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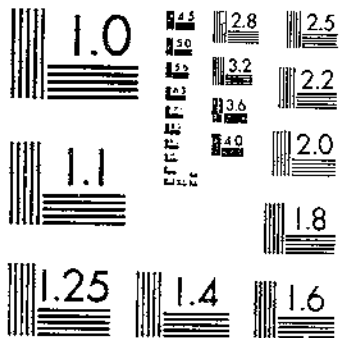
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INHERITANCE OF WINTER HARDINESS, GROWTH HABIT, AND STEM-RUST REACTION

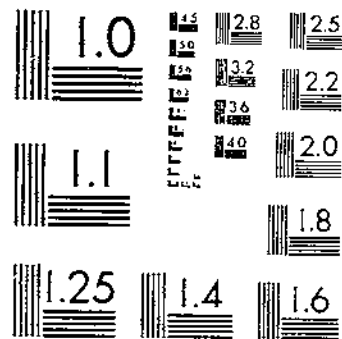
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UNITED STATES DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

INHERITANCE OF WINTER HARDINESS, GROWTH
HABIT, AND STEM-RUST REACTION IN CROSSES
BETWEEN MINHARDI WINTER AND
H-44 SPRING WHEATS¹

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RESEARCH AND BREEDING PROBLEMS

In order to plan intelligently a method of attack upon the problem of breeding an improved variety of wheat, plant breeders should have a knowledge of the manner of inheritance of the characters in question. Many characters that have to do with the reaction of the plant to its environment may be complicated in inheritance. Because of this, much research is needed to arrive at a thorough understanding of these factors.

The purpose of the present study was to obtain more fundamental information on the inheritance of winter hardiness, winter-spring growth habit, and rust reaction, and the interrelations of these characters in a winter × spring wheat cross. These characters are influenced by environment, and a study of their inheritance is difficult.

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² The writer wishes to express his appreciation to H. K. Hayes, chief of the division of agronomy and plant genetics, University of Minnesota, for his suggestions in outlining and conducting these experiments and in providing certain facilities for carrying them out; to E. C. Stakman, professor of plant pathology, for suggestions as to methods of conducting the studies of rust reaction; to J. Allen Clark, senior agronomist, Office of Cereal Crops and Diseases, Bureau of Plant Industry, for making available for this study the necessary facilities of the western wheat project; and to C. G. Colcord, scientific aide, Office of Cereal Crops and Diseases, for checking all calculations.

HISTORICAL REVIEW

Some work has been done already on the inheritance of the more important characters involved in this study, i. e., winter hardiness, winter habit, and stem-rust reaction.

WINTER HARDINESS

Winter wheats vary greatly in their ability to resist cold and to survive the winter. Many reports have been published on the relative resistance of varieties of wheat to killing by cold, but few data are available on the inheritance of this character. Nilsson-Ehle (30)³ crossed two varieties of intermediate hardiness and obtained some lines that were more hardy and other lines that were less hardy than the parents. He concluded that winter resistance behaved as other quantitative characters, being controlled by several genetic factors. Åkerman (4) also crossed two varieties intermediate for resistance to cold with much the same results.

From a Turkey × Odessa cross, Hayes and Garber (19) reported the development of new wheats more cold resistant than the Odessa parent. One of the wheats, Minhardi, was determined by Clark, Martin, and Parker (8) to be the most hardy winter wheat tested in the United States and Canada.

Guines as reported by Schafer (35) found that hardiness was recessive to lack of hardiness in a cross, Turkey × Jenkin.

Martin (24) studied F_3 lines of Kanred × Minhardi for hardiness, but was unable to determine the number of genetic factors involved, although most of the strains were intermediate between the parents in resistance to cold.

Hayes and Aarnodt (18) reported a study on the inheritance of cold resistance and growth habit in a cross of Marquis (spring) and Minhardi and Minturki (winter) wheats. This work was continued from the F_1 through the F_4 generation. They agreed with Nilsson-Ehle that cold resistance is inherited in the same manner as other quantitative characters, although they, likewise, were unable to determine the number of factors involved. The relation between cold resistance and winter-spring growth habit also was studied, but due to the large number of plants eliminated in F_2 from fall-sown material a definite inheritance could not be established. They did find a close correlation in F_3 between spring-growth habit and low winter resistance. Some lines were obtained, however, which were cold resistant and which headed when spring sown. In all cases these cold-resistant spring wheats were later in maturity than Marquis, the spring parent.

Summarizing 10 years' work on breeding for winter hardiness, Quisenberry and Clark (33) concluded that the winter-hardiness character, while heritable, is very complex and is greatly influenced by environment. From a large number of crosses between winter wheats of varying degrees of hardiness, segregates were obtained which were as hardy as, and in some cases hardier than, the hardy parents. Most of the lines obtained were intermediate between the two parents.

As pointed out by various workers (24, 33), relative cold resistance often is rather difficult to determine in the field. The winter may be

³ Italic numbers in parentheses refer to Literature Cited, p. 43.

mild and little or no killing will occur, or a severe winter may wipe out an entire experiment. Salmon (34) points out that winterkilling may be due to any or all of the following four causes: (1) Heaving, (2) smothering, (3) physiological drought, and (4) direct effect of low temperature on plant tissues. The present study, dealing with the inheritance of winter hardiness, is not concerned with the nature of winter hardiness, and only such studies as bear directly on the determination of relative hardiness will be considered.

Newton (27, 28, 29) attempted to find some chemical or physical measure that would give an indication of resistance to cold. He used six varieties of wheat of known relative winter hardiness—Minhardi and Buffum, both very hardy; Kanred and Turkey, intermediate; and Super and Fulcaster, tender. He concluded that the hardier the variety the lower the moisture content of the leaves, and that in hardened-off leaves this moisture is held under a greater force. He found that the volume of press juice per 100 grams of hardened tissue was inversely proportional to hardiness. The quantity of hydrophylic colloids in the press juice was directly proportional to hardiness.

Martin (24) conducted experiments similar to those of Newton and concluded that none of these chemical or physical measures offered a more accurate test of resistance to cold than did a careful field study. Martin carried his tests further and made artificial freezing studies on a few F_2 lines of Kanred \times Minhardi, and, although these studies were not entirely satisfactory, he concluded that this method offered the greatest promise of any laboratory method for the study of resistance to cold. Martin pointed out that considerable care must be exercised in properly hardening off the material before subjecting it to low temperatures.

Hill and Salmon (22) subjected to artificial freezing a series of winter-wheat varieties varying in degree of hardiness. In their experiments Kanred and Kharkof were more hardy than Minhardi, which does not agree with field tests. This result was undoubtedly due to the methods of hardening off which were used, since Minhardi seems to be unable to withstand sudden changes in temperature until after it has been well hardened off. In general, however, their results agreed fairly well with field studies.

Working chiefly with winter wheats, Tumanov and Borodin (38) studied laboratory methods of determining hardiness of plants by direct freezing and indirectly by determining the percentage of dry matter in the expressed sap and the freezing point of the sap. In general, the correlation between laboratory and field tests was good. These workers state that the resistance to frost of the seedlings depended in a high degree on the temperature at which germination had taken place.

Nilsson-Leissner (31), reviewing a book by Åkerman, points out that Åkerman suggests the use of artificial refrigeration in the study of resistance to cold and that by using this method he was able to show transgressive segregation in some hybrid material.

GROWTH HABIT

Wheats usually are classified (7) as having either winter-growth or spring-growth habit. True winter wheats do not produce heads if sown in the spring. They may or may not have the ability to survive

severe winter weather. Spring wheats, on the other hand, head normally when spring sown and as a rule do not survive severe winter weather when fall sown. Some workers (10, 13) recognize a third or intermediate group, consisting of forms that survive the winter when fall sown and head normally when spring sown. Selections of this latter type that bred true were obtained by Hayes and Aamodt (13) from crosses of Marquis by Minturki and Minhardi.

No sharp line of demarcation can be drawn between winter and spring wheats, since there is every gradation between extremes of the two types, and since environment may modify the expression of this seasonal growth character. A slight variation in the date of spring sowing has a marked effect on the amount of heading that occurs, for instance, in winter varieties. As a rule the earlier the date of sowing the greater the amount of heading. Earliness is relative, however for each variety, and all varieties do not react in the same manner.⁴

Several investigators have crossed winter and spring wheats and have studied the behavior of the segregating hybrids. Because segregation is so greatly influenced by environment, results have seemed contradictory and are not at all conclusive. In some cases (12, 36) there was a dominance of winter-growth habit over spring-growth habit; in others (6) the F_1 was intermediate in time of ripening, and in F_2 the bulk of the plants were earlier than the late parent.

Vavilov and Kouznetsov (39) report that in crosses between spring and winter wheats spring-growth habit was dominant over winter-growth habit. In the F_2 generation they obtained 9.6 springs to 1 winter. F_3 lines were obtained which were homozygous for different dates of heading. They conclude that growth habit is controlled by several factors. Aamodt (1) and Gaines and Singleton (14) report results similar to those of Vavilov and Kouznetsov.

Cooper studied several winter \times spring wheat crosses (10). When Marquis was used as the spring parent he obtained a ratio of 13 spring forms to 3 winter forms. Using Haynes Bluestem (Minnesota No. 169) as the spring parent, the ratio was 3 springs to 1 winter. To explain these results Cooper assumed that the winter varieties used in his crosses had the genetic constitution SSii. Marquis was assumed to be ssII, the II factor inhibiting winter habit. Haynes Bluestem (Minnesota No. 169) was assumed to be SSII.

In crosses of Marquis and Kota with Kanred, Aamodt (3) obtained in the F_2 generation a ratio of 15 springs to 1 winter. In the F_3 generation grown from a random F_2 , segregation approximated 7 pure springs, 8 heterozygous, and 1 pure winter. The results were explained by assuming that Marquis and Kota each possess two pairs of dominant factors for spring habit, the winter Kanred possessing their recessive allelomorphs.

RUST REACTION

Several publications giving complete summaries of previous work on breeding rust-resistant wheat are available. The interested reader is referred to papers by Hayes and Stakman (20); Hayes, Stakman, and Aamodt (21); and Aamodt (3). Work similar to the present investigations only will be considered.

⁴ BAYLES, B. B., and MARTIN, J. F. GROWTH HABIT AND YIELD IN WHEAT AS INFLUENCED BY TIME OF SEEDING. [In manuscript.]

In a Marquis \times Kanred cross Melchers and Parker (26) found a single-factor difference for rust reaction, immunity being dominant when the plants were inoculated at heading time in the greenhouse. Aamodt (1) and Hayes and Stakman (20) also worked with Kanred \times Marquis crosses. They found that in the seedling stage one genetic factor or a group of factors may control the reaction to several physiologic forms of rust. Lines resistant to stem rust in the greenhouse may be susceptible in the field, owing entirely to the presence of different physiologic forms under field conditions or to differences in reaction at various stages of growth. In studying a Marquis \times Kota cross, Hayes and Aamodt (17, p. 1011) concluded that—

the study of F_2 seedlings in the greenhouse in their reaction to Forms XIX and XXVII was not satisfactory as a means of isolating F_2 lines which would exhibit the Kota type of resistance under field conditions.

Crossing Marquillo, which is resistant in the mature stage in the field but susceptible in the seedling stage in the greenhouse, with Marquis \times Kanred lines, which are immune in the seedling stage to 11 forms of rust, Hayes, Stakman, and Aamodt (21) found that the Marquis \times Kanred seedling reaction in the greenhouse is controlled by a single pair of factors. The field reaction of Marquillo was best explained as being controlled by two major genetic factors, although minor modifying factors were involved. The factors for field resistance of the Marquillo parent appeared to be inherited independently of the factors for greenhouse immunity of the Kanred parent. Homozygous types were obtained which combined the two types of reaction.

Aamodt (2) assumed that lines showing immunity or resistance in the greenhouse would probably be resistant in the field.

In a cross of H-44 \times Marquis, Goulden, Neatby, and Welsh (15) found no relation between the greenhouse seedling reaction to forms 21 and 36 and the field reaction of the mature plant. It was assumed that different genetic factors controlled resistance in the greenhouse and in the field. It was concluded that two genetic factors were necessary to explain the reaction in the greenhouse to form 36. The studies conducted in the field indicated that resistance was controlled by a single pair of factors.

In crosses of Hope with Marquis and Reliance, Clark and Ausemus⁵ have shown that in the mature stage there are immune, resistant, and susceptible strains breeding true and that there are four segregating types. After a study of the F_2 and F_3 generations of these crosses, the results were explained on the basis of a 2-factor difference. Phenotypic ratios for the immune, resistant, and susceptible groups were approximately 4:11:1. In a Hope \times Ceres cross, however, they found only a single-factor difference or a 3:1 ratio for the immune and resistant groups.

It is known that there may be several types of resistance, i. e., physiological (37), morphological (23), or functional (16). During the seedling stage in the greenhouse the reaction may be due to physiological or true protoplasmic resistance. In the mature stage in the field the reaction may be due to physiological resistance, to

⁵ CLARK, J. A., and AUSEMUS, E. R. INHERITANCE OF IMMUNITY FROM BLACK STEM RUST, YIELD, AND PROTEIN CONTENT IN HOPE WHEAT CROSSES WITH SUSCEPTIBLE AND RESISTANT VARIETIES. Washington, 1928. [mimeographed, p. 8.]

morphological resistance, such as the size of the collenchyma bundles, or to functional resistance, such as the time when the stomata open in the morning. Thus the reaction of seedlings in the greenhouse and of mature plants in the field may be due to different phenomena, each controlled by independent genetic factors.

MATERIAL AND METHODS

The problem in the present study was to combine winter hardiness and rust resistance in a single variety. No available winter variety possesses the degree of rust resistance desired. It therefore was necessary to use a highly rust-resistant spring variety and a very hardy winter variety.

PARENT MATERIAL

The two varieties used for parents in this study are both common wheats, *Triticum vulgare* Vill.

MINHARDI

The winter parent, Minhardi, is a selection from an Odessa × Turkey cross made at the Minnesota Agricultural Experiment Station, University Farm, St. Paul, Minn., in 1902. Minhardi has an awnless spike and a soft red kernel. It is susceptible to black stem rust. As previously mentioned, this is one of the most hardy varieties so far tested in the United States and Canada. The Minhardi parental material was from a single head obtained from the wheat classification herbarium in the Office of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture.

H-44

The spring parent, H-44, is an unnamed selection from a Marquis × Yaroslav-emmer cross made in 1916 by McFadden (25). The selection H-44, made in 1923, has been grown at University Farm, St. Paul, Minn., since 1925. The H-44 is bearded, has a hard red kernel, and is highly resistant to stem rust, leaf rust, loose smut, and bunt. It is susceptible to black chaff and root rot. The H-44 strain and Hope, a named selection from the same cross, seem to possess much of the disease resistance of emmer. The H-44 parental material used in crossing was from a plant selection made in the fall of 1925, obtained from H. K. Hayes, University Farm, St. Paul, Minn.

CONTRASTED CHARACTERS

The contrasting characters of the parents are as follows:

Characters	Minhardi	H-44
Winter hardiness.....	Hardy.....	Tender.
Growth habit.....	Winter.....	Spring.
Stem-rust reaction.....	Susceptible.....	Highly resistant.
Heading period.....	Late.....	Early.
Awnedness.....	Awnleted.....	Awned.
Coleoptile color.....	Green.....	Purple.

METHODS

Crosses were first made by the writer in a greenhouse at the Arlington Experiment Farm, Rosslyn, Va., during the winter of 1925-26. Reciprocal crosses were made by G. F. Sprague at North Platte, Nebr., in 1926, and by V. H. Florell at Davis, Calif., in 1927. Seven F_1 plants of the Minhardi \times H-44 cross were grown from spring seeding at Bozeman, Mont., in 1926. These plants matured so late that the seeds were badly frosted before harvest with consequent reduction in germination to about 40 per cent. A number of F_1 plants of the cross were grown in a greenhouse at the Arlington Farm during the winter of 1926-27. Additional F_1 plants were grown from spring seeding at Moccasin, Mont., in 1927.

The F_2 generation was grown from fall seeding at Davis, Calif., during 1927-28. The kernels were spaced 6 inches apart in rows 1 foot apart, and the crop was irrigated as necessary, in order to obtain as much seed as possible from each plant. At this station both winter and spring wheats survive from fall seeding, and all types head at nearly the same time in the spring. A random selection of the F_2 population was made as a basis for continuing the study in the F_3 generation.

In the fall of 1928 the F_3 generation was sown at University Farm, St. Paul, Minn. From the seed of each F_2 plant, duplicate 5-foot rows were space planted with 25 kernels each. A few rows were similarly planted with F_1 kernels and some with F_2 kernels. Check-rows of Minhardi were sown every tenth row, and every fiftieth row was sown with H-44.

A duplicate planting of the F_3 material was made at the Judith Basin substation, Moccasin, Mont., except that the F_1 and F_2 material was not included. In so far as seed was available, each F_3 line was sown in duplicate 5-foot rows at both stations.

For determining segregation for growth habit, 50 kernels of each F_3 line were sown in a single 10-foot row at University Farm in the spring of 1929. More F_1 and F_2 material also was grown from spring seeding. A check of the H-44 parent was grown in every tenth row, and the Minhardi parent was grown in every fiftieth row.

At University Farm artificial stem-rust epidemics were produced on both the fall-sown and the spring-sown material, by transferring wheat seedlings covered with urediniospores from the greenhouse to the field. When the hybrid plants were starting to shoot they also were sprayed with a suspension of urediniospores. For producing the artificial epidemic in the field, about 15 physiologic forms of stem rust were used.

For the greenhouse rust studies, known physiologic forms were used, the plants being inoculated when the first leaf was about 2 inches long. The physiologic forms of rust for these studies were supplied and identified by E. C. Stakman and M. N. Levine, University Farm, St. Paul, Minn.

For laboratory freezing tests the plants were grown in 4-inch pots, five plants per pot. When the plants were 6 weeks old they were exposed to artificially produced low temperatures and then allowed to recover. The methods used in conducting this phase of the experiment are explained by presenting the results.

From the foregoing outline it will be seen that a good yield of seed from each F_2 plant was necessary in order to carry on the F_3 tests. From the seed of each F_2 plant 100 kernels were sown in the fall, 50 kernels were sown in the spring, 60 kernels were used for the freezing tests, and between 40 and 80 kernels were used for the greenhouse rust studies. By growing the F_2 material at Davis, Calif., under irrigation, it was possible to obtain the necessary seed, but it was not possible to obtain F_2 data on most of the characters, the study, of necessity, therefore, being based upon F_3 results. For the study of winter hardiness in fall-sown material and the study of growth habit in spring-sown material all the F_2 plants that matured sufficient seed were continued. For the laboratory studies a random sample of the F_2 plants was taken.

RESULTS

Experimental results on winter hardiness, growth habit, rust reaction, heading period, coleoptile color, and awnedness are presented in this same order.

WINTER HARDINESS

The following method was used in taking the notes on winter hardiness: Before growth stopped in the fall, counts were made of the total number of plants in each row. In the spring, after growth was well started, the number of surviving plants were counted. The surviving plants were classified as "strong" or "weak," depending upon the vigor of growth. In obtaining a mathematical measure of survival for each row the number of strong plants was multiplied by 1 and the number of weak plants by 0.5. The sum of these two calculations divided by the total number of plants in the row, in the fall, gave a survival percentage which was weighted for the spring condition of the plants. This percentage is termed hardiness index, and although arrived at in a slightly different manner, is the same value as that used by Hayes and Aamodt (18).

AT ST. PAUL, MINN.

The entire nursery at University Farm was sown on September 7, 1928. A week of cool, damp weather immediately following caused poor germination, resulting in a reduced number of plants per row. In general the fall was mild, and while there were nights when the temperature dropped below freezing, there was no subzero weather until December 5, when -1° F. was recorded. Throughout the early part of December there were several light snows, but the ground was not covered long at a time. Temperatures below zero were recorded on two occasions when little or no snow covered the ground. An inspection of the nursery on December 27 showed that the plants apparently were still in good condition, although a few H-44 plants showed signs of killing. The weather was very mild from December 24 to 29, and nearly all the snow melted. Following this mild weather it suddenly turned very cold, the mean temperature for January being 1.9° , with a low of -24° . Throughout this cold weather, however, there was a good covering of snow over the entire nursery. The weather remained cold through February, with no thaw occurring until early in March, when the weather warmed up and the snow quickly melted. It was feared that the cold weather of January

following so quickly the thaw of late December might have killed the entire nursery, but apparently the plants were well hardened off, and with the protection afforded by the snow cover some plants were able to survive.

In Table 1 are given the survival data for fall-sown F_1 and F_2 plants compared with parent plants grown in adjacent rows. None of the H-44 plants survived, while the Minhardi parent had a survival percentage of 90.8 and a hardiness index of 89.6. Only four F_1 plants came up in the fall, and all of these died. The hardiness index of the F_2 plants was 48.4, this being about halfway between the indexes of the two parents. Approximately half of the surviving F_2 plants were classed as "strong."

TABLE 1.—Hardiness indexes of fall-sown parents and F_1 and F_2 plants of Minhardi \times H-44 crosses grown at University Farm, St. Paul, Minn., winter of 1928-29

Variety or cross	Total plants	Number of plants classified as—			Percentage of survival	Hardiness index
		Strong	Weak	Dead		
H-44.....	81			81	0	0
Minhardi.....	163	144	4	15	90.8	89.6
Minhardi \times H-44 F_1	4			4	0	0
Minhardi \times H-44 F_2	350	158	23	169	51.7	48.4

A total of 620 F_2 lines were grown in the field-hardiness study. Because of poor germination the number of plants per line was smaller than anticipated, but it is believed that numbers were large enough to give an indication of the relative resistance to cold of the different lines. The hardiness index was determined for each row, and the duplicate rows of a given line were averaged to obtain the hardiness index for the line. In Table 2 these data are arranged in frequency distributions.

TABLE 2.—Hardiness index classes of parents and 620 F_2 lines of H-44 and Minhardi wheat crosses grown at University Farm, St. Paul, Minn., 1928-29

Variety or cross	Number of lines with hardiness indexes indicated										Total number of lines	Mean	
	0	5	15	25	35	45	55	65	75	85			95
H-44.....	14	1										15	0.3±0.2
Minhardi.....								1	10	37	41	89	88.3±.5
H-44 \times Minhardi.....	33	60	38	23	20	32	24	21	17	11	5	293	31.6±1.1
Minhardi \times H-44.....	37	68	57	30	26	24	15	23	20	16	6	327	30.6±1.0
Total hybrids.....	70	128	95	53	55	56	39	46	37	27	11	620	31.1±.7

Fifteen rows of H-44 were grown in each replication. In one of these rows one plant survived, and it was classed as "weak." This plant did not mature. Minhardi had an average hardiness index of 88.3. An inspection of Table 2 shows that the F_2 lines ranged from those totally killed to those that were as hardy as the winter parent. Of the total number of hybrid lines grown, 31.9 per cent

had a hardness index of 5 or less, which was the range of the spring parent, 18.3 per cent fell within the range of the winter parent, and 49.8 per cent were intermediate. The distribution on a percentage basis is shown graphically in Figure 1. This distribution is a little different from that usually obtained from quantitative characters. As a rule one would expect to have more piling up in the intermediate classes.

It is impossible to know whether any of the F_3 lines were less hardy than H-44, since in this test practically all plants of this strain were killed. The Minhardi parent had a rather wide range of survival, many of the rows having a hardness index of 100. A total of 11 F_3 lines had a hardness index above 91, and, of these, two were above 95. In no case did an F_3 line have a hardness index of 100. It seems safe to conclude, however, that lines as hardy as the Minhardi parent were obtained.

As noted previously, each F_3 line was grown in duplicate 5-foot rows. Replication is desirable in the study of a character such as resistance

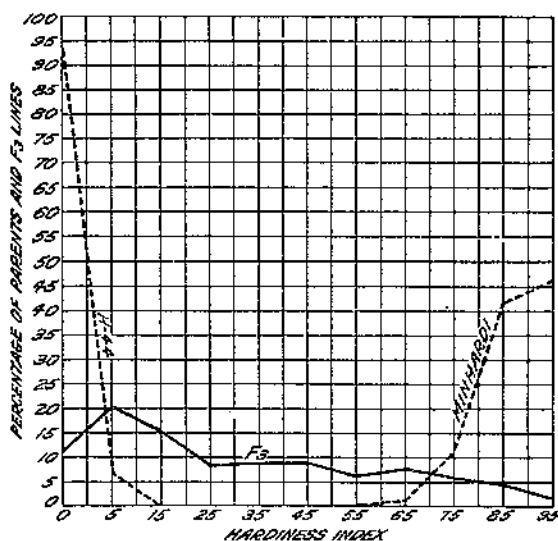


FIGURE 1.—Hardness indexes of parent and F_3 lines of H-44 and Minhardi wheat crosses grown at St. Paul, Minn., 1928-29

to cold, since soil or slight topographic variations might cause differences in killing not due to heredity. In this study there was some variation in survival between the replications, as there were spots in the field where killing, based on the behavior of the checkrows, was much greater than in other places. In a few cases a line was completely killed in one replication and had a good survival in the other replication. In general, however, the results were fairly consistent, as the hardness index of each F_3 line in the first replication when correlated with that of the second replication gave a value of $r = +0.631 \pm 0.017$.

AT MOCCASIN, MONT.

At the Judith Basin substation,⁶ Moccasin, Mont., only F_3 and parental material was grown. All of the F_3 lines of which there was sufficient seed were sown in duplicate 5-foot rows. The nursery was sown August 23-24, 1928. Germination was very good, many of the rows having perfect stands. The plants made a vigorous fall growth and went into the winter in good condition. The winter was long and cold, but with a heavy snow cover. The deep snow gave enough protection to the plants, so that killing was rather light.

In Table 3 are presented survival data of the 608 F_3 lines and their parents. Fifteen rows of H-44 were grown in each replication, and in 7 of these rows there were surviving plants. The average hardi-

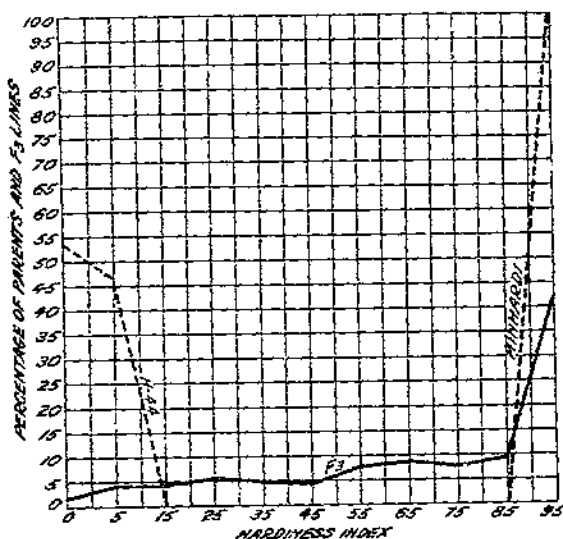


FIGURE 2.—Hardiness indexes of parent and F_3 lines of H-44 and Minhardi wheat crosses grown at Moccasin, Mont., 1923-29

ness index of H-44 at Moccasin was 2.3. The 90 rows of Minhardi had a hardiness index ranging between 91 and 100, that of the majority being 100, showing that killing was much less severe than at St. Paul. Of the 608 F_3 lines, 5.9 per cent had a survival within the range of H-44, 41.9 per cent were within the range of Minhardi, and 52.2 per cent were intermediate. In Figure 2 are shown the distributions by hardiness indexes of the parents and hybrid lines charted on a percentage basis. In this case there is a piling up on the hardy end of the curve, while at St. Paul the piling up was at the opposite end of the curve.

⁶ The writer wishes to thank B. B. Bayles and J. L. Sutherland for growing the material and taking the survival notes at Moccasin.

TABLE 3.—Hardiness index classes of parents and 608 F_2 lines of H-44 and Minhardi wheat crosses grown at the Judith Basin substation, Moccasin, Mont., 1928-29

Variety or cross	Number of lines indicated with hardiness indexes											Total number of lines	Mean
	0	5	15	25	35	45	55	65	75	85	95		
H-44.....	8	7										15	2.3±0.4
Minhardi.....												90	95.0
H-44 × Minhardi.....	9	23	15	17	18	15	23	26	23	27	87	282	61.4±1.3
Minhardi × H-44.....	0	5	10	10	11	11	25	20	25	29	108	326	76.1±1.9
Total hybrids.....	9	27	25	33	29	20	48	52	48	56	255	608	69.3±1.8

The average hardiness index of all F_2 lines grown at Moccasin was 69.3, while at St. Paul it was 31.1. The smaller amount of killing in Montana is a reasonable explanation for the different types of distribution of the hybrid lines obtained at the two places. At St. Paul killing was probably due chiefly to low temperature, while at Moccasin additional factors may have been of importance, particularly drought, soil blowing, and root rots.

In the Montana experiments the F_2 lines of H-44 × Minhardi had an average hardiness index of 61.4 ± 1.3 , while the average for the Minhardi × H-44 lines was 76.1 ± 0.9 . This difference, 14.7 ± 1.6 , might be considered significant, except that at St. Paul the reciprocal crosses had nearly identical averages. There was some variation in hardiness index between the replications grown at Moccasin, although in general the results agreed fairly well. The correlation between the hardiness indexes of the F_2 lines in the first and those in the second replication was $r = +0.552 \pm 0.018$. The killing seemed to be heaviest, however, in the series where the first replication of the H-44 × Minhardi cross was sown. Both replications of the Minhardi × H-44 cross were grown under slightly more favorable conditions. This probably accounts for the difference in survival between the reciprocal crosses at Moccasin.

RELATION BETWEEN HARDINESS AT ST. PAUL AND AT MOCCASIN

Since the same F_2 lines were grown at both St. Paul and Moccasin, it is possible to correlate survival at the two places. In Table 4 is presented a correlation surface showing the relation of hardiness indexes at the two places. A total of 607 F_2 lines were used in this comparison, in which $r = +0.416 \pm 0.023$. The correlation ratio was 0.422 ± 0.023 , and the difference between r^2 and r^2 is 1.9 times its probable error. This value, while not large, shows that lines hardy at one place tend to be hardy at the other, indicating that the same factor, low temperature, was the chief cause of winterkilling at both places.

TABLE 4.—Correlation between the hardiness indexes of F_2 lines of H-44 and Minhardi wheat crosses grown at Moccasin, Mont., and the hardiness indexes of the same lines grown at St. Paul, Minn., 1928-29

Hardiness index at St. Paul (per cent)	Hardiness index at Moccasin											Total number of lines
	0	5	15	25	35	45	55	65	75	85	95	
0	2	7	5	6	4	4	4	9	4	3	17	65
5	3	12	7	9	13	6	10	15	10	7	34	126
15		3	6	10	6	7	12	7	8	11	24	94
25	1	3	3	3	2	3	8	6	4	2	17	52
35	2		3	3		2	2	3	7	4	25	64
45	1		1	1	1	1	3	4	5	13	25	55
55		1		1	1	1	3	4	3	4	22	49
65		1		1	2	1	2	1	2	6	23	37
75							3	1	4	3	26	26
85						1				2	9	10
95										1		
Total lines	9	27	25	33	29	26	48	52	47	56	255	507

$$r = +0.416 \pm 0.023. \quad \eta = 0.422 \pm 0.023. \quad \frac{\eta^2 - r^2}{P.E.} = 1.0.$$

A study of the correlation surface gives a possible explanation as to why the coefficient of correlation was not higher. Many of the lines that had low survivals at St. Paul had high survivals at Moccasin. Of the 191 lines which at St. Paul fell in the hardiness index classes of 5 and less, 99 had hardiness indexes of 65 or more at Moccasin. Among the more hardy lines the correlation in survival at the two places was greater. In other words, the test in Montana was not severe enough to kill many of the less hardy lines.

From the data on winter hardiness obtained in the field the complicated nature of the character is shown. It is easily seen that environment greatly influences results, making any detailed explanation of inheritance out of the question. It is probable, however, that several factors are involved, their expression being greatly influenced by environment.

LABORATORY STUDIES:

Laboratory freezing tests were made on 118 F_2 lines of the H-44 and Minhardi wheat crosses, selected at random. Each of the lines used for this test also was grown from fall seeding in the field at both St. Paul and Moccasin. A large number of plants of each parent also were grown in the laboratory.

Four-inch clay pots were filled with steam-sterilized soil, made up of a mixture of 3 parts loam to 1 part sand. After the pots were filled they were thoroughly wet down previous to sowing on November 6. From six to eight seeds were placed in each pot in order to insure a uniform stand of five plants per pot.

A total of 12 pots were sown for each line. In order to overcome variations in growth due to difference in light and temperature at various places in the greenhouse, the pots of each line were systematically distributed in groups of three each at four different places on the greenhouse benches. Parent check material was similarly distributed so as to be wholly comparable.

⁷ The writer expresses his appreciation to R. B. Harvey, University Farm, St. Paul, Minn., for his valuable suggestions and kind cooperation in conducting these tests, and to S. C. Salmon, Kansas State Agricultural College, Manhattan, Kans., for suggestions in planning the experiment.

Germination was slow and mice caused some damage, making necessary a small amount of reseeded and some transplanting in order to have a uniform number of plants in each pot. The temperature was held near 70° F. until emergence was complete on November 14, and then lowered to between 55° and 60°. It was desired to maintain a temperature as near 55° as possible, but during the middle of the day the temperature occasionally went up before the ventilators could be opened and the heat shut off. There were no automatic controls in the house in which this material was grown, making close regulation of the temperature difficult.

By November 21 the plants had reached the second-leaf stage, and from this time on the temperature was slowly lowered until December 2, when the mean temperature was below 40° F. In Figure 3 is presented a curve of the daily mean air temperature from November 6, the date of planting, until December 14, when the last pots were frozen. On December 4 the minimum temperature dropped to 28°, causing the plants and soil to freeze. The temperature was raised in order to thaw out the plants and soil, and afterwards the temperature was held between 32° and 40° as far as possible. Owing to a very mild spell of weather, it was very difficult to maintain the desired low temperature. On clear days, between



FIGURE 3.—Daily mean air temperature in the greenhouse during the period of growing the plants for freezing studies

10 a. m. and 2 p. m., the temperature would go up above 40°, but would fall quickly after the sun went down. It will be seen from the chart that the mean temperature was below 40° from December 2 to 9, when the weather warmed up again, and as a result the greenhouse temperature went up, although all heat was shut off.

Throughout the period of growth the pots were watered whenever they seemed to be dry. No attempt was made to give equal quantities of water to each pot, but the pots were kept uniformly moist in so far as it was possible to do so from inspection only.

The low-temperature equipment of the department of botany, University of Minnesota, was used for the freezing. Preliminary tests were run on parental material to determine the proper temperatures and duration of exposure, as the amount of hardening off would largely determine how low a temperature the plants would be able to withstand.

From these preliminary trials a 23-hour exposure at 14° F. was chosen for the first test. On the evening of December 10 four pots of each of the F_3 lines, one from each replication, together with parent checks, a total of 600 pots, were placed in the cold room at the same time. The pots were allowed to remain in the low-temperature room for about 23 hours. Owing to unavoidable accidents, good temperature control was not obtained. During more than 6 of

the 23 hours the temperature was below 14° F. For 4 hours the temperature was below 10°, dropping as low as 3° for about 20 minutes. Temperatures were automatically recorded every 10 minutes, and the mean of all these readings was 11.5°. After removing the pots from the cold room, they were placed in a greenhouse to thaw out.

The second test was set for 23° F. and ran for about 23 hours. As before, 4 pots of each of the F₃ lines, with parent checks, a total of 600 pots, were tested. Temperature control again was poor, and for 6 hours the temperature was below 10°, being as low as 1° to 2° for about 40 minutes. The average temperature for this test was 15.6°.

A third test, using the final 600 pots of F₃ hybrid and parent material, also was set at 23° F. In this test the temperature remained relatively constant, varying only about 5°, the mean temperature for the entire 23-hour period being 23.5°.

After freezing, the material from all three lots was placed in a greenhouse, held at a temperature of 55° to 60° F., and kept well watered in an attempt to revive the plants. Ten days after freezing, records were taken on plant condition. These records took into account numbers of living and dead plants and also the degree of injury in surviving plants. A number of pot cultures selected to show the different degrees of killing are illustrated in Plate 1. In arriving at a numerical measure of condition, the plants in each pot were graded according to the criteria given in Table 6. If all five plants were uninjured, the condition value for the pot was 5×20, or 100. If the pot had two dead plants and three weak plants the value was 2×0+3×8, or 24. The average value for the four pots of each F₃ line was taken as the measure of hardiness for that line in the test concerned.

TABLE 5.—Pot cultures of wheat plants graded to show different degrees of killing caused by exposure to artificially produced freezing temperatures

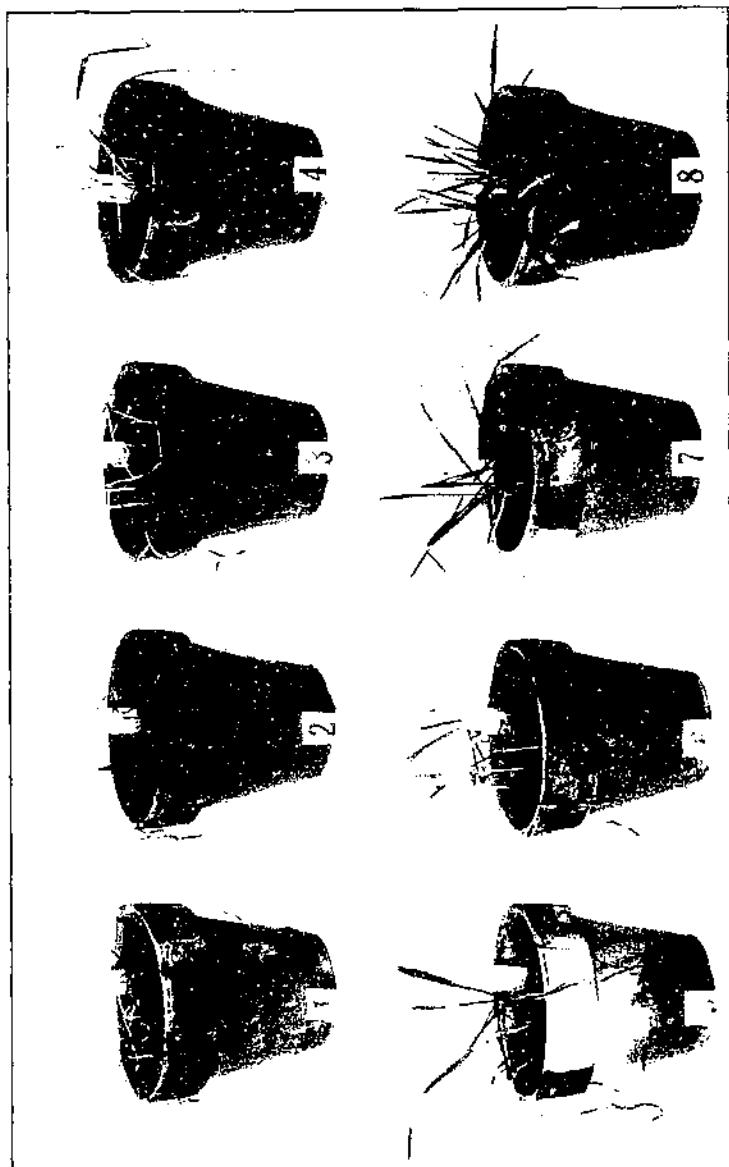
Pot No.	Parent or cross	Condition 10 days after freezing	Survival 30 days after freezing
		Per cent	Per cent
1	H-44	0	0
2	H-44 × Minhardi F ₃	15	0
3	do	48	0
4	do	20	20
5	do	36	60
6	do	60	100
7	do	68	100
8	Minhardi	100	100

TABLE 6.—Criteria for evaluating plant condition 10 days after exposure to low temperature

Description	Visible criteria	Assigned numerical value
Dead	No sign of life	0
Very weak	Showing only small amounts of living tissue	4
Weak	Leaves more than half killed	8
Heavy injury	Leaves about half killed	12
Light injury	Tips of leaves killed	16
No injury	No sign of killing	20

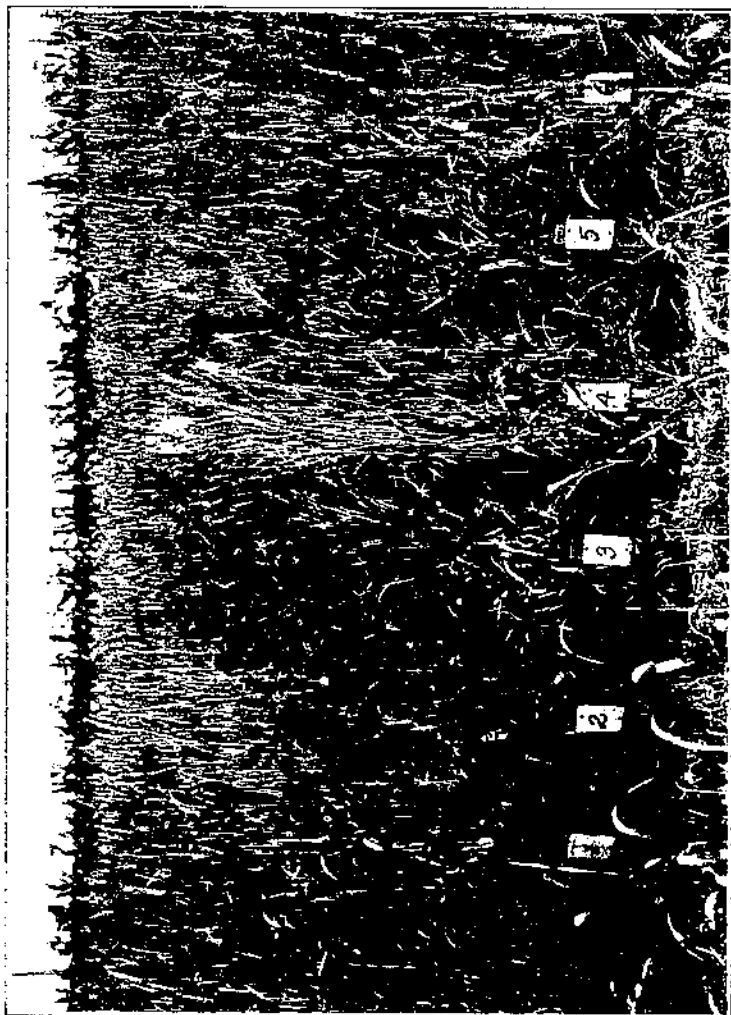
A second observation was made 30 days after the freezing test. At this time the plants were classed as dead or alive, no attempt being made to segregate the living plants as to vigor of growth. It seemed certain that by this time all the plants that had not died were not injured severely enough to prevent ultimate recovery.

Data on plant condition 10 days after freezing are presented in Table 7. In the first test, at a mean temperature of 11.5° F., the H-44 plants were nearly all killed, the average condition being only 0.5, while the Minhardi plants had an average condition of 67.8. The condition of the 118 F₂ hybrid lines ranged from 0 to 52.5 per cent, some lines being as tender as H-44, none as resistant as Minhardi, and the majority falling into the less resistant classes. In the second test, at a mean of 15.6° F., the average condition of H-44 was 0.9 and Minhardi 79.1, Minhardi being considerably higher than in the first test. In this test also some of the F₂ lines were as tender as the H-44 parent and two lines were within the limits of Minhardi. The general distribution for the F₂ lines in the two tests was about the same.



WHEAT PLANTS SHOWING DIFFERENT DEGREES OF INJURY

These injuries were caused by exposure to artificially produced freezing temperatures. The plants were photographed 10 days after freezing and were graded as shown in Table 5.



GROWTH HABIT IN THE NURSERY OF F. LINES OF H 44 AND MINHARDI WHEAT CROSSES AND PARENT ROWS

No. 1, early spring line; Nos. 2 and 3, winter lines; Nos. 4 and 6, H 44 spring parent; and No. 5, Minhardt winter parent.

In the third test, at a mean of 23.5° F., the material was not frozen hard enough to give good differentiation between the hardy and nonhardy lines. The data, however, show no F_3 lines less hardy than H-44. While there was not the wide difference between the two parents shown by the tests at lower temperatures, the general trend of the hybrids was similar to that in the other tests.

Data from the third test were not averaged with those from the first and second tests, since they did not show sufficient killing or differentiation. The average data of the first two tests show that five F_3 lines fell within the limits of the H-44 parent and two within the limits of Minhardi, the remainder of the lines being intermediate between the two parents. Data on parents and hybrids are presented graphically in Figure 4.

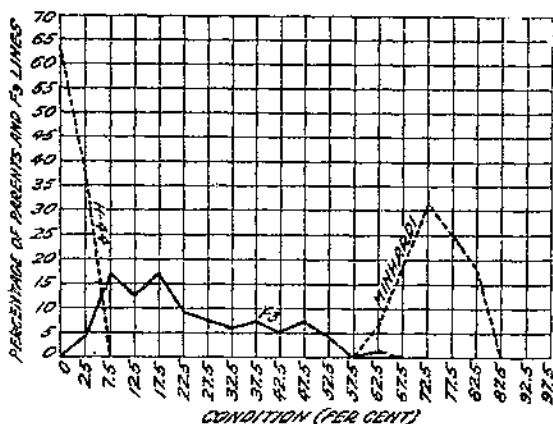


FIGURE 4.—Condition of parents and F_3 lines of H-44 and Minhardi wheat crosses 10 days after freezing

Despite the slightly different temperatures of the first and second tests, the correlation for the 118 F_3 lines in the two tests was highly significant, $r = +0.822 \pm 0.020$. This correlation is higher than that between replications in the field or between the data from St. Paul and from Moccasin.

Data taken 30 days after freezing are presented in Table 8. Data from the first two freezing tests only are given, since in the third test practically all plants survived. No H-44 plants survived in either of the two tests, while Minhardi had an average survival of 86.3 per cent. The spring parent and some F_3 lines were totally killed, while in both tests a few hybrid lines had survivals within the limits of Minhardi. Averaging the two tests, 10 lines had no survivals and 5 lines had survivals within the limits of Minhardi. The correlation between the percentage of plants alive in the first freezing test and in the second was $r = +0.761 \pm 0.026$.

TABLE 8.—Survival of parents and 118 F₂ lines of H-44 and Minhardi wheat crosses 30 days after freezing

Test and variety or cross	Number of lines having survival (per cent) of—																						Total number of lines	Mean survival
	0	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	82.5	87.5	92.5	97.5			
First test, 14° F.:																								
H-44.....	10																						10	0
Minhardi.....																							10	88.1±1.1
H-44 and Minhardi crosses.....	20	7	13	0	12	10	6	6	4	7	3	2	4	3	1	2		2	4	4	2	4	118	21.9±1.3
Second test, 23° F.:																								
H-44.....	10																						10	0
Minhardi.....																							10	81.6±1.5
H-44 and Minhardi crosses.....	10	5	18	10	13	15	7	5	7	6	6	3	1	1	2	3	1	3	5	0	1	1	118	22.6±1.2
Average of two tests:																								
H-44.....	10																						10	0
Minhardi.....																							10	80.3±1.1
H-44 and Minhardi crosses.....	10	11	13	10	14	5	10	7	8	4	4	2	5	1	0	1		2	2	7	3	1	118	23.1±1.2

The relative value of the two sets of hardness data, the one taken 10 days and the other 30 days after freezing, is of interest. Using averages, in both cases, the correlation between condition 10 days after freezing and survival 30 days after freezing was $r = +0.910 \pm 0.011$. This high correlation indicates that either method can be used to measure hardness.

RELATION BETWEEN FIELD AND LABORATORY HARDNESS RESULTS

Although freezing studies can be conducted in the laboratory under controlled conditions, the results are of practical value only in so far as they are correlated with field results. In these studies the same F_3 lines were exposed to freezing temperatures in the laboratory and were grown from fall planting in the field, both at St. Paul and at Moccasin. Since plant condition 10 days after freezing and survival 30 days after freezing were highly correlated, only one of these criteria need be considered in determining the correlation between field and laboratory studies. Survival 30 days after freezing seems to be more comparable with the field results and is used in comparing the laboratory and field methods. Survival in the laboratory when correlated with the hardness index as determined in the field at St. Paul gave a correlation $r = +0.582 \pm 0.041$. Survival in the laboratory correlated with the hardness index in the field at Moccasin results in a slightly higher coefficient, $r = +0.629 \pm 0.038$. Using the average of the hardness indexes at Moccasin and St. Paul as the measure of the field reaction and correlating with survival in the laboratory, the coefficient is still higher, $r = +0.713 \pm 0.031$. The correlation surface for this comparison is shown in Table 9.

TABLE 9.—Correlation between average field hardness index and laboratory survival 30 days after freezing for 118 F_3 lines of H-44 and Minhardi wheat crosses

Laboratory survival (per cent)	Number of lines with a field hardness index (per cent) of—														Total number of lines		
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5		72.5	77.5
5	7		2														9
15	6	5	1	1													13
25	2	3	3	2		1											11
35	2	1	3	2	1	1											10
45	3	2	4	2		1	2										14
55	1	1	1	1	1	1	2	1	2	1	1	1					14
65			4	1	2	2	1	2		2		2	1				15
75		1	1	1	1	2	1	2	1	1		2	1				19
85				1		2	2	3	2	1		2			1	2	16
95						2		1			1					2	6
Total number of lines.....	21	13	10	14	5	10	7	8	4	4	2	5	1	0	1	4	118

$$r = 0.713 \pm 0.031, \quad \sigma = 0.776 \pm 0.025, \quad \frac{r^2 - r^2}{P.E.} = 2.0.$$

In general, the relation between field and laboratory tests is very good. The five lines with outstanding hardness in the field also showed a high degree of resistance to artificially produced low temperatures. None of the lines with a low survival in the greenhouse were hardy in the field, but a few of the lines which appeared to be resistant to cold in the greenhouse were not hardy in the field. From this rather limited test it would seem that artificial freezing offers considerable promise in eliminating hybrid lines susceptible to cold.

By subjecting hybrid material to artificially produced low temperatures it should be possible to select the more cold-resistant lines, and these could then be tested in the field for final selection. Freezing tests can be conducted during the winter regardless of extreme changes in temperature and without the danger of failing to get a test or of losing all of the plant material.

GROWTH HABIT

Growth habit designates the general characteristics that separate winter and spring wheats. True spring wheats when spring sown will produce heads, while true winter wheats remain vegetative and produce few if any heads when spring sown under Minnesota conditions. This study of growth habit is based almost entirely on spring-sown F_3 material, grown at University Farm. Some data were obtained, however, on the behavior of F_1 and F_2 plants, grown with the F_3 lines.

The absence or presence of heads and the date of heading were used to separate the winter, spring, and segregating lines. Three days after the first head appeared all plants upon which at least one head had completely emerged were tagged. Three days later all the plants that had headed since the tagging of the first group were tagged. This method of tagging was continued for eight periods or 24 days after the first head appeared in the nursery. By this time the number of plants heading had decreased so materially that the tagging was continued only at 6-day intervals, designated as periods 10 and 12. The plants that had not headed by the twelfth period, 36 days after heading started, were considered to be winter plants. Such plants began to die at this time.

Of the 3,608 plants of the H-44 parent grown as checks with the F_1 , F_2 , and F_3 material at University Farm, 57.8 per cent headed in period 1, 32.8 per cent in period 2, 8.9 per cent in period 3, and 0.5 per cent in period 4. Not a single plant of the Minhardi parent produced heads, and after the twelfth period they all dried up, due to hot weather and a heavy epidemic of leaf rust.

Data on the growth habit of F_1 and F_2 hybrids and of some parent material are presented in Table 10. Of the 267 plants of H-44 grown in rows adjacent to the F_1 and F_2 plants, most of the plants headed in the first two periods, a few in period 3, and 1 in period 4. A total of five F_1 plants were grown, all of which headed somewhat later than the spring parent. Other F_1 material grown from spring sowing in previous years behaved in about the same manner. In 1926 seven F_1 plants grown at Bozeman, Mont., headed 10 days later than the H-44 parent. In 1927 an F_1 plant grown at Moccasin from spring sowing headed 13 days later than the spring parent. A number of F_1 plants grown in a greenhouse at the Arlington Experiment Farm headed slightly earlier than H-44 plants sown at the same time. These observations indicate a dominance of spring-growth habit in this cross.

TABLE 10.—Growth habit of F_1 and F_2 hybrids and parents of H-44 and Minhardi wheat crosses grown at St. Paul, Minn.

Variety or cross	Number of plants of heading period stated												Total number of plants	
	Spring period											Winter period		
	1	2	3	4	5	6	7	8	10	12				
H-44	138	107	21	1										267
Minhardi													74	74
Minhardi × H-44, F_1						3								3
H-44 × Minhardi, F_1				1	1									2
Minhardi × H-44, F_2	1	31	38	32	37	12	7	8	16	12	22		216	
H-44 × Minhardi, F_2	2	14	30	37	38	18	7	16	21	11	20		223	
Total F_2 hybrids	3	45	77	69	75	30	14	24	37	23	42		439	

Of the 439 F_2 plants, 48 headed in periods 1 and 2, resembling the H-44 parent. A total of 221 plants, or more than half the population, headed in periods 3, 4, and 5, resembling the F_1 . Some plants headed in periods 6 to 12, or much later even than the F_1 . Only 42 true winter plants failed to head.

The F_2 data, grouped on the basis of spring and winter types, together with theoretical numbers calculated from several ratios, are presented in Table 11. The observed numbers do not fit closely the calculated numbers for any of these theoretical ratios. The observed number of winter types falls nearly half way between the calculated numbers for a 15:1 ratio and a 55:9 ratio. Although the deviation of observed from calculated is lowest for the 15:1 ratio, the odds favor the 55:9 ratio.

In 1927 a small F_2 population was grown from spring sowing at Moccasin, Mont. Here the observed ratio was 175 spring to 6 winter. The deviation from the calculated 15:1 ratio, 5.3 ± 2.2 , was only 2.4 times its probable error.

TABLE 11.—Segregation of 439 F_2 plants of H-44 and Minhardi wheat crosses for growth habit, compared with calculated numbers for 15:1, 13:3, and 55:9 ratios

Theoretical ratio	Number of F_2 plants having growth habit of—		Deviation	Probable error	Deviation + probable error	Odds
	Spring	Winter				
15:1						
Observed	397.0	42.0				
Calculated	411.0	27.4	14.6	3.42	4.3	207:1
13:3						
Observed	397.0	42.0				
Calculated	356.7	82.3	40.3	5.52	7.3	High.
55:9						
Observed	397.0	42.0				
Calculated	377.3	61.7	10.7	4.91	4.0	142:1

In the F_3 generation grown at St. Paul from spring seeding, there were 622 lines which were selected entirely at random. These lines when separated into the two phenotypic-growth habit groups give

589 spring to 33 winter. These numbers are compared with the theoretical ratios, 15:1, 13:3, and 55:9, in Table 12. In this case the fit to a 15:1 ratio is very close. Since an F_3 test is more reliable than an F_2 test, it would seem that segregation for growth habit in this cross best fits a ratio of 15 spring to 1 winter. Two genetic factor pairs therefore are necessary to explain the segregation.

TABLE 12.—Segregation of 622 F_3 lines of H-44 and Minhardi wheat crosses for growth habit, compared with calculated numbers for 15:1, 13:3, and 55:9 ratios

Theoretical ratio	Number of F_3 lines having growth habit of—		Deviation	Probable error	Deviation \pm probable error	Odds
	Spring	Winter				
15:1:						
Observed.....	589.0	33.0				
Calculated.....	583.1	38.9	5.9	4.07	1.4	1.9:1
13:3:						
Observed.....	589.0	33.0				
Calculated.....	505.4	116.6	83.6	6.57	12.7	High.
55:9:						
Observed.....	589.0	33.0				
Calculated.....	534.6	67.4	54.4	5.89	9.2	High.

In order to analyze the F_3 lines more fully they were classified into six genotypic groups, depending upon their breeding behavior. The groups are distinguished as follows:

- (1) Early spring, where all plants headed as early as the spring parent.
- (2) Late spring, where all plants headed during a relatively short period, but later than the spring parent.
- (3) Segregating spring, where all plants headed but the heading extended over several periods.
- (4) Segregating like F_2 , where all types appeared in proportions similar to the F_2 .
- (5) Segregating spring and winter, where segregation occurred for late spring and winter types.
- (6) Winter, where no plants headed.

While it is not desirable to give all the data obtained on growth habit, a few examples of the various types of segregation are given in Table 13. In making up this table an attempt was made to give a reasonable example of the method of classification. It will be seen that F_3 lines were recovered which headed within the limits of the spring parent, also spring lines which were apparently homozygous for later heading. The amount of variability present also can be seen from the data in this table. In Plate 2 the different types of growth habit are illustrated.

TABLE 13.—Types of segregation for growth habit obtained in F₃ lines of H-44 and Minhardi wheat crosses in comparison with the parents

Name of parent or hybrid No.	Number of plants of heading period stated											Total number of plants	
	Spring period												Winter period
	1	2	3	4	5	6	7	8	10	12			
Parents:													
H-44.....	36	3	2										41
Do.....	9	27	5										41
Do.....	11	22	4	1									38
Do.....	32	10											42
Minhardi.....													43
Do.....													40
Do.....													39
F₃ hybrid lines:													
Early spring—													
1C-1-6.....	3	23	15										41
1C-1-43.....	10	15	6										40
1C-2-19.....	5	27	4										36
Late spring—													
2C-2-113.....			17	18	9								44
1C-3-16.....					8	27	2	1					38
1C-1-105.....						13	21	4	2				40
Segregating spring—													
1C-2-35.....	5	6	15	9	1	2	1						39
1C-2-6.....			15	11	6	7	1	2					42
1C-1-101.....			1	1	5	10	11	4	1	1			40
Segregating like F₂—													
1C-1-2.....	6	11	3	3	2			2	7	7		2	42
1C-1-68.....	1	11	11	2	4	3				3		4	43
1C-1-100.....	1	2	10		6	5	1	2	2	1		5	35
Segregating spring and winter—													
1C-2-37.....						5	2		2	7		26	42
1C-2-26.....				5	4	2	2	2	1	7		17	40
2C-1-14.....					3	5	1	2		12		12	35
Winter—													
1C-1-92.....												38	48
1C-2-1.....												29	26
1C-2-51.....												42	42

The number of F₃ lines that could be placed in each of the six growth-habit groups enumerated above are given in Table 14. The data show that 40 lines were classed as early spring, 68 late spring, 33 winter, and the remainder in the segregating groups. Since the number of early spring and winter types each closely approximate one-sixteenth of the total, calculated numbers based on a 1:2:4:4:4:1 genotype ratio were obtained. The observed and calculated numbers, compared by the goodness-of-fit method, are shown together in Table 14. The value of $P=0.38$ indicates that 38 times in 100 trials a poorer fit than the one obtained would be expected, due to chance alone.

TABLE 14.—Segregation of 622 F₃ lines of H-44 and Minhardi wheat crosses for growth habit, compared by the goodness-of-fit method with a calculated 1:2:4:4:4:1 genotypic ratio

Growth-habit groups	F ₃ lines		O-C	$\frac{(O-C)^2}{C}$
	Observed	Calculated		
	Number	Number		
Early spring.....	40	38.9	1.1	0.03
Late spring.....	68	77.7	-9.7	1.21
Segregating spring.....	169	165.5	4.5	.13
Segregating like F ₂	176	165.5	19.5	2.46
Segregating spring and winter.....	146	155.6	-9.5	.58
Winter.....	33	38.9	-5.9	.89
Total.....	622	622.0		

$\chi^2=5.29$. $P=0.38$.

The following hypothesis is suggested to explain the observed segregation: Assuming spring-growth habit to be dominant and two factors necessary to explain the segregation, the early spring parent, H-44, may be considered to have the genotype *AABB* and the Minhardi winter parent the genotype *aabb*. The F_1 would be *AaBb* and head as a late spring wheat. The F_2 genotypes and their breeding behavior in the F_3 generation would be as follows:

F_2 genotype	Parts of 16	Breeding in F_3 as—
<i>AABB</i> -----	1	Early spring.
<i>AAbb</i> -----		
<i>aaBB</i> -----	2	Late spring.
<i>AABb</i> -----		
<i>AaBB</i> -----	4	Segregating spring.
<i>AaBb</i> -----		
<i>AaBb</i> -----	4	Segregating like F_2 .
<i>Aabb</i> -----		
<i>aaBb</i> -----	4	Segregating spring and winter.
<i>aabb</i> -----		
<i>aabb</i> -----	1	Winter.

In general, it seems that the 2-factor hypothesis here advanced satisfactorily explains the results obtained, although the writer believes that such a definite interpretation might not always hold true, since expression of the growth-habit character is so greatly influenced by environment. It is possible that in a different season or with different dates of seeding the segregation might have been materially changed. In grouping the F_3 lines it was necessary to keep constantly in mind the fact that environmental factors, such as soil, moisture, and stand, had a considerable effect upon growth habit. In general, the results obtained on growth habit agree with the work of Aamodt (8) and of Vavilov and Kouznetsov (39).

RELATION BETWEEN WINTER HARDINESS AND GROWTH HABIT

Since each of the F_3 lines was fall sown at Moccasin and St. Paul and spring sown at St. Paul, and all the lines tested for hardiness in the laboratory were spring sown, it is possible to determine the relationship between growth habit and hardiness, as determined both in the field and in the laboratory.

IN THE FIELD

The data for hardiness indexes are given by growth-habit groups in Table 15. Hardiness data for both St. Paul and Moccasin and the average for the two stations are given. The data from each station and the averages show the same general relations, regardless of the fact that killing was much less severe at Moccasin than at St. Paul. The lines classed as early spring had the lowest average hardiness indexes, although some of these lines were more hardy than the spring parent. The lines classed as late spring were more hardy on the average than the early spring lines. At St. Paul the lines classed as segregating spring were less hardy on the average than the late spring lines, while at Moccasin the reverse was true. For the average of the two stations the segregating spring and late spring lines are not significantly different as to hardiness indexes. The lines segregating

like F_2 were still more hardy, as were the lines that segregated for late springs and winters. The lines classed as winter, while few in number, had the highest average hardiness indexes. At St. Paul about half of the lines classed as having winter-growth habit were less hardy than the lower limit of Minhardi. Spring lines more hardy than the spring parent were obtained. Some early spring lines were obtained that were as hardy as some of the winter lines. The segregating lines that contained some winter types were more hardy than the lines having no winter types.

In Figure 5 the average hardiness indexes at St. Paul and Moccasin by growth-habit classes are shown graphically.

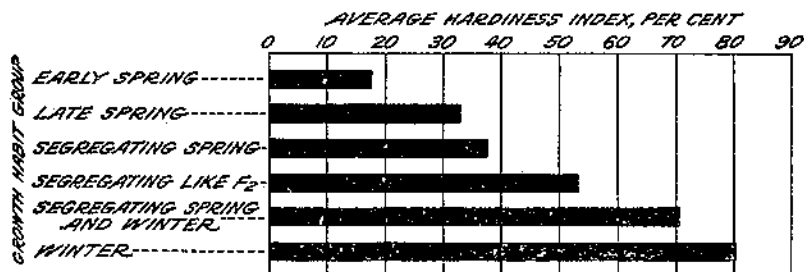


FIGURE 5.—Diagram showing the average hardiness indexes of F_2 lines of H-44 and Minhardi wheat crosses by growth-habit groups

TABLE 15.—Relation between hardiness indexes and growth habit of parents and F_2 lines of H-44 and Minhardi wheat crosses grown in the field at St. Paul, Minn., and at Moccasin, Mont., in 1929

Parents and F_2 lines by growth-habit groups	Number of lines with hardiness index of—											Total number of lines	Mean hardiness indexes		
	0	5	15	25	35	45	55	65	75	85	95				
St. Paul:															
Parents—															
H-44	14	1												15	0.3±0.2
Minhardi								1	10	37	41			80	89.3±.3
F_2 lines—															
Early spring	10	16	12	2										40	7.8±.7
Late spring	5	22	12	12	5	3	2	1	2	1	1			68	19.3±1.6
Segregating spring	32	44	23	17	9	8	5	5	1	1	1			145	16.7±1.1
Segregating like F_2	15	35	34	12	20	22	11	14	6	5				174	20.1±1.2
Segregating spring and winter	5	10	13	9	16	21	15	23	23	16	8			159	31.2±1.4
Winter		1	1	1	5	1	0	0	5	4	3			33	60.2±2.7
Moccasin:															
Parents—															
H-44	8	7												15	2.3±.4
Minhardi														90	95.0
F_2 lines—															
Early spring	4	8	5	9	4	5	1	1	1	1	2			41	28.7±2.7
Late spring	3	8	7	9	4	5	9	7	2	2	11			57	45.5±2.6
Segregating spring	2	10	8	12	11	12	16	10	12	8	35			145	58.0±1.7
Segregating like F_2		1	5	3	0	6	17	17	23	28	69			172	76.2±1.2
Segregating spring and winter					1	3	7	8	10	16	108			153	87.9±.7
Winter											1			31	94.7±.3
Average for both stations:															
F_2 lines—															
Early spring	2	13	12	4	5	3	1							40	17.8±1.5
Late spring		9	13	14	10	5	7	4	3	2				67	32.9±1.8
Segregating spring		9	18	23	31	28	22	6	4	2	1			144	37.6±1.0
Segregating like F_2		1	7	9	21	36	34	34	19	8	3			172	58.3±.9
Segregating spring and winter			1		3	14	28	25	27	38	17			153	70.6±.9
Winter								1	5	7	12			31	80.5±1.3

IN THE LABORATORY

The relation between the percentage of plants alive 30 days after freezing and growth habit is shown in Table 16. As in the field, the average resistance to cold is in direct relation to lateness of heading or to the percentage of winter-habit plants in the class. The early heading group, however, contains some lines with greater resistance to cold than the H-44 parent. The winter-habit lines gave the highest average survival of any of the growth-habit groups, although the difference between the winter group and the segregating spring and winter group is not significant in the light of its probable error.

It would have been desirable to test a larger number of early spring and winter lines, but when the laboratory experiments were made information on growth habit was not available and of necessity the selection of lines was entirely at random.

Both field and laboratory data show a relation between growth habit and winter hardiness. It is possible that a factor or factors responsible for winter-growth habit also may be responsible for resistance to cold. It also is possible that factors for growth habit and factors for resistance to cold are linked. This linkage, if present, is not complete, or it would be impossible to obtain spring lines more hardy than the spring parent or winter lines less hardy than the winter parent. Because of the complicated nature of resistance to cold it would seem that many factors are involved in the expression of this character, and undoubtedly factors other than those having to do with growth habit are concerned.

The relationship of hardiness and growth habit also is of some importance with spring wheat. The production of hardy wheats having a spring-growth habit should be of considerable economic importance in extending wheat production into higher latitudes or altitudes. In practice the extreme recombinations are probably lost in large part, since spring wheats will not survive severe winters such as are encountered in Minnesota; and the tender winter segregates are lost, since they do not head from spring seeding and are not able to withstand the severe winters.

STEM-RUST REACTION

One of the important phases of the present study is the reaction of the hybrid lines to black-stem rust, *Puccinia graminis tritici*. Studies were conducted in the greenhouse on F_3 lines only and in the field on all the material growing at St. Paul. The field studies did not cover a true random sample of the hybrid population, since many plants and lines were lost from winterkilling in fall-sown material, and some spring-sown lines and plants failed to head and rust notes could not be obtained.

FIELD STUDIES

When grown in the field, H-44 shows a high degree of resistance to stem rust, while Minhardi is very susceptible. The field-rust notes were taken about one week before the plants were ripe, and are designated as the mature-plant reaction. In taking notes the plants were classed in three rust-reaction groups—resistant, semiresistant, and susceptible. Plants that showed little or no rust were called resistant, those heavily rusted were classed as susceptible, and the plants having an intermediate infection were classed as semiresistant.

TABLE 16.—Relation between survival 30 days after freezing and growth habit of parents and F₂ lines of H-44 and Minhardi wheat crosses

Parents and F ₂ lines by growth-habit groups	Number of lines having a percentage of survival of—																			Total number of lines	Mean survival (per cent)			
	0	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	82.5	87.5			92.5	97.5	
Parents:																								
H-44.....	16																						16	0
Minhardi.....																							10	80.3±1.1
F ₂ lines:																								
Early spring.....	3	3			1																		7	3.6±1.5
Late spring.....	4	3	3	2	1	1		1					1										16	11.6±2.5
Segregating spring.....	2	4	4	0	5	1	2		1			1				1							30	16.0±1.9
Segregating like F ₂	1	1	4	5	5	3	4	4	1		1		1										30	21.1±1.0
Segregating spring and winter.....			2	3	2		3	2	3	4	3	1	3	1				3					30	30.3±2.5
Winter.....							1		3								1						6	43.5±5.3

SPRING-SOWN MATERIAL

The H-44 parent grown in rows adjacent to F₁ and F₂ plants was classed as resistant. (Table 17.) None of the Minhardi plants headed and no rust data were taken on them.

TABLE 17.—Rust reaction of F₁ and F₂ plants of H-44 and Minhardi wheat crosses and the H-44 parent grown from spring sowing

Variety or cross	Number of plants			Total
	Resistant	Semiresistant	Susceptible	
Parent: H-44.....	267			267
Hybrids:				
H-44 × Minhardi F ₁		2		2
Minhardi × H-44 F ₁		3		3
H-44 × Minhardi F ₂	39	109	55	203
Minhardi × H-44 F ₂	49	94	51	194
Total F ₂ hybrids.....	88	203	106	397

Five F₁ plants were grown from spring sowing, and these were all classed as semiresistant or intermediate in rust reaction. Rust notes were obtained on a small F₂ population of 397 plants. The 88 resistant, 203 semiresistant, and 106 susceptible plants approach a theoretical 1:2:1 ratio. Comparing these data with those calculated on a 1:2:1 ratio by the χ^2 method (Table 18), the value $P=0.41$ indicates that 41 times in 100 trials a worse result would be expected, owing to chance alone.

TABLE 18.—Goodness-of-fit to a 1:2:1 ratio for rust reaction of F₂ generation of H-44 and Minhardi wheat crosses grown from spring sowing

Class	Observed	Calculated	O-C	$\frac{(O-C)^2}{C}$
	Number	Number		
Resistant.....	88	99.25	-11.25	1.28
Semiresistant.....	203	198.50	4.50	.10
Susceptible.....	106	99.25	6.75	.46
Total.....	397	397.00		

$\chi^2=1.84$. $P=0.41$.

A summary of the data from the spring-sown F₂ lines is shown in Table 19. The F₃ plants were described as resistant, semiresistant, and susceptible, and the lines later were classed as to breeding behavior into the six breeding groups shown in the table. The rust epidemic was fairly heavy in some parts of the nursery, while in other parts the infection was much lighter. Since the F₃ families were grown only in single rows, it is possible that the true rust reaction of some families was not obtained.

TABLE 19.—Rust reaction of the parent H-44 and of 589 F₂ lines of H-44 and Minhardi wheat crosses grown from spring sowing

Variety or cross	Number of lines having breeding behavior of—						Total number of lines
	Resistant	Semiresistant	Segregating			Susceptible	
			Resistant to semiresistant	Resistant to susceptible	Semiresistant to susceptible		
Parent: H-44.....	94						94
Hybrids:							
H-44 × Minhardi F ₁	72	2	27	122	10	43	276
Minhardi × H-44 F ₁	92	1	16	174	5	25	313
Total F ₂ lines.....	164	3	43	296	15	68	589

The data in Table 19 do not indicate a simple single-factor inheritance, because in the extreme classes there are too few susceptible and too many resistant lines, and also because three families bred true for semiresistance. There were segregating lines containing only resistant and semiresistant plants and others containing only semiresistant and susceptible plants. It is impossible, therefore, to explain these data on the basis of a single genetic factor difference between the resistant and susceptible parents.

FALL-SOWN MATERIAL

Rust data were taken on the few F₂ plants of the Minhardi × H-44 cross that survived the winter at St. Paul, and these are given in Table 20. The Minhardi plants, which were grown in rows adjacent to the F₂ material, were all classed as susceptible. Of the 159 F₂ plants, 90 were resistant, 35 semiresistant, and 34 were susceptible. Combining the resistant and semiresistant against the susceptible plants, the numbers are 125 to 34. The deviation from a calculated 3:1 ratio is 5.75 ± 2.24 , indicating a very good fit, although for a single-factor explanation to be tenable there should be no more resistant than susceptible plants.

TABLE 20.—Rust reaction of the parent Minhardi and of 159 F₂ plants of the Minhardi × H-44 cross grown from fall sowing

Variety or cross	Number of plants having reaction class of—			Total number of plants
	Resistant	Semiresistant	Susceptible	
Minhardi.....			159	159
Minhardi × H-44 F ₂	90	35	34	159

The rust data from the F₂ material are summarized in Table 21. In a total of 492 F₂ families, 100 were classed as susceptible, suggesting an approach to one-fourth of the lines. However, there were 25 F₂ families that bred true for semiresistance, 74 families that segregated for resistant and semiresistant plants, and 44 families that segregated for semiresistant and susceptible plants only. A single factor does not explain this segregation, for it could not account for the lines

breeding true for semiresistance and those segregating for only two of the three classes.

TABLE 21.—Rust reaction of the parent Minhardi and of 492 F₃ lines of H-44 and Minhardi wheat crosses grown from fall sowing

Variety or cross	Number of F ₃ lines having breeding behavior of—						Total number of lines
	Resistant	Semi-resistant	Segregating			Susceptible	
			Resistant to semi-resistant	Resistant to susceptible	Semi-resistant to susceptible		
Parent: Minhardi.....						89	89
Hybrids:							
H-44 × Minhardi.....	37	13	36	77	22	46	231
Minhardi × H-44.....	50	12	38	85	22	54	261
Total F ₃ lines.....	87	25	74	162	44	100	492

A single-factor segregation is suggested by the data obtained from the F₂ grown from spring sowing and also from the number of susceptible plants from the fall-sown F₂. In the F₃ generation from both fall and spring seeding, however, lines were obtained which so behave that a single-factor explanation is inadequate.

RELATION BETWEEN RUST REACTION OF FALL-SOWN AND SPRING-SOWN MATERIAL

Since all the F₃ lines were grown at St. Paul from both fall and spring seeding, it is possible to compare the rust reaction of a line when fall sown with the reaction of the same line when sown in the spring. Plants of 466 F₃ families headed from both fall and spring seeding, and the rust reactions of these lines are shown in Table 22. While there was some correlation between the rust reaction of a line when fall sown and when spring sown, the correlation was not absolute. For example, of the 86 families that were classed as resistant in the fall-sown nursery, only 45 were also resistant when spring sown, 3 being susceptible and the remainder segregating in various ways. There were 94 F₃ families that were susceptible when fall sown, and of these 32 were susceptible when spring sown and 8 were resistant, 1 semi-resistant, and 53 segregated in various ways.

TABLE 22.—Comparison of the rust reaction of F₃ lines of H-44 and Minhardi wheat crosses grown from fall and spring sowing

Rust reaction of lines when fall sown	Number of lines having rust reaction of lines when spring sown—						Total number of lines
	Resistant	Semi-resistant	Segregating			Susceptible	
			Resistant to semi-resistant	Resistant to susceptible	Semi-resistant to susceptible		
Resistant.....	45		0	30	2	3	86
Semi-resistant.....	4	1	1	17	2		25
Resistant to semi-resistant.....	40		0	26			72
Resistant to susceptible.....	24		10	86	4	7	160
Semi-resistant to susceptible.....	4	1	1	24		0	30
Susceptible.....	8	1	3	45	5	32	94
Total.....	135	3	38	228	13	51	466

The exact cause for the difference in behavior is not known, although there are several possible explanations. Since the nurseries were about a mile apart, it is possible that different physiologic forms of stem rust were present, although the epidemic was first started in the guard rows surrounding the fall-sown nursery, and inoculum from these rows was used in starting the epidemic on the spring-sown material. It is possible that different genetic factors are involved. The same factor or factors that control rust reaction when the plants are spring sown may partly control the reaction when they are fall sown. In addition to the main factor or factors, however, there may be additional factors of minor importance which operate when the material is grown over a longer period from fall sowing. It also might be possible that factors for rust reaction are linked with factors for growth habit. The fact that in the spring-sown material there were proportionately more resistant F_3 lines and in fall-sown material more susceptible lines would tend to support such a conclusion. However, when the rust data from both fall-sown and spring-sown material were recorded by growth-habit classes there was little or no indication of any gradual change in rust reaction as the groups changed from spring to winter growth habit.

Because of the nature of the material, a complete study could not be made. The data cover only a part of the population, since the less hardy lines were eliminated from the fall-sown nursery by winter-killing, and the winter types were eliminated from the spring-sown nursery by their failure to head. Rust readings could not be obtained for the F_3 lines thus eliminated, and even for many of the lines on which data were taken the numbers of plants surviving the winter or heading from spring seeding were probably too small to give a true picture of breeding behavior. In disease reaction two organisms, the plant and the pathogene, are involved, both of which are influenced by environment. In this particular case the inadequacy of the material due to environmental effects and the complicated nature of the character involved certainly justify no definite conclusions.

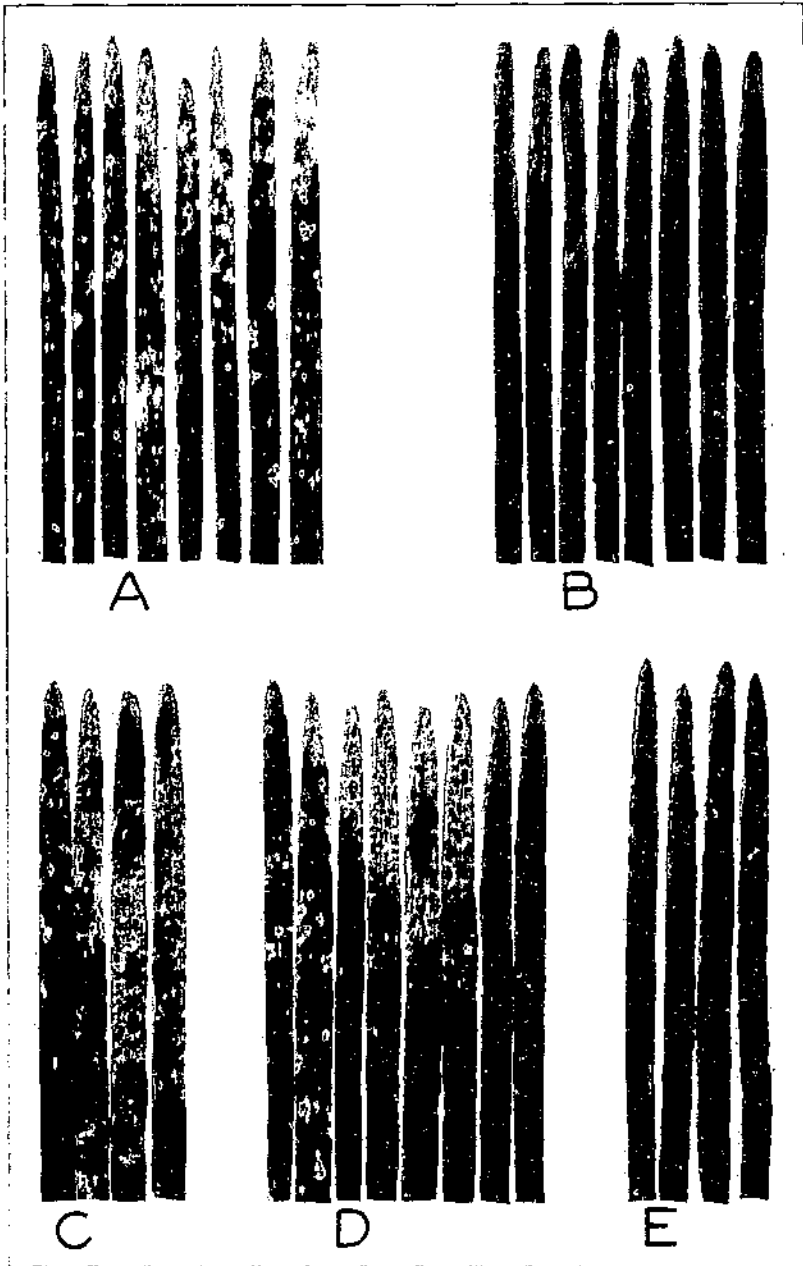
LABORATORY STUDIES

Rust studies, using known forms of rust, were made in the greenhouse on seedling plants of parents and F_3 hybrid lines. For this study stem-rust forms 36 and 60 were used. The methods of conducting such greenhouse seedling rust tests and the taking of data have been described (1, 21).

REACTION TO FORM 60

In the seedling stage H-44 is highly resistant to form 60. A total of 972 plants of H-44 were infected with form 60, and of these 933 were classed as type 1 in reaction and 39 as type 2, both being resistant reactions. Minhardi, on the other hand, was very susceptible to this form of rust. A total of 980 plants were infected, all of which had a type 4 or susceptible reaction. (Pl. 3.)

The data from the greenhouse studies with form 60 are shown in Table 23. In all, 264 F_3 lines of H-44 \times Minhardi and 216 F_3 lines of Minhardi \times H-44 were grown. Since the reaction was very distinct, it was comparatively easy to separate the F_3 lines into three breeding groups—resistant, segregating, and susceptible. (Pl. 3.)



SEEDLING REACTION IN THE GREENHOUSE TO RUST FORM 60

Parent: A, H B resistant, and B, Minharch, susceptible. F lines of H, H and Minharch wheat crosses. C, Resistant, D, segregating, and E, susceptible.

The number of families falling into each group were 114, 265, and 101, respectively. These are compared in Table 24 with a similar total calculated on a 1:2:1 ratio, using the goodness-of-fit method. The value of $P=0.05$ indicates that only 5 times in 100 trials would a result as bad or worse be expected due to chance alone. The poor fit is due chiefly to the fact that there were too few susceptible and too many segregating lines recovered. Although the agreement between the observed and the calculated ratios is not good, the writer believes that a single-factor difference is largely responsible for the results, since only one type of segregation was observed in the heterozygous lines.

TABLE 23.—Reaction to stem rust form 60 of parents and 480 F_2 lines of H-44 and Minhardi wheat crosses grown in the greenhouse

Variety and cross	Number of lines having reaction of—			Total number of lines
	Resistant	Segregating	Susceptible	
Parents:				
H-44	24			24
Minhardi			21	21
Hybrids:				
H-44 × Minhardi F_1	63	145	56	264
Minhardi × H-44 F_1	51	120	45	216
Total F_2 lines	114	265	101	480

TABLE 24.—Reaction to stem rust form 60 of 480 F_2 lines of H-44 and Minhardi wheat crosses, compared with a calculated 1:2:1 ratio by the goodness-of-fit method

Breeding groups	Number of lines		O - C	$\frac{(O-C)^2}{C}$
	Observed	Calculated		
Resistant	114	120	-6	0.30
Segregating	265	240	25	2.60
Susceptible	101	120	-19	3.01
Total	480	480		

$\chi^2=5.01$. $P=0.05$.

Some variation was observed in the expression of resistance to form 60 in the seedling stage. It was pointed out that the reaction of H-44 was mostly type 1, with some type 2. A majority of the pots of H-44 had all plants classed as type 1. Among the 114 resistant hybrid lines, 10 lines had all plants classed as having type 1 reaction. Fifty-seven lines had more type 1 than type 2 plants, 47 lines had more type 2 than type 1 plants, and 1 line was classed as all type 2.

In the rust tests one pot of each line was run at one time and a second pot later, in order to check certain inconsistencies. The lines giving both type 1 and type 2 reaction were separated into two groups—those giving the same reading both times and those giving reversed readings in the two tests. If a line had more type 2 than type 1 plants both times, it was placed in the first group; but if in the first test there were more type 2 than type 1 plants and in the second

test more type 1 than type 2, the line was put in the second group. Of the 113 lines giving types 1 and 2, 39 showed reversed reaction in the two trials. This indicates that while minor factors may have been operating in the resistant lines, environmental fluctuation was so great as to make a study of these minor factors impossible.

REACTION TO FORM 36

A second experiment was conducted on 150 hybrid lines to determine their reaction to form 36. The parental reaction to this form was identical with that for form 60, H-44 being resistant, mostly type 1 with a few type 2 plants, and Minhardi susceptible. The hybrid lines were chosen on the basis of their reaction to form 60. Sixty lines resistant to form 60, 60 susceptible lines, and 30 segregating lines were selected. In all cases reaction was the same as for form 60, indicating that the same genetic factor or factors control the seedling reaction to these two forms of rust in the greenhouse.

RELATION BETWEEN SEEDLING AND MATURE-PLANT REACTION

To be of practical value, seedling-rust reaction in the greenhouse must give an indication of the mature-plant reaction in the field. The greenhouse seedling reactions of 459 F_3 lines are compared with the field reaction of the same lines grown from spring sowing. (Table 25.) Of the 105 lines which were resistant in the greenhouse, only 42 were resistant when grown in the field, and 7 of the lines bred true for susceptibility. More than half of the 257 lines segregating in the greenhouse also segregated in the field, 65 were resistant and 18 susceptible. There were 97 susceptible lines in the greenhouse, and of these 12 proved to be resistant and 31 susceptible in the field. There was some relationship between the greenhouse and the field reactions. It would seem that the factors or group of factors that control seedling-rust reaction only partly control the reaction of the plants in the mature stage. In addition there are other independent factors controlling the mature-plant reaction.

TABLE 25.—Seedling-rust reaction in the greenhouse of 459 F_3 lines of H-44 and Minhardi wheat crosses compared with the mature-plant field reaction of the same lines when spring sown

Greenhouse seedling reaction	Number of lines having mature-plant field reaction of—						Total number of lines
	Resistant	Semi-resistant	Segregating			Susceptible	
			Semi-resistant to resistant	Resistant to susceptible	Semi-resistant to susceptible		
Resistant.....	42	2	16	37	1	7	105
Segregating.....	65		20	145	0	18	257
Susceptible.....	12		5	45	4	31	97
Total.....	119	2	41	227	14	56	459

Comparing the greenhouse-seedling reaction with the mature-plant field reaction of the F_3 lines grown from fall seeding (Table 26), there is less correlation than for the spring-sown field material. Of the 84 lines classed as resistant in the greenhouse, 15 were resistant and

10 susceptible in the field. Among the 87 lines that were susceptible in the greenhouse, 11 were resistant in the field and 26 were susceptible.

TABLE 26.—Seedling-rust reaction in the greenhouse of 380 F_2 lines of H-44 and Minhardi wheat crosses compared with the mature-plant field reaction of the same lines when fall sown

Greenhouse-seedling reaction	Number of lines having mature-plant field reaction of—						Total number of lines
	Resistant	Semiresistant	Segregating			Susceptible	
			Resistant to semiresistant	Resistant to susceptible	Semiresistant to susceptible		
Resistant.....	15	7	16	25	11	10	84
Segregating.....	37	9	27	77	21	38	209
Susceptible.....	11	6	10	27	7	26	87
Total.....	63	22	53	129	39	74	380

Here again the data indicate the presence of additional factors for mature-plant reaction in the field. It would seem that in this case the additional factors have as much influence on rust reaction in the field as the factor for controlling seedling reaction. It is hardly possible to explain the results on the basis of two independent factors, for the reason that a single factor will not explain the results obtained in the field. Additional factors would have to be assumed for a complete explanation.

The conclusion that different factors control the reaction of the seedlings in the greenhouse and the mature plants in the field is in agreement with the work of Hayes and Aamodt (17) and Goulden, Neatby, and Welsh (15).

HEADING PERIOD

It was impossible to make a careful study of the time of heading in the fall-sown material, as many plants winterkilled. Early heading is an important character in winter wheat, however, and notes were taken to determine whether some of the hybrids were as early as or earlier than Minhardi in time of heading. A single date was recorded for each row, being the date when heading was general in the row. The data from the two stations are presented in Table 27.

In the material grown at St. Paul the Minhardi checkrows headed from June 17 to June 24, with most of the rows heading between June 18 and June 21. Among the hybrids, heading started June 14 and continued until June 28. The mode and mean dates of heading of the hybrids are earlier than for the Minhardi parent. Of the surviving lines, 18.5 per cent headed before the earliest date for Minhardi, and 2.6 per cent after the latest date for Minhardi.

In Montana, Minhardi headed from June 22 to June 28, most of the rows heading between June 25 and June 27. The hybrid lines started heading on June 16 and continued until June 30. A total of 65.6 per cent of the hybrid lines headed before the earliest row of the Minhardi, and only 1.3 per cent of the hybrid lines headed later than the latest Minhardi row.

TABLE 27.—Date of heading of Minhardi and F₂ lines of H-44 and Minhardi wheat crosses grown from fall seeding at St. Paul, Minn., and Moccasin, Mont.

Variety or cross	Number of lines heading June—																Total number of lines	Mean date of heading— June	
	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29			30
St. Paul:																			
Minhardi.....				6	18	25	17	15	5	5	1							89	19.5±0.1
H-44 × Minhardi.....	1	11	23	67	49	45	13	8	3	3	1	5	1				230	18.1± . 1	
Minhardi × H-44.....	2	21	33	79	52	32	17	7	9	2	2	4	2		1		263	17.9± . 1	
Total hybrids.....	3	32	60	146	101	77	30	15	12	5	3	9	3		1		493	18.0± . 1	
Moccasin:																			
Minhardi.....									1		5	10	34	31	3		90	26.1± . 1	
H-44 × Minhardi.....			2	9	60	60	21	30	18	13	15	19	13	17	0	5	260	21.4± . 1	
Minhardi × H-44.....			5	88	92	35	24	33	31	24	9	7	13	6	5	2	324	20.2± . 1	
Total hybrids.....			7	47	142	85	45	63	49	37	24	26	26	23	11	7	593	20.7± . 1	

Many more hybrid lines were earlier than Minhardi at Moccasin than at St. Paul. There may be at least two explanations for this behavior. At Moccasin killing was less severe and more spring-growth habit types may have survived, these types tending to head earlier. It is known that under different environments varieties of wheat may head at relatively different periods, and it is possible that Minhardi heads relatively later at Moccasin than at St. Paul, thus giving a different standard of comparison.

The date of heading at St. Paul was correlated with the date of heading at Moccasin for 476 F_3 lines heading at both places. The coefficient $r = +0.468 \pm 0.024$ shows a tendency for the lines to react the same for date of heading at both stations. This correlation between date of heading for the hybrid lines grown at the two stations is slightly higher than that for winter hardiness at the two places, the latter correlation being $+0.416 \pm 0.023$.

COLOR OF COLEOPTILE

As the young wheat plant emerges from the soil its first foliage leaf is inclosed in the plumule sheath or coleoptile. Near the tip there is a slit through which the foliage leaf emerges. Percival (32) has described the coleoptile in some forms of wheat as pale green or colorless, while in others it is pink.

The coleoptiles of H-44 plants when emerging from the soil in the greenhouse have a rather distinct purple color. This color persists after the foliage leaves grow out of the coleoptile, and in some cases the base of the first leaf shows the purplish tinge. Minhardi, on the other hand, has a light-green coleoptile. In growing the hybrid plants for the laboratory freezing tests and for the greenhouse rust studies it was possible to obtain data on the color of the coleoptile of the parents and hybrids. The number of plants available for study in each of the hybrid lines varied from 12 to nearly 100, and in addition a large number of parent plants were classified. All the studies were made on F_2 material, but since the lines were selected at random, they probably are more accurate than if made on F_2 material only.

The development of coleoptile color proved to be extremely variable, apparently being considerably influenced by temperature and sunlight at the time of germination and emergence. Since pots of the same lines were grown at several different times, it was possible to obtain data that revealed the variability of the character under varying conditions. All the data for a given F_3 line were combined to determine its breeding behavior.

The plants were described and grouped in three classes—dark purple, light purple, and green. The plants of H-44 were classed as dark purple and light purple, there being 1,703 dark purple and 288 light purple. Minhardi plants, of which 2,203 were grown, were all classed as green. Out of 480 F_3 hybrid lines, 33 proved to be homozygous for green. The ratio of 447:33 deviates from a calculated 15:1 ratio by 3.0 ± 3.58 .

Although the expression of the purple color was somewhat variable, making classification difficult, the F_3 lines were classed into six groups, as shown in Table 28. The observed numbers are compared with calculated numbers based on a 2-factor difference. Observed and calculated data do not agree very well, the goodness-of-fit test giving

a value of $P=0.09$, indicating that 9 times in 100 trials a result as bad or worse would be expected from chance alone. The high χ^2 and low P values are caused by wide deviations in the true dark-purple and true light-purple groups and in the groups segregating for light purple and green. It is believed that these discrepancies were caused by difficulties of classification incident to the variable expression of the purple color. The homozygous green lines were distinct, and the expression of the green color was uniform, so it is believed that this group was properly classified. On this basis it seems evident that at least two genetic factors are needed to explain the results.

TABLE 28.—Breeding behavior for coleoptile color of 480 F_3 lines of H-44 and Minhardi wheat crosses compared with a calculated genotypic 1:2:4:4:4:1 ratio by the goodness-of-fit method

Breeding behavior for coleoptile color	Number of lines		O-C	$\frac{(O-C)^2}{C}$
	Observed	Calculated		
True dark purple.....	21	36	-9	2.70
True light purple.....	60	68	-10	1.67
Segregating dark purple to light purple.....	109	120	-11	1.01
Segregating dark purple to green.....	127	120	7	.41
Segregating light purple to green.....	140	120	20	3.33
True green.....	33	80	3	.80
Total.....	480	480		

$$\chi^2=9.42. P=0.09.$$

The following hypothesis is presented. Assuming as present in H-44 two duplicate dominant factors, cumulative in effect for dark-purple coleoptile ($P_1P_1P_2P_2$), and as present in Minhardi the recessive allelomorphs $p_1p_1 p_2p_2$ causing green coleoptile color, the F_1 would be $P_1p_1 P_2p_2$, while the F_2 genotypes and F_3 breeding behavior would be as follows:

F_2 genotype	Parts of 16	F_3 breeding behavior
$P_1P_1P_2P_2$	1	True for dark purple.
$P_1P_1 p_2p_2$	2	True for light purple.
$p_1p_1 P_2P_2$		
$P_1p_1 P_2p_2$	4	Segregating for dark purple and light purple.
$p_1P_1 P_2P_2$		
$P_1p_1 P_2p_2$	4	Segregating for dark purple, light purple, and green.
$p_1P_1 P_2p_2$		
$P_1p_1 p_2p_2$	4	Segregating for light purple and green.
$p_1p_1 P_2P_2$		
$p_1p_1 p_2p_2$	1	True for green.

This hypothesis gives the genotypic 1:2:4:4:4:1 ratio used in Table 28. The discrepancies between observed and calculated data have been previously explained as probably due to difficulties of classification due to the variable expression of the purple color. A 2-factor hypothesis, therefore, seems to give an adequate explanation of the segregation observed. These results are in agreement with those obtained by Goulden, Neatby, and Welsh (15) in an H-44 \times Marquis cross.

AWNEDNESS

The H-44 parent is awned, while Minhardi is classed as awnless, although there are short awnlets at the tip of the spike. The F_1 hybrid of this cross had slightly longer awnlets than the Minhardi parent. The F_2 plants were, therefore, described in three classes—awnleted like Minhardi, strongly awnleted like F_1 , and awned like H-44.

The data from F_2 plants obtained at Davis, Calif., in 1928 and at St. Paul in 1929 are given in Table 29. The Davis material was a true random sample, there being no elimination due to winterkilling or to plants failing to head. In this population there were 501 awnleted and strongly awnleted to 122 awned. The wide deviation from a 3:1 ratio, 33.75 ± 7.29 , was caused by a deficiency of awned plants. Inspection of the data shows that the separation of the F_2 material into homozygous awnleted and heterozygous or strongly awnleted classes also was not good, as too many were classed as awnleted.

TABLE 29.—Segregation for awn development of F_2 plants of H-44 and Minhardi wheat crosses

Cross	Number of plants			
	Awnleted	Strongly awnleted	Awned	Total
Davis, Calif., 1927-28:				
H-44 × Minhardi.....	94	146	53	293
Minhardi × H-44.....	106	155	69	330
Total F_2	200	301	122	623
St. Paul, Minn., 1928 (spring sown):				
H-44 × Minhardi.....	57	96	50	203
Minhardi × H-44.....	45	107	42	194
Total F_2	102	203	92	397

The F_2 material grown at St. Paul was not a true random sample, because the winter plants failed to head. In this material there were 305 awnleted to 92 awned, which deviated 7 ± 5.82 from a calculated 3:1 ratio. In this case the observed and calculated ratios agree reasonably well.

Data on breeding behavior for awn development were taken on all F_3 hybrid lines. This made possible a comparison of the F_2 classification with the F_3 breeding behavior and a correction of the F_2 classification.

The data in Table 30 show that in F_2 it was difficult to separate the homozygous from the heterozygous awnleted types. Of the 199 plants classed in F_2 as awnleted, 43 produced segregating progeny in F_3 , while 12 of the 301 plants classed as strongly awnleted bred true in F_3 . All of the plants classed as awned in F_2 bred true in F_3 .

Correcting the F_2 ratio of the Davis material on the basis of F_3 breeding behavior and comparing the observed numbers with a calculated 1:2:1 ratio by the goodness-of-fit method gives a value $P = 0.008$. (Table 31.) This very low probability is due to the small number of awned plants in F_2 , although all of these when grown bred true.

The F_2 generation grown at St. Paul, while not a true random sample, did not show this lack of awned plants. In spite of the apparent lack of agreement in the Davis F_2 material, caused by the deficiency of true-breeding awned lines, the fact that there was only one type of segregation in F_3 makes it almost certain that only a single genetic-factor difference controls the awn situation in this cross. It is possible that this poor fit, as well as those observed for some of the other characters, could be due in part to the abnormal chromosomal behavior of H-44, as reported by Elders (11). This single-factor difference is similar to the early results of Biffen (5), those of Hayes and Aamodt (17), Gaines and Singleton (14), Goulden, Neatby, and Welsh (15), and Clark and Quisenberry (9) in crosses between awnleted and awned wheats.

TABLE 30.—Breeding behavior for awn development of F_3 lines of H-44 and Minhardi wheat crosses compared with the F_2 awn classification

Classed in F_2 as—	Breeding behavior in F_3 lines			Total number of lines
	Awnleted	Segregating	Awned	
Awnleted.....	156	43		199
Strongly awnleted.....	12	289		301
Awned.....			122	122
Total.....	168	332	122	622

TABLE 31.—Comparison of the F_3 breeding behavior for awn development of H-44 and Minhardi wheat crosses with a calculated 1:2:1 ratio by the goodness-of-fit method

Breeding group	Number of lines		O-C	$\frac{(O-C)^2}{C}$
	Observed	Calculated		
Awnleted.....	168	155.5	12.5	1.00
Segregating.....	332	311.0	21.0	1.42
Awned.....	122	155.5	-33.5	7.22
Total.....	622	622.0		

$$\chi^2=0.64. \quad P=0.008.$$

CHARACTERS NOT ASSOCIATED

Throughout the foregoing presentation the more important associations of the characters have been presented and discussed. It was shown, for example, that winter-growth habit and cold resistance were associated, as well as date of heading of fall-sown material and hardness.

All data were taken so as to make it possible to study the association of the various characters. No relation was found between awn type and date of heading in the F_2 material grown from spring sowing at St. Paul. This study was limited, of course, to the plants that headed. In this same material no significant relation was found between rust reaction and date of heading. There was only a slight tendency for such association, and this was probably due to the fact that these later plants had a better chance to become infected, since

there was a greater abundance of inoculum present late in the season. There also was no relation between awn type and rust reaction in F_2 lines.

In the F_3 material there was no relation between awns and average hardness index. There was no relation in F_3 between growth habit and date of heading when fall sown. The purple coleoptile color of H-44 was not associated with seedling resistance to rust.

DISCUSSION

A study of the inheritance of hardness is difficult to conduct. If studied in the field the work must be done in a locality where differential killing can be obtained. If the winter is mild, very little or no killing will occur, depending upon the hardness of the material being studied. On the other hand, if the winter is very severe, with continued low temperatures and little or no snow covering, all of the material may be lost. Such conditions make necessary the growing of material at more than one place, and, for a thorough test, over a period of several years. No chemical test yet devised can be used satisfactorily as a substitute for actual freezing, either in the field or in the laboratory. The data here presented show that artificial freezing in the laboratory may be used on breeding material, with reasonable assurance of success. The correlation between survival from artificial freezing and survival from field experiments is fairly good, even though there is reason to believe that laboratory methods might be improved.

There are reasons why field and laboratory hardness tests may never completely agree. The laboratory freezing test gives a measure of the resistance to cold of a variety or a hybrid strain at the time the test is made. The weakness of the artificial test lies in the fact that it is very difficult to harden off the material thoroughly, in order to get an absolutely correct picture of the resistance of the strains to cold. No doubt varieties differ greatly as to their speed in hardening off and ability to build up resistance. Another disturbing factor is that in the field tests, while resistance to cold usually is of first importance, there are other factors, such as drought, soil blowing, and heaving, which cause winterkilling.

The data presented indicate a correlation between winter-growth habit and winter hardness. This relationship seemed to go still farther, since in general the earlier-heading spring types were less hardy than the later-heading spring types. This association was not complete, however, since early spring-habit lines were obtained that were more hardy than H-44. Winter-habit lines also were obtained that were less hardy than Minhardi. This fact is of practical importance in winter-wheat breeding work. For certain areas, especially in Montana and Minnesota, it is necessary to have a hardy winter-wheat variety, the date of maturity being of secondary importance. In southern Nebraska and in Kansas a successful variety should have both winter hardness and early maturity. The data indicate that the production of such a variety is difficult but not impossible. It does emphasize, however, the difficulty of breeding hardy adapted varieties for the more southern areas when the breeding operations are confined solely to those areas. The problem can be met, however, by dividing the seed of selected lines, growing part where a measure of winter hardness can be obtained and the other

part when there will be a true expression of time of maturity. From the two sets of data it should be possible to select among the early types adapted to the southern area those that are more winter hardy and vice versa.

SUMMARY

Crosses were made between H-44, a spring wheat, and Minhardi, a winter wheat, and the segregation for winter hardiness, winter-growth and spring-growth habit, rust reaction, and other plant characters was determined.

The field studies on winter hardiness were conducted at University Farm, St. Paul, Minn., and at Moccasin, Mont. At St. Paul the killing of the F_3 material was heavy, and there was a piling up at the less hardy end of the curve. In Montana, where killing was less severe, there was a piling up on the hardy end of the curve. The correlation between the hardiness of the F_3 lines at Moccasin and at St. Paul, however, was $+0.416 \pm 0.023$, showing that in general the same condition, chiefly low temperature, caused the killing at both places. The winter-hardiness character appears to be controlled by several genetic factors, the final expression being greatly influenced by the environment under which the material is grown.

In laboratory freezing tests the F_3 lines varied in cold resistance from the tenderness of the H-44 parent to the hardiness of the Minhardi parent, with a preponderance of tender lines. A correlation of $+0.713 \pm 0.031$ was obtained between cold resistance, as measured by the laboratory freezing test, and field survivals, showing that cold resistance was the principal character determining winter hardiness.

Growth-habit studies were conducted on F_2 and F_3 material. Limited F_2 data indicated a ratio of 15 having spring growth to 1 having winter-growth habit. A genetic explanation for growth-habit segregation in F_3 is suggested by assuming duplicate dominant factors for spring-growth habit, H-44 (spring) having the genotype *AABB* and Minhardi (winter) having the genotype *aabb*. This hypothesis gave an adequate explanation of the results obtained. The presence of a dominant factor or factors gives spring forms varying in earliness from those as early as H-44 to those which head very late.

A correlation was found between winter-growth habit and winter hardiness, as expressed by both field and laboratory tests. The association was not complete, since winter forms were obtained that were less hardy than Minhardi as well as spring forms that were more hardy than the spring parent.

Data on rust reaction in the field at St. Paul were none too satisfactory, since from the fall sowing many plants were killed and from spring sowing many plants failed to head. A single-factor difference for resistance and susceptibility was indicated by the F_2 results from the material grown from both fall and spring sowing. The F_3 studies, however, proved such an explanation to be inadequate. In addition to the major genetic factor involved, other minor modifying factors must be assumed to explain the reaction obtained.

There was little relation between the rust reaction of a line when fall sown and the same lines when spring sown, indicating the presence of different forms of rust or a different expression of the genetic factors due to the different length of the growing period.

In the greenhouse a segregation approximating 1 resistant, 2 segregating, and 1 susceptible was obtained from F_3 lines inoculated with

physiologic form 60 of stem rust. There was an indication of minor factors influencing the expression of rust reaction, even in the greenhouse. The behavior of the lines was the same when inoculated with form 36, showing that the same factor or factors control the reaction of the seedlings to these two forms of rust.

No close relation was found between the greenhouse-seedling reaction and the reaction of the mature plants in the field. It would seem that genetic factors, in addition to those controlling the reaction in the seedling stage, are necessary to explain the reaction in the mature-plant stage.

Data on the date of heading were obtained at both stations on the F_3 lines that survived the winter, a single note being taken on each row. At St. Paul the F_3 lines started heading before Minhardi and continued later. The mode for heading in the hybrids was earlier than the mode of the winter parent. At Moccasin, the hybrid lines started heading six days before Minhardi, the majority being headed before Minhardi started. The correlation between date of heading at St. Paul and at Moccasin was $+0.468 \pm 0.024$.

Greenhouse seedlings of H-44 have a purple-colored coleoptile, while seedlings of Minhardi have a green coleoptile. A ratio of 15 purple or segregating lines to 1 homozygous green line was obtained in the F_3 , indicating dominant duplicate factors. It is assumed that H-44 has the genetic constitution $P_1P_1 P_2P_2$ and Minhardi $p_1p_1 p_2p_2$.

H-44 is awned, while Minhardi is classed as awnless or awnleted. Segregation of this character indicates that a single genetic factor is involved.

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