathery stigma; c= ovary.
5. Stigmatic branch with two attached pollen grains (x 30).
6. Cross-section of floret when the anthers are still green (x 18). a= anther sac; b= immature pollen grains; c= lemma; d= feathery stigma; e= palea; f= barb.
7. Mature pollen grains (x 450).
8. Two lodicules which attach to the base of the ovary and lie between it and the lemma (x 9).

TABLE XIII

Average Percentage Seed-Setting Obtained in Selfed Strains of Rye, 1921 to 1925

1921			1922				1923				1924				1925				
Cult. No.	No. of plants	Percentage seed-setting of strain	Cult. No.	No. of plants	Percentage seed-setting		Cult. No.	No. of plants	Percentage seed-setting		Cult. No.	No. of plants	Percentage seed-setting		Cult. No.	No. of plants	Percentage seed-setting		Years selfed
					Parent plant	Strain			Parent plant	Strain			Parent plant	Strain			Parent plant	Strain	
											Minn. No. 92				R 2	7		1.5	1
											do				3	7		1.4	do
											do				4	1		0.4	do
											do				5	3		1.4	do
											do				6	2		0.8	do
											do				7	2		2.4	do
											do				9	2		3.7	do
											do				10	1		0	do
											do				11	1		0.3	do
											do				12	2		1.2	do
											do				13	4		5.5	do
											do				14	4		8.4	do
											do				15	1		1.1	do
											do				16	5		5.8	do
											do				17	5		1.0	do
											do				18	4		5.4	do
											do				19	4		1.9	do
											do				20	3		6.4	do
											do				21	3		7.7	do
											do				22	4		4.1	do
											do				23	3		0.8	do
											do				24	2		2.6	do
											do				25	4		1.6	do
											do				26	3		0.1	do
											do				27	4		4.0	do
											do				28	4		3.2	do
											do				29	4		2.6	do
											do				30	3		1.5	do
											do				31	3		4.4	do

TABLE XIII—*Continued*

AVERAGE PERCENTAGE SEED-SETTING OBTAINED IN SELFED STRAINS OF RYE, 1921 TO 1925

1921			1922				1923				1924				1925				Years selfed
Cult. No.	No. of plants	Percentage seed-setting of strain	Cult. No.	No. of plants	Percentage seed-setting: Parent plant	Percentage seed-setting: Strain	Cult. No.	No. of plants	Percentage seed-setting: Parent plant	Percentage seed-setting: Strain	Cult. No.	No. of plants	Percentage seed-setting: Parent plant	Percentage seed-setting: Strain	Cult. No.	No. of plants	Percentage seed-setting: Parent plant	Percentage seed-setting: Strain	
							Minn. No. 2				R 1	11		14.0	R32	1	11.3	4.8	1
							do				38	20		15.3	33	3	73.3	2.2	do
							do				38				34	3	5.6	2.3	do
							do				87	13		11.0	35	5	6.9	2.2	do
			Minn. No. 2				R20	12		6.1	2	16	45.3	3.1	36	4	17.9	0.6	2
			do				39	16		7.6	3	17	53.1	12.6	37	4	37.5	3.2	do
			do				58	11		15.6	4	23	61.3	12.7	38	5	13.2	2.3	do
											4				39	4	16.1	0.2	do
			do				58				5	22	60.7*	4.5	40	5	14.8	5.4	+1
											6	4	61.7	32.1	41	2	34.0	23.6	2
			do				58				7	3	1.3	5.7	42	4	5.4	1.1	do
			do				64	6		0.7	8	4	1.8	2.0	43	1	1.7	1.4	do
R 5	41	2.6	R 5	6	38.6*	2.3	8	6	9.4	0.2	9	2	0.8	9.2	44	2	18.3	0	3
5			6	11	56.8*	6.4	9	10	17.6	0.8	10	7	4.6*	2.3	45	3	5.2	7.8	1+1, 3
			6				10	6	13.6	1.1	11	4	2.6	5.7	46	3	6.9	8.2	3
6	9	21.2	11	19	42.5*	13.2	21	9	48.3	2.5	12	8	23.5*	2.3	47	4	1.7	2.0	1+1
			11				22	7	26.2	1.3	13	3	2.3	0.3	48	3	0.8	1.9	3
							23	15	19.5	1.5	14	8	57.3*	12.6	49	3	5.5	0.3	1+1
											14				50	3	81.3	1.2	do
			11				25	16	31.5	2.6	15	15	18.3	7.6	51	4	22.7	2.0	3
8	19	0.2	13	9	42.6*	4.3	27	7	17.5	1.2	16	12	40.9*	2.6	52	4	6.3	4.5	1+1
9	19	0.6	15	7	17.2*	3.0	30	7	3.5	10.2	17	17	50.0	24.6	53	3	52.9	5.2	3
											17				54	1	9.1	7.3	do
6	9	21.2	11	19	42.5*	13.2	24	7	62.5	2.2	18	10	13.8	5.0	55	6	19.8	1.2	do
											18				56	3	5.5	24.2	do
14	23	2.1	21	15	78.4*	20.9	36	12	33.1	2.2	19	3	0.8	2.2	57	2	2.4	4.6	do
											19				58	3	1.8	1.1	do
			21				37	9	44.0	1.0	21	12	51.7*	9.2	59	4	9.2	20.3	1+1

* = Sib crosses, i.e., heads of two sibs bagged together. † = Open pollinated.

+ in years selfed column = Sib cross, thus 2+2 = 2 years selfed followed by a sib cross one year and two successive years selfed.

TABLE XIII—*Continued*

AVERAGE PERCENTAGE SEED-SETTING OBTAINED IN SELFED STRAINS OF RYE, 1921 TO 1925

1921			1922				1923				1924				1925				
Cult. No.	No. of plants	Percentage seed-setting of strain	Cult. No.	No. of plants	Percentage seed-setting		Cult. No.	No. of plants	Percentage seed-setting		Cult. No.	No. of plants	Percentage seed-setting		Cult. No.	No. of plants	Percentage seed-setting		Years selfed
					Parent plant	Strain			Parent plant	Strain			Parent plant	Strain			Parent plant	Strain	
R15	52	1.7	R25	21	73.5†	7.9	R41	6	41.0	4.7	R23	4	2.1	29.7	R60	1	1.5	0.3	3
											23				61	4	76.1	51.5	do
15			26	11	37.1*	8.3	42	9	21.6	0.8	24	5	1.9	3.0	62	3	10.0	0.9	do
19	11	0.7	33	13	71.7†	6.2	46	12	21.1	1.2	28	8	4.5	12.6	63	5	81.7	19.2	do
5	41	2.6	1	2	2.4	51.4	2	14	67.6	1.5	29	12	13.8	15.1	65	5	14.1	6.2	4
					.		2				30	4	1.3	12.2	66	1	10.1	0	do
5			2	8	9.6	3.5	4	11	12.5	5.0	31	11	7.5	19.5	67	5	76.8	31.4	do
											31				68	4	3.0	3.8	do
5			1	2	2.4	51.4	3	5	35.1	11.1	32	5	51.1	35.3	69	2	50.9	30.6	do
5			2	8	9.6	3.5	4	11	12.5	5.0	33	15	29.5	7.5	70	1	5.0	2.8	do
5			3	7	19.7	2.9	5	12	9.4	1.1	34	8	3.2	3.1	71	2	4.1	2.9	4, 2+1
											M.No.2				72	4		13.1	1
5			3	7	19.7	2.9	6	8	10.9	2.9	35	11	19.5	4.0	73	4	2.7	3.8	4
5			4	11	44.1	3.7	7	6	4.5	0.1	36	10	29.0*	8.9	74	2	2.6	40.0	2+1
14	23	2.1	20	7	3.3	18.3	33	8	9.6	4.8	37	11	14.8	8.8	75	5	10.5	25.9	4
			20				34	10	61.1	0.8	39	5	4.7	15.5	76	4	73.2	18.5	do
			20				35	11	21.3	3.9	40	4	4.1	3.5	77	4	10.2	0.6	do
15	52	1.7	23	4	12.8	6.0	38	10	18.1	2.7	43	13	16.4	9.2	78	4	43.4	1.3	do
											43				79	5	6.2	34.1	do
15			24	8	4.1	1.4	40	4	2.2	1.1	44	5	1.4	2.3	80	3	1.3	25.7	do
23	47	1.7	38	10	35.9	11.7	51	10	34.1	0.2	46	8	10.9*	4.7	81	2	13.9	2.2	2+1
			38				52	10	26.0	0.9	47	2	20.5*	3.3	82	4	5.6	1.2	do
24	61	2.8	40	9	3.2	7.4	53	8	21.6	3.2	48	5	4.9	8.8	83	7	15.3	11.4	4
			40				54	9	14.7	3.3	49	3	4.8	49.3	84	1	38.5	16.5	do
24			41	8	15.3	16.6	56	9	41.0	5.6	52	15	39.9*	9.5	85	5	18.7	1.3	2+1
											52				86	4	3.6	4.3	do

* = Sib crosses, i.e., heads of two sibs bagged together. † = Open pollinated.
\+ in years selfed column = Sib cross, thus 2+2 = 2 years selfed followed by a sib cross one year and two successive years selfed.

TABLE XIII—*Concluded*

AVERAGE PERCENTAGE SEED-SETTING OBTAINED IN SELFED STRAINS OF RYE, 1921 TO 1925

1921			1922				1923				1924				1925				
Cult. No.	No. of plants	Percentage seed-setting of strain	Cult. No.	No. of plants	Percentage seed-setting: Parent plant	Percentage seed-setting: Strain	Cult. No.	No. of plants	Percentage seed-setting: Parent plant	Percentage seed-setting: Strain	Cult. No.	No. of plants	Percentage seed-setting: Parent plant	Percentage seed-setting: Strain	Cult. No.	No. of plants	Percentage seed-setting: Parent plant	Percentage seed-setting: Strain	Years selfed
R24			R42	8	27.8	17.7	R59	7	30.4	8.6	R53	14	20.2	16.5	R87	4	81.8	28.4	4
											53				88	1	7.3	14.3	do
			42				60	6	54.8	8.7	54	11	26.5	20.4	89	2	47.5	8.5	do
							60				55	14	7.2	11.2	90	4	27.4	3.2	do
6	9	21.2	7	5	4.0	3.1	11	16	9.5	1.2	56	9	4.7	6.4	91	4	8.3	0.3	5
6			8	10	15.0	4.1	13	8	6.6	4.9	58	10	14.3	7.2	92	4	19.2	6.3	do
			8				14	12	64.7*	2.5	60	6	12.2	10.2	93	5	34.0	9.2	2+2
6			9	14	51.7	3.0	16	10	3.6	0.3	61	8	27.7*	5.8	94	4	27.7	6.3	3+1
6			10	12	60.9	13.5	18	8	2.7	2.3	62	4	4.3	27.3	95	4	80.3	14.5	5
											62				96	3	1.7	6.5	do
			10				19	11	54.3	0.9	63	4	1.3	16.8	97	6	66.4	9.9	do
9	19	0.6	14	4	2.4	19.9	28	11	9.3	3.2	64	7	6.2	19.7	98	2	1.9	3.0	do
8	19	0.2	12	1	1.9	80.3	26	7	80.3	16.8	65	1	69.6	55.0	99	6	55.0	10.0	do
10	6	0.6	16	1	1.5	35.4	31	6	35.4	3.9	67	5	1.9	11.1	100	3	35.4	22.7	do
11	16	0.6	18	2	2.8	6.3	32	14	12.5	3.1	69	7	6.6	6.0	101	5	14.0	0.9	do
18	7	0.5	29	1	1.3	12.5	43	4	12.5	14.6	70	8	56.4	53.2	102	6	91.1	3.2	do
21	10	2.3	34	6	4.7	22.8	48	14	25.5	6.2	72	10	6.6	17.7	103	9	31.4	11.2	do
			34				49	4	51.1	0.8	74	18	45.5*	39.3	104	6	71.7	26.9	3+1
											74				105	1	1.8	0	do
18	7	0.5	30	1	7.8	1.2	65	1	1.2	1.3	75	3	1.3	13.4	106	3	17.5	3.5	5
							102-1				83	7	5.7	24.8	107	5	3.8	5.1	2
							15 yld. test				84	6		6.0	108	4	17.6	10.0	1
							42 yld. test				85	7		11.4	109	6	9.1	4.9	do
											1501				110	1		4.2	do

* = Sib crosses, i.e., heads of two sibs bagged together. † = Open pollinated.
+ in years selfed column = Sib cross, thus 2+2 = 2 years selfed followed by a sib cross one year and two successive years selfed.

TABLE XIV

Yield and Height of Selfed Strains in Comparison with Commercial Minnesota No. 2 Rye Used as a Check

1925 Cult. No.	No. years selfed	Yield						Height					
		1923		1924		1925		1923		1924		1925	
		Grams	Per cent	Grams	Per cent	Grams	Per cent	Inches	Per cent	Inches	Per cent	Inches	Per cent
C-3	1					132.2	96					48	108
5	do					183.8	134					52	117
7	do					121.4	88					50	112
6	do					135.2	98					52	117
4	2			141.0	60	109.7	80			60	102	48	108
9	do			239.3	102	123.2	90			66	112	50	112
10	do			239.3	102	158.1	115			66	112	50	112
11	+1			194.2s	83	97.8	71			58s	98	42	94
12	2			85.3	36	11.9	9			54	92	36	81
13	do					101.5	74					44	99
15	3	60	48			9.4	7	50	104			40	90
11 (1924)	1+	123	99	101.1s	43			49	102	60s	102		
16	3	123	99	187.8s	80	176.0	128	49	102	56s	95	45	101
13 (1924)	1+	91	73	143.3s	61			42	88	58s	98		
15 (1924)	do	109	88	140.8s	60			46	96	58s	98		
17	1+1	109	88	140.8s	60	25.8	19	46	96	58s	98	42	94
18	3	75	60	154.9	66	172.8	126	46	96	58	98	44	99
19	1+1	64	52	87.8s	37	108.5	79	46	96	52s	88	42	94
21	3	67	54	26.2	11	5.6	4	47	98	54	92	36	81
22	3	82	66	291.8	124	122.6	89	49	102	62	105	36	81
22 (1924)	1+	98	79	323.2s	138			52	109	58s	98		
23	1+1	72	58	121.0s	52	179.3	130	49	102	58s	98	40	90
24 (1924)	1+	94	76	210.3s	90			46	96	50s	85		
24	3	94	76	210.3s	90	37.5	27	46	96	50s	85	32	72
25 (1924)	2	38	31	10.7	5			42	88	46	78		
25	3	149	120	173.4s	74	31.4	23	48	100	56s	95	38	85
27	4	119	96	245.3	104	176.9	129	53	111	56	95	44	99
28	do	119	96	245.3	104	92.8	68	53	111	56	95	40	90

s = sib-pollination.

TABLE XIV—*Continued*

YIELD AND HEIGHT OF SELFED STRAINS IN COMPARISON WITH COMMERCIAL MINNESOTA NO. 2 RYE USED AS A CHECK

1925 Cult. No.	No. years selfed	Yield						Height					
		1923		1924		1925		1923		1924		1925	
		Grams	Per cent	Grams	Per cent	Grams	Per cent	Inches	Per cent	Inches	Per cent	Inches	Per cent
C-29	4	28	23	256.2	109	30.2	22	45	94	58	98	38	85
30	do	145	117	60.5	26	27.2	20	40	84	44	75	32	72
30 (1924)	3	28	23	256.2	109			45	94	58	98		
31 (1924)	do	124	100	157.4	67			50	104	54	92		
31	2+1	81	65	145.7s	62	141.3	103	45	94	52s	88	42	94
33	4	75s	60	243.7	104	44.6	32	46s	96	52	88	38	85
34	do	117	94	132.3s	56	244.0	178	52	109	56s	95	44	99
36 (1924)	3	20	16	198.9	85			48	100	58	98		
35	4	95	77			140.3	102	44	92			44	99
36	2+1	42	34	201.8s	86		123	46	96	56s	95	36	81
37	4	80	65	103.1	44	52.5	38	49	102	54	92	42	94
39	do	53	43	200.7	85			46	96	58	98	32	72
41 (1924)	3	76	61	108.7	46			48	100	54	92		
40	2+1	86	69	154.7s	66	30.1	22	57	119	54s	92	40	90
41	4	69	56	81.3	35	45.2	33	46	96	54	92	32	72
42	do	69	56	81.3	35	30.1	22	46	96	54	92	30	67
43	do	72	58	99.6	42	189.4	138	47	98	46	78	32	72
45	do	72	58	125.7	54	116.7	85	47	98	48	81	34	76
46	5	170	137	198.0s	84	211.5	154	52	109	56s	95	44	99
49	do	87	70	55.3	24	63.2	46	47	98	54	92	44	99
51	2+2	160s	129	229.0	98	116.4	85	49s	102	56	95	42	94
52	3+1	22	18	148.2s	63	112.8	82	46	96	56s	95	42	94
53	5	94	76	156.0	66			46	96	56	95	39	88
54	do	20	16	236.4s	101	202.5	147	41	86	56s	95	40	90
55	do	110	89	249.2s	106	152.6	111	49	102	60s	102	44	99
57	do	53	43	75.8	32			41	86	48	81	36	81
58	do	34	27	105.0	45	55.3	40	49	102	58	98	30	67
59	do			128.2	55	149.1	109			58	98	40	90
60	do	14	11	63.8	27	58.1	42			56	95	36	81
61	do	127	102	107.2	46	212.8	155	51	106	54	92	48	108
63	3+1	44	35	184.3s	78	143.5	104	46	96	58s	98	40	90
66	1			181.2	77	155.0	113			60	102	44	99

s = sib-pollination. + in years selfed column = Sib cross, thus 2+2 = 2 years selfed followed by a sib cross one year and two successive years selfed.

TABLE XIV—*Concluded*

YIELD AND HEIGHT OF SELFED STRAINS IN COMPARISON WITH COMMERCIAL MINNESOTA NO. 2 RYE USED AS A CHECK

1925 Cult. No.	No. years selfed	Yield 1923 Grams	Yield 1923 Per cent	Yield 1924 Grams	Yield 1924 Per cent	Yield 1925 Grams	Yield 1925 Per cent	Height 1923 Inches	Height 1923 Per cent	Height 1924 Inches	Height 1924 Per cent	Height 1925 Inches	Height 1925 Per cent
C4 (1924)	1			200.7	85					60	102		
63 do	4			97.1	41					58	98		
70 do	do			59.0	25					44	75		
71 do	do			40.5	17					38	64		
72 do	do			36.7	16					56	95		
6 (1923)	2	114	92					50	104				
16 do	3	87	70					43	90				
44 do	do	14	11										
47 do	do	34	27					49	102				
48 do	2	34	27					46	96				
63 do	3	14	11										
65 do	3	22	18					45	94				
76 do	2	83	67					50	104				
88 do	do	8	6										
Minn. No. 2		73	59	209.1	89	131.4	96	46	96	60	102	52	117
do		140	113	306.7	131	86.7	63	43	90	64	108	48	108
do		147	119	239.3	102	133.2	97	48	100	60	102	44	99
do		113	91	306.8	131	197.7	144	48	100	58	98	44	99
do		134	108	266.6	114	135.3	98	46	96	56	95	44	99
do		138	111	253.7	108	68.2	50	44	92	58	98	44	99
do		132	106	249.8	106	61.6	45	49	102	56	95	44	99
do		103	83	252.2	107	146.1	106	49	102	56	95	40	90
do		77	62	282.1	120	217.3	158	50	104	58	98	44	99
do		98	79	208.8	89	143.3	104	48	100	58	98	44	99
do		118	95	162.3	69	190.3	139	51	106	62	105	44	99
do		112	90	182.2	78	137.5	100	48	100	60	102	42	94
do		160	129	209.8	89			52	109	60	102		
do		159	128	158.3	67			50	104	60	102		
do		130	105					48	100				
do		149	120					46	96				
Mean of checks		124	100	234.8	100	137.4	100	47.9	100	59	100	44.5	100

s = sib-pollination. + in years selfed column = Sib cross, thus 2+2 = 2 years selfed followed by a sib cross one year and two successive years selfed.