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C. R. Rohde

C. F. Pulham

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C. R. Rohde
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C. R. Rohde and C. F. Pulham[2]

Interest in growing winter barley in the winter wheat areas of central and northwestern United States has increased considerably in recent years because of governmental acreage limitations on the growing of wheat.

Barley is one of the few crops which can be considered a fairly successful substitute for wheat in central and northwestern areas. Its culture is almost identical to that of wheat, making it possible for farmers to grow it with no major changes in their farming practices or machinery requirements.

Under conditions of little or no winterkill, winter barley generally produces higher yields of grain than does spring barley. However, the level of winter hardiness plant breeders have been able to attain in present winter varieties is much below that attained in winter wheat. The major hazard in growing winter barley is its lack of winter hardiness.

An important obstacle toward the development of winter barley varieties with a higher level of winter hardiness has been the deficiency of genetic information on this character. The primary objective of these studies was to obtain information on the genetics of the winter hardiness of a group of 18 winter barley varieties which originated from widely different geographic areas of the world. It was hoped that this information might be helpful in determining whether or not it would be possible for barley breeders to combine different genetic sources of winter hardiness and attain a higher level of hardiness than presently exists.

A major hindrance in the breeding of hardy winter barley varieties is the infrequency of the occurrence of winter field conditions that reliably evaluate the winter hardiness of varieties and new hybrids.

During many years conditions prevail, such as mild temperatures or a cover of snow, that even the most tender varieties survive, or temperatures and environmental conditions are so severe that all materials are winterkilled. A second objective of these studies was to determine whether or not two methods used somewhat successfully in the breeding of other crop plants might be useful in evaluating the winter hardiness of winter barley varieties. These were:

[2]C. R. Rohde, formerly Research Associate, Department of Agronomy, University of Nebraska, now Associate Professor of Agronomy, Pendleton Branch Experiment Station, Pendleton, Oregon. C. F. Pulham, formerly Assistant in Agronomy, University of Nebraska, now deceased.

(1) To make estimates of the amount of leaf damage that occurs during periods of low temperature in the winter.

(2) To determine the survival of field-hardened plants grown in greenhouse flats and frozen in a refrigerator.

A high correlation between the results of one or both of these methods and the winter survival observed in the field would make it possible for the breeder to make faster progress in developing winter hardy winter barley varieties.

LITERATURE REVIEW

The problem of winter hardiness in winter barley has been recognized for many years in the United States. In 1917 Kiesselbach and Ratcliff (12) stated that "Winter barley also lacks in hardiness, and for this reason is an unsafe and unsatisfactory crop . . . The development of a hardy strain of winter barley would doubtless be a valuable achievement." Literature dealing particularly with the inheritance of winter hardiness in winter barley is extremely limited, further emphasizing the need of this study. This review summarizes the advances which have been reported in the understanding of winter hardiness and cold resistance in wheat, oats, and barley. By far the greatest amount of information has been reported in wheat.

According to Smith (25), Schiemann, Andersson, and Ziegenbein concluded that cold resistance in barley was inherited in a quantitative manner. Andersson and Ziegenbein obtained transgressive segregates more cold-resistant than either parent. However, Smith stated that Tschermak considered winter hardiness to approach a 1:2:1 ratio in the F_2.

Poehlman (18) pointed out that Kearney, C. I. 7580, had the highest average survival in the 1949 and 1950 regional barley winter hardiness nurseries. According to Wiebe and Reid (31), this variety was a selection from a composite of hybrids of all possible single crosses of 13 barley varieties. At least 10 varieties of this group were winter varieties or exhibited a winter-like habit of growth. These varieties ranged in hardiness from some such as Wisconsin Winter and Tennessee Winter with only fair hardiness to tender types such as Orel, Winter Club, Esaw, and Trebi. This would indicate that through the proper combination of genetic factors, transgressive segregation can result in the production of winter barley varieties with a high level of winter hardiness, that is, higher than that of the most hardy parent.

Inheritance studies in oats by Coffman (8), Mather and Andersson (16), and Rosen, *et al.* (22) also indicated that cold resistance was inherited as a quantitative character. Mather and Andersson obtained hybrids which were more hardy than Grey Winter, the most winter hardy parent. Rosen, *et al.* observed hybrids with all gradations of hardiness, from those that were less hardy than the tender

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parent to those which were more hardy than the hardy parent. Coffman pointed out ". . . that further progress in breeding hardier oats may well be expected from crossing among present hardy varieties." He cited Wintok, a selection from a cross between Hairy Culberson and a hardy selection from Fulghum, C. I. 2500, as being more winter hardy than either parent. Wintok was the most hardy variety in the cooperative uniform winter hardiness nurseries in the period 1942-1946.

Numerous workers have reported studies on the inheritance of winter hardiness in winter wheat. In general, they found that winter hardiness was inherited as a quantitative character. However, it was a character which was greatly influenced by environment. Hayes and Aamodt (9), in crosses between Marquis, a spring variety, and Minturki and Minhardi, very hardy winter varieties, found the F_1 to be winter tender, winterkilling 100 percent. The average survival of the F_2 was about midway between that of the parents. The progeny of strong F_2 plants was, on the average, superior to the progeny of weak ones. They obtained F_3 and F_4 lines which appeared to be as hardy as the hardy parents, however, the frequency was quite low. They obtained a low correlation between the survival of the F_3 lines and the F_4 progeny of these lines, the r-value being $+0.19$. This low correlation was explained by the fact that tender plants in heterozygous lines would be winterkilled in the F_3 generation, with the result that the F_4 progeny from such lines would be substantially more winter hardy than the lines from which they came.

Carpenter (6) and Quisenberry (19) both observed that the average survival of F_3 lines, in relation to their parents, depended on the location of the experiments. Both observed that under conditions of severe winterkilling, the average survival of the F_3 lines was intermediate but closer to that of the tender parent, while under less severe conditions, the average survival was nearer that of the hardy parent. In contrast to the phenotypic dominance of low survival observed by Hayes and Aamodt, Martin (15) and Rosenquist (23) reported a tendency for hardiness to be phenotypically dominant. Worzella (33) reported lack of dominance in winter hardiness, that is, the survival of the F_1 was intermediate between that of the parents. Rosenquist, however, had a small percentage of crosses in which dominance was lacking, and some in which lack of hardiness or winter tenderness was dominant. It would appear that the expression of dominance depends on the parents involved and the conditions under which the tests were made.

Numerous research workers have observed transgressive segregation in their studies of winter hardiness in winter wheat. Worzella (33) and, according to Hayes and Aamodt (9), Nilsson-Ehle and Akerman in Sweden obtained hybrid lines which were more tender than either parent. The latter workers in Sweden and Quisenberry

and Clark (20) also report obtaining hybrid lines which were hardier than the more hardy parent. An excellent example of the exploitation of transgressive segregation in the production of winter hardy wheat varieties was the development of the varieties Minhardi and Minturki at Minnesota. These varieties are selections from the cross Turkey × Odessa. Both parental varieties are very hardy. However, an even higher level of hardiness was attained in Minhardi and Minturki.

The use of artificial freezing in evaluating cold resistance of wheat varieties has been used extensively by many research workers. Its use on barley and oats has been very limited. However, Mather and Andersson (16), working with winter oats in Sweden, obtained good agreement between the survival of winter oat varieties in artificial freezing tests and their survival in field tests. Artificial freezing tests conducted by Salmon (24) with a variety of winter barley, a variety of winter oats, and several varieties of winter rye indicated that cold resistance was the predominating factor in determining their adaptation and distribution.

Several workers (2, 10, 11, 14, 15, 19, 30, 34) have obtained rather high correlations between the field survival of winter wheat varieties and their survival in artificial freezing tests. Correlation coefficient values ranging from 0.58 obtained by Salmon (24), to 0.87 obtained by Weibel and Quisenberry (30), have been reported. These tests included all gradations of field hardening, various levels of artificial hardening, and material which was not hardened at all. Weibel and Quisenberry (30) obtained the highest correlation where they artificially froze field hardened material in December. They observed that varieties differed in their rate of attaining or losing hardiness. This was noted also by Anderson and Kiesselbach (2), Suneson and Peltier (28), Hill and Salmon (10), and Worzella and Cutler (34). This observation was used to explain the changes in rank of hardiness which often occur among varieties in field survival tests. Ausemus and Bamberg (4) reported results of artificial freezing tests which did not correlate well with field survival tests. They suggested that the low correlation may have been due either to the fact that the strains and varieties tested were all rather highly cold resistant or that field tests do not always bring out the true differences in cold resistance.

Factors, other than degree of hardening, which have been noted to cause a variation in the results from artificial freezing tests in wheat are stage of growth (14, 17, 29, 34), time of freezing whether day or night (14, 24), fertility of soil in which plants were grown (34), amount of Hessian fly infestation in seedlings (34), quickness with which plants were frozen (2), speed with which plants were thawed out after freezing (2), and amount of moisture in the soil, when plants were frozen (19, 24).

Estimates of leaf damage in wheat after freezing have been used in artificial freezing tests as a measure of cold resistance. Laude (13), Aamodt and Platt (1), Salmon (24), and Martin (14) obtained correlation coefficients varying from 0.64 to 0.95 between the amount of leaf damage in artificial freezing tests and survival in field or survival in artificial freezing tests. This method also appears to be a fairly reliable method for evaluating the cold resistance of varieties of oats, barley and rye.

Recently, Andrews (3) reported the results of freezing sprouted seeds of winter wheat. The seeds were germinated at 22° for 16 hours; placed in a constant temperature room at 0.5° C. for four to six weeks; and then frozen at −15° C for 16 hours. After 2 to 3 weeks survival counts were made. With 20 varieties of winter wheat, a correlation coefficient of 0.85 was obtained between the survival from this test and the survival in field tests. This compares with a correlation coefficient of 0.75 obtained by Weibel and Quisenberry (30) in artificial freezing tests with seedling plants using this same group of varieties.

MATERIALS AND METHODS

In 1942, Wiebe[1], of the U. S. Department of Agriculture, initiated a study to assemble a group of winter barley varieties that contained the best sources of winter hardiness from the various winter barley growing areas of the world. This study was begun by surveying the 700 to 800 varieties of the world collection of winter barley varieties which had been collected by the Division of Plant Exploration and Introduction and maintained by the Crops Research Branch of the U. S. Department of Agriculture. This collection was fall sown at six experiment stations in 1942. On the basis of the results of these tests, the eight most winter hardy varieties representing the major source areas for winter hardiness in winter barley were selected for further comparison with the most hardy commercial varieties. This second group of tests was conducted in the crop years 1944-1945 and 1945-1946 as part of the Uniform Barley Winter Hardiness Nursery. A summary of the results of these studies is shown in Table 1. These studies indicated that the best source areas were Korea, China and Caucasus. The five foreign introductions, Suchow, Derbent, Caucasus, Kura, and Apsheron were added to this winter hardy group in order to provide a more adequate sampling of the better source areas for winter hardiness of winter barley. The commercial varieties Dicktoo, Reno, Kentucky I, and Randolph were selected because they represent the most hardy varieties in the United States. Randolph was added primarily because it possesses a combination of winter hardiness and the ability to pro-

Table 1. Percent winter survival of 17 winter barley varieties tested at several experiment stations in the United States during the years 1943, 1945 and 1946.

Variety	C.I. No.	Origin	5 station average (1942-43)	24 station average (1944-45)	28 station average (1945-46)	Grand average
Reno	6561	United States	78.0	87.5	82.5	82.7
Dicktoo	5529	United States	81.0	81.6	84.6	82.4
Kido	5145	Korea	81.0	79.8	85.7	82.2
Shonan	5255	Korea	76.0	78.0	82.6	78.9
Kentucky I	6050	United States	75.0	82.0	75.1	77.4
Meimi	5136	Korea	76.0	78.0	76.3	76.8
Khayyam	1117	United States	73.0	73.9	70.5	72.5
Sabbaton	1266	China	69.0	73.4	71.6	71.3
Peking	4202-2	China	67.0	73.3	67.9	69.4
Marm	5562	Caucasus	59.0	78.3	70.3	69.2
Hokudo	5176	Korea	62.2	71.6	69.0	67.6
Black Russian	2202	Caucasus	54.0	58.3	49.1	53.8
Suchow	5091	China	57.2			
Derbent	5008	Caucasus	51.0			
Caucasus	4334	Caucasus	49.0			
Kura	4306	Caucasus	43.0			
Apsheron	5557	Caucasus	25.0			

duce extremely vigorous growth when sown early in the fall. In order to have a 2-row variety in the group, Khayyam was added. Thus, a group of eighteen varieties was assembled.

Since the extensive series of tests showed that none of the foreign introductions were more winter hardy than the most hardy commercial varieties, it was hoped that this group of varieties contained diverse sources of germ plasm for winter hardiness. Furthermore, it was thought that a higher level of winter hardiness might be attained by the proper combination of genes from this presumably diverse group of genes controlling winter hardiness.

One of the objectives of the study herein reported was to obtain information as to the nature of the inheritance of the winter hardiness of this diverse group of eighteen varieties. To facilitate making the 153 possible crosses among these varieties in one season, a male sterile gene (ms), was introduced into each variety by the backcross method. This male sterile gene (ms), a result of a recessive mutation in a seed row of Composite Cross selection, C. I. 5368-1, at Davis, California in 1936, was found by Suneson (27), and has been used extensively by him and his co-workers. In 1940 male sterile plants of C. I. 5368-1 were crossed with Barbless, C. I. 5105. The F_1 of this cross was backcrossed to Barbless and male sterile plants of the F_2 of this cross were crossed to the eighteen varieties of winter barley used in this study. Each of these crosses were backcrossed to the original varieties three times and male sterile plants in the F_2 from the last backcross were used as female plants in crosses with each of the other original varieties. For example, the cross of Khayyam x Sabbaton, the male sterile derivative of Khayyam was crossed to the original variety Sabbaton, while in the cross of Black Russian x Khayyam, the male sterile derivative of Black Russian was crossed to the original variety Khayyam. These crosses were made in the greenhouse at Beltsville, Maryland, during the winter of 1949-50. The F_1's were then fall sown at Sacaton, Arizona in 1950-51 and an abundant supply of F_2 seed was harvested for all 153 crosses, except Marm x Kido and Reno x Kido.

Field plantings of the F_2 progenies and 18 parent varieties were made at five experiment stations in 1951-52 to obtain data on winter survival. The five stations were Manhattan and Hays, Kansas; Lafayette, Indiana; Urbana, Illinois; and Lincoln, Nebraska. Lincoln, Nebraska was the only station that was able to make plantings of all 153 crosses. Due to a shortage of seed of the two above mentioned crosses, 151 F_2 progenies and the 18 parent varieties were grown at the other four locations. At these four locations, the material was planted in single row plots, either eight or ten feet long and replicated twice. The rows were ridged at planting time in the Urbana test. At Lincoln, Nebraska, field plantings of the 153 F_2 progenies and the 18 parent varieties were made in ten-foot rows

with six replications. The six replications were divided into three groups of two replications each and treated as follows: (a) space-sown, seed sown at about one-half the normal rate (4 grams per row); (b) close-sown, seed sown at the normal rate (8 grams per row); and (c) close-sown, protected, normal seeding rate with a light soybean straw covering applied on November 10, 1951. These methods of seeding were used in order to maximize the chances of having differential survival.

Leaf damage notes were taken on the Lincoln, Nebraska field tests on November 10 and December 1, 1951 and on February 26, 1952. Temperatures of 11° F and 16° F occurred on November 2 and November 24, 1951, respectively. The first two readings gave estimates of the damage which occurred then. Unusually mild temperatures occurred during January and the first half of February. This was followed by a low temperature of 12° F on February 21. The last reading thus gave an estimate of the damage which occurred at that time. These notes were taken on the space-sown and non-protected close-sown replicates only. The scale used was 1 to 10, where 10 = no leaf damage.

The F_2 progenies and the parent varieties were also tested in the freezing chamber at Lincoln, Nebraska. About 30 seeds of each entry were planted in each replication on October 7 and 8, 1951. A randomized block design with three replications was used. The freezing chamber method used was similar to that described by Kiesselbach and Anderson (11) and Suneson and Peltier (28). The freezing chamber had a temperature variance of ± 2.0° C. The capacity was sufficient to permit the freezing of an entire replication at one time. The first replicate was frozen at − 16° C on December 3, and replications 2 and 3 were frozen at − 14° C on December 10 and 12, 1951, respectively. All replicates were in the freezing chamber for a 24 hour period. After freezing, the flats were placed immediately in the greenhouse which was maintained at a temperature of about 21° C. The survival was determined by making stand counts immediately after freezing and making counts of the live plants two weeks later.

Winter survival notes were taken on all field tests; however, differential winter survival did not occur at Manhattan, Kansas, and Urbana, Illinois in 1951-52, therefore, these data were not used in the analyses.

In the crop year 1952-53, bulk F_2 populations of each cross except Dicktoo x Kido and Kentucky I x Kido were grown at Sacaton, Arizona where no winterkilling occurred. Seed from these plantings was used to plant bulk F_3 populations and the parent varieties at North Platte and Lincoln, Nebraska, during the crop years 1953-54 and 1954-55. It was necessary to obtain bulk F_3 seed for the two crosses, Dicktoo x Kido and Kentucky I x Kido from the F_2 progenies grown at Lincoln in 1952. Winter survival notes were taken on all

four tests. Leaf damage notes were taken on this material at Lincoln, Nebraska on December 30, 1953, January 6, 1954 and March 2, 1955. The data from all experiments and all locations were analyzed by the analysis of variance. Missing plot values were computed for the two crosses which were not grown at Hays, Kansas and Lafayette, Indiana, using a procedure similar to that given by Cochran and Cox (7). Correlation coefficients were calculated for various combinations of the data.

Since all the crosses were segregating for the male sterility (ms) gene, this provided an opportunity to study the segregation of this character after the F_2 populations had been exposed to winterkilling. It is known that this gene character segregates in a simple 3:1 ratio, with normal fertility being dominant. A significant deviation from 3:1 in the F_2 would indicate that there may have been differential survival of the normal and male sterile plants. Such a deviation would suggest the possibility of a linkage between the male sterility gene and a gene or genes controlling winter survival.

Average plant height determinations and counts on number of tillers per plant were made on the normal and the male sterile plants. This made it possibe to determine whether or not the male sterility (ms) gene had an effect on these characters or whether or not linkage was involved.

The varieties Black Russian, Caucasus, and Derbent possessed the black lemma character (B,B) and Khayyam was a 2-row (V,V) variety, thus, it was possible to study the segregation of these characters also. Significant deviations from 3:1 for colored vs. non-colored lemma and for non-6 row vs. 6-row head types were assumed to indicate possible linkages of these genes with a gene or genes controlling winter survival. Studies also were made to determine whether or not these qualitative characters were associated or linked in their inheritance. The segregations and associations of the above mentioned characters were studied by the chi-square method. All studies of the qualitative characters, plant height and tillering were carried out on the field grown material at Lincoln, Nebraska.

The junior author was responsible for taking the notes on the tests grown at Lincoln, Nebraska, while data at the other locations were taken by the cooperators at those stations.

RESULTS AND DISCUSSION
Winter Survival of Bulk F_2 and Parents

Differential winter survival data were obtained on the 18 parent varieties and 151 bulk F_2 progenies from crosses of these varieties at Lafayette, Indiana and at Hays, Kansas, while at Lincoln, Nebraska similar data were obtained on the 18 parent varieties and all possible 153 bulk F_2 progenies. Since the material at Lincoln was handled in three different ways, data from five different experiments was avail-

Table 2. Winter survival data of 18 winter barley varieties, their bulk F_2 progenies, and the mid-parent averages obtained at Lincoln, Nebraska, Lafayette, Indiana and Hays, Kansas in 1952.[1]

Parent of crosses	Kentucky I	Randolph	Kido	Reno	Dicktoo	Meimi	Peking	Khayyam	Shonan	Marm	Suchow	Sabbaton	Hokudo	Caucasus	Kura	Derbent	Black Russian	Apsheron	Average of its 17 progenies
Kentucky I	*83.0*	86.3	88.0	87.2	39.3	92.2	88.5	77.7	80.3	82.2	85.2	84.3	85.3	67.2	72.1	76.3	74.5	55.5	80.7
Randolph	81.5	*80.0*	85.3	79.6	85.0	84.0	81.3	81.0	80.0	76.2	80.0	83.7	67.0	69.5	69.0	80.3	73.0	40.2	76.6
Kido	85.4	83.8	*87.7*	85.3²	79.2	78.7	78.2	70.9	83.2	84.4²	76.5	74.5	76.0	67.0	76.0	63.5	60.0	63.0	75.9
Reno	85.4	83.9	87.8	*87.8*	85.8	80.5	82.3	73.8	79.5	81.5	76.5	79.5	73.5	66.3	58.5	70.5	65.5	49.0	75.0
Dicktoo	88.0	86.5	90.4	90.4	*93.0*	76.0	89.0	77.8	84.0	76.0	79.5	68.0	67.5	85.5	81.2	49.2	62.5	37.0	74.9
Meimi	86.1	84.6	88.4	88.5	91.1	*89.2*	69.0	78.5	81.0	84.5	77.5	71.5	78.0	63.8	71.0	32.3	67.3	71.5	74.0
Peking	75.3	73.8	77.6	77.7	80.3	78.4	*67.6*	79.2	82.5	84.0	81.5	73.8	76.0	44.2	62.7	74.0	51.0	51.2	73.4
Khayyam	79.8	78.4	82.2	82.2	84.8	83.0	72.2	*76.7*	80.8	78.0	69.5	79.0	81.7	55.2	65.5	64.0	63.5	60.0	72.7
Shonan	84.5	83.0	86.8	86.9	89.5	87.6	76.8	81.4	*86.0*	87.6	64.0	78.0	65.5	78.2	67.5	52.0	51.6	35.5	72.4
Marm	77.0	75.5	79.4	79.4	82.0	80.1	69.3	73.8	78.5	*71.0*	75.5	75.0	75.0	60.7	63.7	52.5	45.5	41.7	71.9
Suchow	77.4	75.8	79.7	79.8	82.4	80.4	69.6	74.2	78.8	71.4	*71.7*	76.5	75.0	67.5	62.5	62.5	71.5	40.0	71.8
Sabbaton	70.8	69.2	73.1	73.2	75.8	73.8	63.0	67.6	72.2	64.8	65.1	*58.5*	75.5	64.5	60.7	67.5	35.7	31.0	69.3
Hokudo	75.0	73.5	77.4	77.4	80.0	78.1	67.3	71.8	67.5	69.0	69.4	62.8	*67.0*	57.2	51.0	55.0	49.6	60.0	68.8
Caucasus	54.2	52.7	56.6	56.6	59.2	57.3	46.5	51.0	55.7	48.2	48.6	42.0	46.2	*25.4*	36.1	52.7	31.9	18.7	58.0
Kura	52.8	51.2	55.1	55.2	57.8	55.8	45.0	49.6	54.2	46.8	47.1	40.5	44.8	24.0	*22.5*	26.1	34.2	1.4	56.4
Derbent	41.5	54.2	58.1	58.2	60.8	58.8	48.0	52.6	57.2	49.8	50.1	43.5	47.8	27.0	25.5	*38.5*	21.9	5.4	53.3
Black Russian	48.0	46.6	50.4	50.4	53.0	51.2	40.4	44.9	49.6	42.0	42.4	35.8	40.0	19.2	17.8	20.8	*13.1*	10.3	51.1
Apsheron	46.2	44.8	48.6	48.6	51.2	49.4	38.6	43.1	47.8	40.2	40.6	34.0	38.2	17.4	16.0	19.0	11.3	*9.5*	39.5
Average of 17 mid-parent values	71.1	70.5	74.2	74.2	76.7	74.9	64.7	69.0	73.4	66.3	66.6	60.4	64.4	44.8	43.5	45.5	39.0	37.4	

[1]The values above the diagonal are the average survival of the bulk F_2 progenies, the values below the diagonal are the average survival of the parents of each cross. The italicized values are those of the varieties themselves.

²Each average is based on four calculated values and the average of six replications at Lincoln, Nebraska.

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able to evaluate this material. In Table 2 a summary is given of the average winter survival of the parents and progeny obtained in these five tests. A summary of the average survival of the parents or mid-parent value of each cross is also presented in this table. The most winter hardy varieties were Dicktoo, Meimi, Reno, Kido, Shonan, Kentucky I, and Randolph. This agrees very well with data from the more extensive tests presented in Table 1. With the exception of Shonan, the bulk F_2 progenies of this group of varieties also had the highest average survival. The average survival of the progenies of Shonan probably were not significantly different from the progenies of some of the other varieties of this group.

The correlation coefficient between the average survival of the parents of each cross, or mid-parent value, and the average survival of their bulk F_2 progenies for the 153 crosses was 0.83. The correlation coefficient between the average survival of each variety, itself, and the average survival of its seventeen crosses for all 18 varieties was 0.95. These high values indicate that, on the average, the performance of the variety was a good measure of how its progeny would perform as measured by its bulk F_2 progeny. Furthermore these high correlation coefficients indicate that the primary gene action is probably additive, even though it is recognized that much of the gene effects due to dominance and epistasis would be reduced in the F_2 generation.

In Table 3 is a summary of the analysis of variance of this group of experiments. Highly significant[1] differences occurred among the experiments, among the crosses, and among the parent varieties. A highly significant difference occurred between the average survival of the parent varieties and the average survival of the bulk F_2 progenies. The average survival of the parent varieties was 62.1 percent and that

[1] Differences at the 5 percent level will be described as significant and those at the 1 percent level as highly significant throughout this paper.

Table 3. **The analysis of variance of the winter survival data obtained on 18 winter barley varieties and 153 bulk F_2 progenies of all possible single crosses of these varieties tested in five experiments in Nebraska, Kansas, and Indiana in the crop year 1951-1952.**

Source of variation	Degrees of freedom		Mean squares
Experiments	4		44,234.36**
Replications within experiments	5		1,777.72**
Entries	170		3,682.04**
Among crosses	152		3,166.15**
Among lines		17	22,046.39**
Within lines		135	788.64**
Among parents	17		8,233.54**
Parents vs. crosses	1		4,721.34**
Entries x experiments	680		314.17*
Error	846[1]		271.89

[1] Four missing plots calculated.
* F-value significant at the 5 percent level.
**F-value significant at the 1 percent level.

of the bulk F_2 progenies was 67.5 percent. This indicates that, on the average, genes for higher winter survival in this group of varieties tend to be at least partially phenotypically dominant to those for low winter survival. However, a close examination of the results in Table 2 shows that the degree of dominance varies from the possibility of complete dominance for high winter hardiness to complete dominance for winter tenderness. One hundred three of the 153 progenies had higher average survival values than that of the average of their parents. Of these 103 progenies, 34 had survival values higher than their high parent. These results can be explained by a complementary interaction of dominant or partially dominant factors for high winter survival resulting in many genotypes having a higher level of winter hardiness than the most hardy parent. These results might also be explained by an overdominance action of the genetic factors for high winter survival. Varieties which had several progenies that had average survivals above that of the high parent were Sabbaton, Peking and Kentucky I. The most extreme example was that of the cross Marm x Peking whose F_2 survival was 84.0 percent, while the survival of Marm was 71.0 percent and that of Peking was 67.6 percent.

In the group of progenies whose average survival was below that of the average of their parents, 19 progenies had average survival values below that of their low parent. This indicates that in some progenies most of the genetic factors for low winter survival were completely or partially phenotypically dominant. Varieties which had several progenies in this category were Shonan, Reno, and Kido. The most extreme example in this case was the F_2 progeny of the cross Meimi x Kido whose average survival was 78.7 percent, that of Meimi was 89.2 percent and that of Kido was 87.7 percent.

Between 15 and 16 of the 17 progenies from the varieties Marm, Caucasus, Kura, Kentucky I, Peking, and Black Russian had average survival values above that of the average of their parents. In the case of Kentucky I, the average survival of its 17 progenies was 80.7 percent, while the average survival of Kentucky I was 83.0 percent. This suggests that the gene or genes for the high winter hardiness possessed by this variety tend to be phenotypically dominant or possibly overdominant in most crosses. Normally, some of the dominance effects are lost in the F_2 which gives added support to this conclusion. Regarding the other varieties in this group whose winter hardiness is medium to low, the results indicate that most of them possess a recessive gene or genes for winter tenderness and the gene or genes they possess for winter hardiness are phenotypically dominant or partially dominant and that they tend to be complementary in their action with the factors for high winter survival possessed by the other varieties.

Most of the progenies of Dicktoo, Meimi, and Shonan had

average survivals below that of the average of their parents. The data from these crosses indicate that the gene or genes for the high winter hardiness possessed by these varieties either lack dominance, or are due to favorable epistatic effects, or are partially recessive to the gene or genes for winter tenderness possessed by the other varieties. Furthermore, these varieties may possess a gene or genes which inhibit the gene or genes for winter hardiness possessed by some of the other varieties. For example, the average survival of the cross Dicktoo x Kido was 79.2 percent, while the average of Dicktoo was 93.0 percent and that of Kido was 87.7 percent.

Results obtained from this latter group of varieties may be explained in another way. Since all crosses were made by using a male sterile derivative of the female parent of each cross, it is possible that some of the winter hardiness was lost in the development of the male sterile derivative and that the derivative was less winter hardy than the original variety. This especially would be likely to occur if the variety concerned contained a large number of genes for winter hardiness or if it contained a gene or genes for winter hardiness which were closely linked to its gene for normal fertility. Therefore, the progeny from crosses involving such a derivative would have a lower level of winter hardiness than if the original variety had been used as the parent. The male sterile derivates of these varieties were not tested so it is not possible to verify this explanation.

The analysis of variance in Table 3 also shows that the between line variance is much greater than the within line variance. According to Sprague and Tatum (26), the between line variance is a measure of the additive gene effects and the within line variance is a measure of non-additive gene effects, such as dominance and epistasis. These data indicate that additive gene action was predominant in these crosses. However, significant non-additive effects were also noted.

Winter Survival of Bulk F_3 and Parents

Differential winter survival data were obtained on the 18 parent varieties and the 153 bulk F_3 progenies at North Platte and Lincoln, Nebraska, in 1954 and in 1955. Thus, a total of four tests were available to evaluate this material. Apparently, in the cross Kido x Suchow, an error was made in the material tested, since this entry did not survive in any of the tests. These results were contrary to previous observations on the bulk F_2 progeny of this cross and to the performance of the parent varieties. These data were considered erroneous. In order to facilitate the analysis of the entire group of data, missing values were calculated, based on the average performance of these varieties in all other crosses in which each appeared.

In Table 4 is a summary of the average winter survival of mater-

Table 4. Winter survival data of 18 winter barley varieties, their bulk F_3 progenies, and the mid-parent averages obtained at Lincoln, and North Platte, Nebraska in 1954 and 1955.[1]

Parent of crosses	Kido	Dicktoo	Shonan	Kentucky I	Meimi	Marm	Reno	Khayyam	Randolph	Sabbaton	Peking	Hokudo	Suchow	Caucasus	Derbent	Black Russian	Kura	Apsheron	Average of its 17 progenies
Kido	*69.4*	70.0	61.9	64.2	54.2	59.2	61.6	51.8	58.3	49.2	51.5	49.2	46.1[2]	38.8	38.1	43.9	45.2	41.9	51.8
Dicktoo	65.7	*70.7*	63.9	62.2	61.5	54.2	55.3	48.6	57.8	51.2	50.7	44.7	42.8	44.5	41.6	48.3	51.8	30.7	51.5
Shonan	63.3	62.6	*54.4*	61.1	57.7	57.7	58.7	55.1	51.8	50.2	54.7	44.0	45.2	48.1	39.1	38.9	43.2	29.7	50.7
Kentucky I	62.4	64.8	56.6	*58.9*	55.7	48.7	51.2	50.1	49.1	53.7	51.6	47.4	48.2	37.1	40.9	39.5	40.0	43.4	49.5
Meimi	62.0	62.6	54.5	56.8	*54.6*	58.6	50.7	49.8	51.9	42.2	50.2	45.5	42.9	42.0	33.7	41.7	40.7	46.4	48.6
Marm	58.8	59.5	51.4	53.6	51.4	*48.3*	46.7	51.5	46.4	51.8	47.7	45.3	48.7	37.6	39.3	37.7	38.8	33.0	47.3
Reno	64.1	64.8	56.6	58.8	56.7	53.6	*58.8*	42.7	45.2	48.7	42.8	38.2	49.2	36.2	41.3	37.8	30.7	30.2	45.1
Khayyam	57.6	58.3	50.2	52.4	50.2	47.1	52.4	*45.9*	43.0	47.1	48.7	46.9	43.5	38.1	39.6	38.8	34.7	36.6	45.1
Randolph	59.0	59.7	51.6	53.8	51.6	48.5	53.8	47.3	*48.7*	49.8	43.2	40.9	43.7	36.2	39.7	41.2	32.2	29.3	44.6
Sabbaton	56.0	56.7	48.6	50.8	48.6	45.5	50.8	44.3	45.7	*42.7*	47.0	47.0	42.3	40.7	42.1	28.7	36.8	24.7	44.3
Peking	56.0	56.7	48.6	50.8	48.6	45.5	50.8	44.3	45.7	42.7	*42.7*	48.4	42.4	29.2	40.9	36.4	36.3	30.8	44.3
Hokudo	52.1	52.8	44.6	46.8	44.7	41.6	46.8	40.4	41.8	38.8	38.8	*34.8*	37.2	39.9	38.9	29.6	31.7	32.9	41.6
Suchow	57.0	57.7	49.6	51.8	49.6	46.5	51.8	45.3	46.7	43.7	43.7	39.8	*44.7*	38.8	35.2	31.3	35.9	16.2	40.6
Caucasus	48.8	49.4	41.3	43.6	41.4	38.2	43.5	37.0	38.4	35.4	35.4	31.5	36.4	*28.2*	28.9	28.2	27.8	28.7	36.5
Derbent	50.8	51.5	43.4	45.6	43.4	40.3	45.6	39.1	40.5	37.5	37.5	33.6	38.5	30.2	*32.3*	30.2	27.2	14.3	35.9
Black Russian	49.0	49.7	41.6	43.8	41.6	38.5	43.8	37.3	38.7	35.7	35.7	31.8	36.7	28.4	30.5	*48.7*	27.1	21.5	35.3
Kura	46.8	47.5	39.4	41.6	39.4	36.3	41.6	35.1	36.5	33.5	33.5	29.6	34.5	26.2	28.3	26.5	*24.3*	13.5	34.9
Apsheron	36.4	44.4	36.2	38.5	36.4	33.2	38.4	32.0	33.4	30.4	30.4	26.4	31.4	23.2	25.2	23.4	21.2	*18.1*	29.6
Average of 17 mid-parent values	49.4	57.0	49.3	51.4	49.4	46.4	51.4	45.3	46.6	43.8	43.8	40.1	44.7	37.0	38.9	37.2	35.1	32.2	

[1]The values above the diagonal are the average survival of the bulk F_3 progenies and the values below the diagonal are the average survival of the parents of each cross. The italicized values are those of the varieties themselves.
[2]Calculated value.

ial in this group of tests. The varieties having the highest average survival were Dicktoo, Kido, Kentucky I, Reno, Meimi, Shonan and Randolph. These results were in close agreement with the average survival of these varieties in the F_2 studies and with the results of the tests shown in Table 1. With the exception of Reno and Randolph, the bulk F_3 progenies of this group of varieties had the highest average survivals. The correlation coefficient for the average survival of the parents of each cross or mid-parent value and the average survival of their bulk F_3 progeny was 0.86. The correlation coefficient between the average survival of each variety and the average survival of its 17 crosses for all varieties was 0.94. These data indicate that, on the average, the performance of a variety is a good indication of its performance in crosses as measured by its bulk F_3 progeny. The correlation coefficients obtained from the bulk F_2 data were almost identical with these, being 0.83 and 0.95, respectively. High correlation coefficients would be expected if the primary gene action were additive, with dominance and epistatic effects either absent or of minor importance. If these latter effects were absent, then the correlation between the survival of the bulk F_2 and the bulk F_3 progenies should be quite high. This correlation coefficient was 0.83. This compares with a comparable correlation coefficient of 0.91 for the average survival value of the parents tested in these two groups. The lower correlation coefficient for the progenies indicate that although there are gene effects other than additive effects in operation, additive effects are probably of major importance.

A summary of the analysis of variance of the bulk F_3 is given in Table 5. Highly significant differences in winter survival occurred among experiments, among crosses, among the parent varieties, and between the average survival of the bulk F_3 progenies and the average survival of the parent varieties. The average survival of the parent varieties was 44.8 percent while that of the bulk F_3 progenies

Table 5. The analysis of variance of the winter survival data obtained on 18 winter barley varieties and 153 bulk F_3 progenies of all possible crosses of these varieties tested at North Platte and Lincoln, Nebraska, in the crop years 1953-1954 and 1954-1955.

Source of variation	Degrees of freedom[1]			Mean squares
Experiments	3			701,373.52**
Replications within experiments	8			586.29**
Entries	169			1,357.70**
Among crosses		151		1,212.61**
Among lines			17	9,136.79**
Within lines			134	207.31**
Among parents		17		2,696.83**
Parents vs. crosses		1		499.79**
Entries x experiments	507			233.77**
Error	1352			70.08

[1] Missing plot values were calculated for the cross Kido x Suchow based on their average performance in all other crosses.
**F-value significant at the 1 percent level.

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was 43.2 percent. This does not agree with what was observed in the bulk F_2 tests. The bulk F_3 tests indicated that, on the average for all crosses, winter tenderness may be partially phenotypically dominant, while the bulk F_2 data indicated the presence of phenotypic dominance for high winter survival.

This observation can be explained in two ways. Since the bulk F_3 tests were conducted under more severe conditions than the F_2 tests, it is possible that the winter hardiness of the heterozygotes was less stable and, therefore, many of the heterozygotes succumbed under severe conditions. If the heterozygotes were killed in the severe tests and survived in the less severe tests, then, when such tests were averaged together, dominance for winter hardiness or winter tenderness would tend to be eliminated. Some evidence of this appeared in both sets of tests. For example, among the bulk F_2 tests the greatest amount of killing occurred in the Hays, Kansas test. In this test the average survival of the bulk F_2 progenies was 47.5 percent while that of the parents was 50.1 percent. Furthermore, in this group of tests, the least amount of killing occurred in the close-sown, protected test at Lincoln, Nebraska. In this test, the average survival of the bulk F_2 progenies was 79.4 percent while that of the parents was 69.1 percent. The difference between the average survival of the parents and the average survival of the bulk F_2 progenies in the Hays test was not statistically significant. However, this difference in the Lincoln test was statistically significant.

The most severe test of the bulk F_3 progenies was at North Platte in 1954. The average survival of the bulk F_3 progenies was 3.6 percent while that of the parents was 7.5 percent. The least severe test was at Lincoln, Nebraska, in 1955. The average survival of the bulk F_3 progenies was 89.7 percent while that of the parents was 88.3 percent. The difference between parents and progenies was highly significant in the North Platte test but was not significant in the Lincoln test. Therefore, both groups of tests tend to support the conclusion that the winter hardiness of the heterozygotes tends to break down under severe conditions. Since the average survival of the F_3 tests was below that of the F_2 tests, the difference in the dominance expressed in these two could be explained in this manner.

A second explanation was alluded to in the discussion of results of the bulk F_2 tests. This was the fact that the female parent in all crosses was a male sterile derivative of the variety and that the entire winter hardiness of the original varieties may not have been recovered in many of the male sterile derivatives. In all probability both explanations were operating simultaneously in these crosses.

It is possible also, that because of increased homozygosity of the bulk F_3 progenies as compared to the bulk F_2 progenies, phenotypic dominance and epistatic effects were reduced. Theoretically, however, these effects should only be reduced by about one-half as com-

pared to the F_2 and, therefore, should still be detectable in the F_3 generation. The analysis of variance in Table 5 indicates that significant non-additive gene effects occurred in this material. However, from a breeding standpoint, they appear to be relatively unimportant compared to the additive effects. In comparing the between line and within line variances of the two groups of tests, as shown in Tables 3 and 5, the between line variance is about 28 times as large as the within line variance in the F_2 tests and about 44 times as large in the F_3 tests. This is in agreement with theoretical expectations, whereby dominance and epistatic gene effects are reduced with each generation of self pollination.

In the bulk F_2 tests a preponderance of the crosses had average survivals above the average of their parents; however, in the bulk F_3 tests, only 60 of the 153 crosses had an average survival above that of their parents. Furthermore, the bulk F_2 tests of the progenies of Marm, Caucasus, Kura, Kentucky I, Peking and Black Russian indicated that winter hardiness tended to be partially or completely phenotypically dominant. In the bulk F_3 tests the progenies of Shonan, Peking, Sabbaton, Hokudo, and Kura indicated some tendency for winter hardiness to be partially to completely phenotypically dominant. Therefore, these two groups of tests together tend to support the conclusion that Peking and Kura possess genetic factors which result in winter hardiness being expressed as partially or completely phenotypically dominant.

In the bulk F_2 tests, the progenies of Dicktoo, Meimi, and Shonan indicated that the high winter hardiness of these varieties tended to be expressed as phenotypically recessive while the F_3 tests indicated that this was true of Reno, Suchow, Meimi, and Randolph. Therefore, these tests combined indicate that the moderately high winter hardiness of Meimi was either controlled by a preponderance of recessive genes or that in the crosses in which it was used as the female parent, its male sterile derivative was less hardy than was the original variety. The latter possibility seems very likely to have occurred with Dicktoo also because in the crosses in which the male sterile derivative of Dicktoo was used, the average survival of its bulk F_2 progenies was 9 percent below the average mid-parent survival. In the crosses in which Dicktoo was used as the pollen parent, the average survival of its bulk F_2 progenies was 4 percent higher than the average mid-parent survival. In the bulk F_3 tests, the average survival of its bulk F_3 progenies, where the male sterile derivative of Dicktoo was used as one parent, was 7 percent below the average mid-parent survival. In these same tests the average survival of its bulk F_3 progenies, where the original variety Dicktoo was used as the pollen parent, was 4 percent below the average mid-parent survival. Therefore, both sets of data tend to indicate that the male

sterile derivative of Dicktoo was probably less winter hardy than the original stock of Dicktoo.

The conclusion that the use of the male sterility factor in the production of these hybrids resulted in a loss of some factors for winter hardiness is supported by data from the U. S. Department of Agriculture 1958 Barley Winter Hardiness nurseries (5). As mentioned previously, seed of the bulk F_2 progenies was grown at Urbana, Illinois, in 1952. However, winterkilling was so severe that it was not possible to obtain reliable differential winterkilling data. Since the F_2 segregated for male sterility, seed was harvested from the male sterile heads because these kernels would be crosses among the surviving plants. These hybrid seeds were grown in Sacaton, Arizona, in 1952-53. A bulk sample from this material was planted at Madison, Wisconsin, in 1953-54, where winterkilling was again severe and seeds were again harvested from male sterile heads. This procedure was repeated for two more cycles. In 1958, plantings of the F_3 of the first three cycles and F_2 of the fourth cycle were compared with a planting of a bulk sample of the parent varieties in the U. S. Department of Agriculture Barley Winter Hardiness nursery. The bulk parent sample was made up of equal numbers of seed of each of the 18 original varieties. The average winter survivals were as follows:

> Bulk parental sample—72.7%
> ms Composite cross 1st cycle—66.0%
> ms Composite cross 2nd cycle—78.7%
> ms Composite cross 3rd cycle—83.2%
> ms Composite cross 4th cycle—83.4%

The average survival of the 1st cycle was somewhat below the parental bulk indicating that some of the winter hardiness of the original parents had been lost with the introduction of the male sterile factor.

This is not a serious difficulty in the use of this method as a breeding technique because every variety, except Kentucky I, was used in its original form in some of the crosses. Therefore, this reservoir of genes has the possibility of containing the genes for the maximum winter hardiness of all the original varieties, except with the possible exception of Kentucky I.

To summarize, a careful evaluation of the bulk F_2 and bulk F_3 winter survival data shown in Tables 2 and 4 indicates that no two varieties behaved similarly in all crosses. This indicates that each variety possesses a different combination of genes controlling winter survival. It is not possible to determine from these data, however, whether or not it would be possible to obtain a gene combination which would give a level of winter hardiness higher than that of Dicktoo, the variety having the highest average survival in these tests.

Table 6. Correlation coefficients showing the relationship between the average winter survival in the field of 18 winter barley varieties grown in nine individual experiments and their average survival in all nine experiments.

Experiment	Number of replications	r-value*
Lincoln, Nebraska, 1952		
Normal seeding rate	2	0.92
Normal seeding rate, seedlings protected	2	0.94
One-half normal seeding rate	2	0.87
Lafayette, Indiana, 1952	2	0.93
Hayes, Kansas, 1952	2	0.86
Lincoln, Nebraska, 1954	3	0.93
North Platte, Nebraska, 1954	3	0.76
Lincoln, Nebraska, 1955	3	0.85
North Platte, Nebraska, 1955	3	0.90

*All values are positive and are significant at the 1 percent level.

Correlation Studies Between Winter Survival Tests

These data provided an opportunity to compare the results of each test with the average of all tests. Correlation coefficients were computed from the data obtained on the parental varieties only and are shown in Table 6. All correlation coefficient values are high with the exception of the 1954 test at North Platte, Nebraska. Very severe killing occurred in this test with the less hardy varieties, Sabbaton, Black Russian, Kura, Caucasus, Derbent, Hokudo, Apsheron, and Marm, winterkilling 100 percent. The results of these tests indicate that two replications were sufficient to give a reliable evaluation of the varieties and that each test gave a fairly good indication of the winter hardiness of this group of winter barley varieties.

Leaf Damage Data on Bulk F_2 and Parents

Previous investigators have shown that in other crops a correlation often exists between the amount of leaf damage in freezing tests and the amount of winter hardiness a variety possesses. During the crop year 1951-52 there were three opportunities to take readings on the amount of leaf damage which occurred at Lincoln, Nebraska. These readings were not taken on the protected plots because the soybean straw tended to obscure the plants in these plots. Below normal temperatures occurred October 30 to November 7, 1951; and November 16 to November 25, 1951. The lowest temperature was 11° F on November 2 in the first period and 16° F on November 24 in the second period. Between these two periods temperatures reached as high as 68° F so that some growth occurred. Leaf damage readings were taken on November 10 and on December 1.

Abnormally mild weather occurred in 1952 during January and the first half of February with temperatures reaching as high as 58° F on January 31 and 65° F on February 11. About two inches of new growth occurred during this period. *Slightly below normal*

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Table 7. Mean leaf damage caused by cold temperature on 18 winter barley varieties, their bulk F$_2$ progenies and the mid-parent values obtained on November 10, December 1, and February 26 at Lincoln, Nebraska, in the crop year 1951-1952.[1]

Parent of crosses	Randolph	Kentucky I	Peking	Dicktoo	Kido	Meimi	Shonan	Reno	Marm	Suchow	Sabbaton	Hokudo	Khayyam	Caucasus	Kura	Derbent	Black Russian	Apsheron	Average of its 17 progenies
Randolph	*8.8*	8.4	8.8	8.9	8.6	8.6	8.2	8.1	7.8	8.2	8.2	7.9	8.0	7.4	7.6	7.7	7.7	7.1	8.1
Kentucky I	8.4	*8.0*	8.2	8.4	8.3	8.4	7.8	7.8	8.1	8.0	7.6	8.0	7.4	7.2	7.3	7.8	7.7	6.8	7.8
Peking	8.6	8.2	*8.3*	8.1	7.8	7.8	7.8	7.7	7.9	7.7	7.7	7.3	7.2	7.1	6.7	7.2	6.6	6.8	7.6
Dicktoo	8.5	8.1	8.3	*8.2*	7.4	7.2	7.9	8.1	7.8	7.4	7.0	7.0	7.2	7.9	7.2	6.0	6.9	6.4	7.5
Kido	8.5	8.0	8.2	8.2	*8.1*	7.0	7.9	7.7	8.0	7.2	7.8	7.2	7.2	7.2	7.2	6.9	6.8	6.3	7.4
Meimi	8.4	8.0	8.1	8.1	8.0	*7.9*	7.7	7.8	7.9	7.6	7.1	7.6	7.2	7.2	7.1	5.7	7.0	6.9	7.4
Shonan	8.1	7.7	7.9	7.8	7.8	7.7	*7.4*	7.5	8.0	7.4	7.4	6.8	6.9	7.3	6.9	6.9	6.6	6.1	7.4
Reno	8.3	7.8	8.0	8.0	7.9	7.8	7.5	*7.7*	7.1	7.5	7.4	6.9	7.1	6.7	7.0	6.8	7.2	6.3	7.3
Marm	8.0	7.5	7.7	7.7	7.6	7.5	7.3	7.4	*7.1*	7.3	7.3	7.6	7.3	6.5	6.5	6.3	6.0	6.2	7.3
Suchow	8.0	7.6	7.8	7.7	7.6	7.5	7.3	7.4	7.1	*7.2*	7.1	7.1	6.4	7.0	7.2	6.9	6.7	5.4	7.2
Sabbaton	7.8	7.4	7.6	7.5	7.5	7.4	7.1	7.3	7.0	7.0	*6.8*	7.5	7.4	6.5	6.9	7.1	5.4	5.5	7.1
Hokudo	8.0	7.5	7.7	7.7	7.6	7.5	7.3	7.4	7.1	7.1	7.0	*7.1*	7.2	6.6	6.6	6.7	6.1	6.8	7.1
Khayyam	7.8	7.4	7.6	7.5	7.5	7.4	7.1	7.3	7.0	7.0	6.8	7.0	*6.8*	6.6	6.8	6.8	6.4	6.2	7.0
Caucasus	7.4	7.0	7.1	7.1	7.0	6.9	6.7	6.8	6.5	6.5	6.4	6.5	6.4	*5.9*	5.9	5.7	5.6	5.8	6.7
Kura	7.3	6.9	7.1	7.0	7.0	6.9	6.6	6.8	6.5	6.5	6.3	6.5	6.3	5.9	*5.8*	5.9	5.6	3.9	6.6
Derbent	7.3	6.9	8.0	7.0	6.9	6.8	6.6	6.7	6.4	6.5	6.3	6.4	6.3	5.8	5.8	*5.8*	5.5	4.1	6.5
Black Russian	7.2	6.8	6.9	6.9	6.8	6.7	6.5	6.6	6.3	6.3	6.2	6.3	6.2	5.7	5.7	5.6	*5.5*	4.8	6.4
Apsheron	6.5	6.0	6.2	6.2	6.1	6.0	5.8	5.9	5.6	5.6	5.5	5.6	5.5	5.0	5.0	4.9	4.8	*4.1*	6.0
Average of 17 mid-parent values	7.9	7.5	7.6	7.6	7.5	7.5	7.2	7.3	7.1	7.1	6.9	7.1	6.9	6.5	6.5	6.4	6.3	5.7	

[1]The leaf damage ratings are on a scale of 1 to 10. 1 = all leaves severely damaged; 10 = no leaf damage. The scores above the diagonal are those for the bulk F$_2$ progenies; those below the diagonal are the mid-parent scores; and the italicized scores are those for the parents themselves. Each score is the average of 12 readings.

temperatures occurred during the period February 20 to February 25, 1952 with the lowest temperature of 12° occurring on February 21. Leaf damage readings were taken on February 26.

Correlation coefficients between the readings obtained at the different dates were as follows: November 10 and December 1, r = 0.85; November 10 and February 26, r = 0.75; and December 1 and February 26, r = 0.76.

In Table 7 is a summary of the average readings obtained for the three dates leaf damage observations were made. The varieties which had the least amount of leaf damage were Randolph, Peking, Dicktoo, Kido, Kentucky I, and Meimi. The progenies of these varieties and those of Shonan also had the least average leaf damage. Sixteen progenies had average leaf damage readings above 8.0. Nine of these progenies had Randolph as one parent and 6 had Kentucky I as one parent. Peking, Dicktoo, and Kido, as varieties, had average leaf damage readings above 8.0 but nearly all of their progenies averaged below 8. The correlation coefficient between the average leaf damage of the parents of each cross, or mid-parent value, and the average of their bulk F_2 progeny for all crosses was 0.87. Furthermore, the correlation coefficient for the average of the variety itself and the average of its 17 progenies for all the varieties was 0.97. Both correlation coefficients indicate that the amount of leaf damage that occurs in a variety is a good indication of the amount of damage that will occur in its bulk F_2 progeny.

The mean square values obtained from the analysis of variance of these tests are given in Table 8. Highly significant differences occurred among dates of taking readings, among the crosses, and among the parent varieties. This analysis also indicates that the crosses and varieties did not behave the same relative to each other on the different dates readings were taken. One possible reason for

Table 8. The analysis of variance of readings of leaf damage caused by cold temperature on 18 winter barley varieties and 153 bulk F_2 progenies of all possible single crosses of these varieties tested at Lincoln, Nebraska, in the crop year 1951-52.

Source of variation	Degrees of freedom		Mean squares
Dates	2		3090.81**
Replications	3		6.26
Error (a)	6		5.90
Entries	170		9.31**
Among crosses	152		8.41**
Among lines		17	60.86**
Within lines		135	1.80**
Among parents		17	17.83**
Parents vs. crosses		1	1.83
Entries x dates	340		1.25**
Error (b)	1530		0.54

** F-value significant at the 1 percent level.

Table 9. The average leaf damage caused by cold temperature in 18 winter barley varieties at three dates at Lincoln, Nebraska, during the crop year 1951-52.[1]

Variety	Leaf damage value			
	November 10 1951	December 1 1951	February 26 1952	Average
Randolph	9.8	9.8	7.0	8.8
Peking	9.8	9.5	5.8	8.3
Dicktoo	9.8	9.0	6.0	8.2
Kido	9.8	8.8	5.8	8.1
Kentucky I	9.0	9.2	5.8	8.0
Meimi	9.5	8.2	6.0	7.9
Reno	9.0	8.0	6.0	7.7
Shonan	9.5	7.8	5.0	7.4
Suchow	9.2	7.0	5.2	7.2
Marm	9.0	7.0	5.2	7.1
Hokudo	9.0	7.2	5.0	7.1
Khayyam	8.8	6.8	5.0	6.8
Sabbaton	9.0	8.0	3.5	6.8
Caucasus	8.5	6.0	3.2	5.9
Kura	8.8	6.0	2.8	5.8
Derbent	8.0	6.5	2.8	5.8
Black Russian	8.2	6.0	2.2	5.5
Apsheron	7.0	3.5	1.8	4.1
Average	9.0	7.5	4.7	

[1]Readings are based on a scale of 1 to 10. 1 = all leaves severaly damaged; 10 = no leaves damaged.

this is that the damage which was recorded on November 10 had an average reading of 8.9, that on December 1 an average of 7.7, and that on February 26 an average of 4.8. Since the damage recorded on November 10 was at a very low level, it is possible that this test was not able to distinguish between progenies which differ only slightly in their leaf damage. These small differences may be detectable only under conditions of severe freezing such as was measured on February 26. Furthermore, it has been observed in winter wheat that varieties differ in the speed with which they gain or lose their hardiness; possibly this is also true in winter barley. When weather conditions change and cold damage occurs, some varieties are found to be relatively much less hardy than they were previously. For example, the data in Table 9 show that the ranking of Shonan was fifth among the parent varieties on November 10, but on February 26 it had dropped to tenth. Likewise, the ranking of Reno was ninth on November 10 and fourth on February 26. However, the ranking of other varieties was about the same at all three dates. Randolph ranked first at all three dates and Apsheron ranked last or eighteenth at all three dates.

It should also be noted in Table 8 that the average leaf damage of the bulk F_2 progeny was not significantly different from that of the parents. This would indicate that, for the average of all crosses, the factors controlling the amount of leaf damage lacked dominance.

However, a close look at Table 7 indicates that the varieties are not consistent in this respect. Kentucky I, Marm, and Sabbaton have several progenies whose average leaf damage was equal to or slightly less than that of the parent with the least amount of leaf damage. This suggests that the leaf damage resistance of Kentucky I and Marm is phenotypically dominant in certain crosses and that the lack of resistance of the variety Sabbaton is phenotypically recessive. On the other hand, Peking, Kido, Dicktoo, and Meimi had several progenies whose average leaf damage was equal to or greater than the parent with the greater amount of leaf damage. This would indicate that the tenderness of these varieties was phenotypically dominant in many of their crosses. However, as was observed in the winter survival results, all gradations of dominance and recessiveness for resistance to leaf damage by cold were observed among the various progenies.

The analysis of variance given in Table 8 also shows that both additive and non-additive gene effects, as measured by the between and within line variances, were observed in the inheritance of resistance to leaf damage. The additive gene effects were much larger than the non-additive gene effects.

Leaf Damage Data on Bulk F_3 and Parents

It was also possible to obtain leaf damage readings on the bulk F_3 progenies and parents at Lincoln, Nebraska, on December 30, 1953, January 6, 1954 and March 2, 1955. Temperatures of 3° and 6° F on December 22 and 23, 1953, respectively; and 1° F on February 24, 1955 provided opportunities for determining leaf damage. These temperatures occurred with no snow cover.

The correlation coefficients between the results obtained at the different dates were highly significant and are shown in Table 10. These r-values show that the correlations between dates was not high, except for the first dates which were taken so close together that the second date probably was strongly influenced by the damage that occurred on the first date. However, they were considered sufficiently high so that the data for the three dates were averaged together for a general evaluation of the material.

Table 10. Correlation coefficients between leaf damage readings taken December 30, 1953, January 6, 1954, and March 2, 1955 on 18 winter barley varieties and 153 bulk F_3 progenies at Lincoln, Nebraska.

Readings correlated	r-values[1]	
	Parents	F_3
December 30, 1953 and January 6, 1954	0.94	0.92
December 30, 1953 and March 2, 1955	0.77	0.58
January 6, 1954 and March 2, 1955	0.79	0.63

[1]All r-values are significant at the 1 percent level.

Table 11. Mean leaf damage caused by cold temperature on 18 winter barley varieties, their bulk F₃ progenies, and the mid-parent values obtained on December 30, 1953, January 6, 1954, and March 2, 1955 at Lincoln, Nebraska.[1]

Parents of crosses	Kentucky I	Dicktoo	Kido	Randolph	Suchow	Meimi	Shonan	Hokudo	Marm	Peking	Khayyam	Kura	Sabbaton	Caucasus	Reno	Black Russian	Derbent	Apsheron	Average of its 17 progenies
Kentucky I	*4.9*	6.0	5.5	5.6	5.8	5.4	5.1	4.7	4.4	5.0	4.3	4.4	4.7	4.2	5.1	3.9	4.5	3.8	4.9
Dicktoo	5.8	*6.8*	4.8	4.7	5.8	5.1	6.9	4.7	4.2	5.4	5.1	5.4	4.3	4.3	4.1	5.0	3.3	2.3	4.8
Kido	5.6	6.6	*6.3*	5.2	4.6²	5.2	5.4	4.8	5.6	4.8	4.6	4.7	5.2	4.2	4.2	4.2	3.7	3.7	4.7
Randolph	5.2	6.1	5.9	*5.5*	5.4	4.6	4.3	4.6	4.2	4.7	5.3	4.1	5.0	4.2	3.9	4.4	3.8	3.6	4.6
Suchow	4.7	5.7	5.4	5.0	*4.6*	4.9	4.1	5.0	4.7	4.1	3.7	5.0	4.4	4.8	4.3	3.9	4.0	2.4	4.5
Meimi	5.0	5.9	5.7	5.3	4.8	*5.1*	4.3	5.3	4.6	4.8	4.6	4.8	3.8	4.3	4.0	3.9	2.8	3.8	4.5
Shonan	5.8	6.7	6.5	6.1	5.6	5.9	*6.7*	4.3	4.7	4.2	4.3	4.9	4.0	4.7	4.7	2.9	3.7	3.1	4.5
Hokudo	4.7	5.6	5.4	5.0	4.5	4.8	5.6	*4.4*	4.8	4.5	5.2	4.4	4.2	4.6	3.6	3.4	3.7	3.6	4.4
Marm	4.6	5.6	5.3	4.9	4.4	4.7	5.5	4.4	*4.3*	4.7	4.1	4.2	4.6	4.2	4.4	3.3	3.6	3.3	4.3
Peking	4.7	5.6	5.4	5.0	4.5	4.8	5.6	4.4	4.4	*4.4*	4.6	4.0	4.3	3.4	3.9	3.2	3.9	3.9	4.3
Khayyam	4.5	5.4	5.2	4.8	4.3	4.6	5.4	4.3	4.2	4.3	*4.1*	3.9	3.9	3.3	3.7	3.3	3.5	3.4	4.3
Kura	3.9	4.9	4.6	4.2	3.8	4.0	4.8	3.7	3.6	3.7	3.5	*2.9*	3.7	3.1	3.3	2.9	3.5	1.8	4.2
Sabbaton	4.6	5.6	5.4	4.9	4.5	4.7	5.5	4.4	4.4	4.4	4.2	3.7	*4.4*	6.3	3.3	2.3	3.4	2.5	4.0
Caucasus	4.0	4.9	4.7	4.3	3.8	4.1	4.9	3.8	3.7	3.8	3.6	3.0	3.7	*3.1*	3.2	3.6	3.4	3.1	3.9
Reno	4.4	5.4	5.2	4.8	4.3	4.5	5.3	4.2	4.2	4.2	4.1	3.5	4.2	3.5	*4.0*	3.2	3.5	2.3	3.8
Black Russian	3.9	4.9	4.6	4.2	3.8	4.0	4.8	3.7	3.6	3.7	3.5	2.9	3.7	3.0	3.5	*2.9*	3.2	3.0	3.5
Derbent	4.1	5.1	4.8	4.4	3.9	4.2	5.0	3.9	3.8	3.9	3.7	3.1	3.9	3.2	3.7	3.1	*3.3*	1.7	3.5
Apsheron	3.7	4.6	4.4	4.0	3.5	3.8	4.6	3.5	3.4	3.5	3.3	2.7	3.4	2.8	3.2	2.7	2.9	*2.5*	3.0
Average of 17 mid-parent values	4.7	5.6	5.3	4.9	4.5	4.8	5.5	4.5	4.4	4.5	4.3	3.7	4.4	3.8	4.2	3.7	3.9	3.5	

[1]Readings are based on a scale of 1 to 10. 1 = all leaves severely damaged; 10 = no leaves damaged. The scores above the diagonal are those for the bulk F₃ progenies; those below the diagonal are the mid-parent values; and the italicized scores are those for the parents themselves. Each score is the average of 9 values.

²Missing plot value calculated based on the average reading of Kido and Suchow in all other crosses.

Table 12. The analysis of variance of readings of leaf damage caused by cold temperature on 18 winter barley varieties and 153 bulk F_3 progenies of all possible single crosses of these varieties when tested at Lincoln, Nebraska, in the crop years 1953-1954 and 1954-1955.

Source of variation	Degrees of freedom[1]		Mean squares
Years	1		1673.52**
Reading dates on 1953-1954 test	1		14.99**
Replications within years	4		3.02**
Replications in 1954		2	3.46**
Replications in 1955		2	2.59**
Dates x replications in 1954	2		0.33
Entries	169		7.39**
Among crosses	151		6.56**
Among lines		17	41.36**
Within lines		134	2.14**
Among parents	17		14.51**
Parents vs. crosses	1		11.03**
Entries x dates	338		0.97**
Error	1014		0.55

**F-value significant at the 1 percent level.

[1] Missing plot values were computed for the cross Kido x Suchow based on the average leaf damage of the progenies of these varieties in all other crosses.

A summary of the average reading for all three dates is shown in Table 11. Varieties whose progenies had the least average amount of leaf damage for the three dates were Kentucky I, Dicktoo, Kido, Randolph, Suchow, Meimi, and Shonan. These varieties themselves also had the least amount of leaf damage; however, they did not rank in the same order as their progenies. The variety which deviated greatest in this respect was Shonan. This variety ranked second in its leaf damage readings, however, its progeny ranked seventh. Since the male sterile derivative of Shonan was used in thirteen of its seventeen crosses, it would appear that a significant amount of the resistance to leaf damage of Shonan was lost in obtaining its male sterile derivative. An indication of this was also noted in the winter survival of its progenies in the bulk F_2 tests, however, this conclusion was not substantiated in the winter survival tests of its bulk F_3 progenies and the leaf damage readings of its bulk F_2 progenies.

In Table 12 is the analysis of variance of the leaf damage data from the parents and bulk F_3 progenies. Highly significant differences occurred among dates, among crosses, and among the parent varieties. The average leaf damage reading of the parent varieties was significantly higher than the average of the bulk F_3 progenies. This differs from the F_2 data where no difference was observed between the average of the parents and the average of the F_2 progenies. Furthermore, there is no indication that the leaf damage of the heterozygous plants changes in relation to the homozygous plants under different levels of leaf damage. Normally, with each genera-

tion of self pollination the progenies approach the average of the parents. Since the data from the F_3 progenies appear to be at a level below the average of the parents, these results indicate that the male sterile derivatives were less resistant to leaf damage than were the original varieties. Furthermore, the shift of the F_3 leaf damage reaction relative to the parents in comparison to the F_2 relative to the parents is downward. This indicates a slight tendency for resistance to leaf damage to be partially phenotypically dominant or at least that non-additive gene action existed.

Kura, Kentucky I, Suchow, and Caucasus had a predominance of progenies whose average leaf damage was less than the mid-parent value. The genetic factors involved in these varieties appear to give a reaction whereby resistance to leaf damage is partially to completely phenotypically dominant. The progenies of Kido, Shonan, and Reno, on the other hand, tend to show a greater amount of leaf damage than the mid-parent value. This indicates that susceptibility to leaf damage was partially to completely phenotypically dominant in the progeny of these varieties or that a substantial amount of the resistance to leaf damage originally possessed by these varieties, was not present in their male-sterile derivatives. When the F_2 and F_3 results are combined, the genetic factors of Kentucky I controlling leaf damage appear rather consistently to show dominance of resistance to leaf damage, while those of Kido show susceptibility to leaf damage as being dominant.

The analysis of variance of the F_3 data indicates that, as was indicated in the F_2 data, both additive and non-additive gene effects occurred in the inheritance of leaf damage caused by cold temperatures; however, the additive gene effects were much larger. The

Table 13. Correlation coefficients between the average winter survival and the average leaf damage caused by cold temperatures in several experiments on 18 winter barley varieties and their 153 bulk F_2 and F_3 progenies tested at Lincoln, Nebraska, in 1951-1952, 1953-1954 and 1954-1955.[1]

Leaf damage experiment	Number of replications	r-value[2]	
		Progeny	Parents
Bulk F_2 tests—			
November 10, 1951	4	0.83	0.82
December 1, 1951	4	0.82	0.80
February 26, 1952	4	0.86	0.94
Av. of three experiments		0.90	0.90
Bulk F_3 tests—			
December 30, 1953	3	0.72	0.84
January 6, 1954	3	0.73	0.85
March 2, 1955	3	0.56	0.76
Av. of three experiments		0.76	0.87

[1]The winter survival data in the bulk F_2 tests are the average of the Hays, Kansas, Lafayette, Indiana, and Lincoln, Nebraska tests. The winter survival data in the bulk F_3 tests are the average survival for two years at North Platte and Lincoln, Nebraska.
[2]All r-values are significant at the 1 percent level.

data also indicate that the entries did not behave the same relative to each other in all the tests. This again suggests the possibility that they may differ in the speed with which they gain or lose their resistance to leaf damage, with the result that variety A might be highly resistant to leaf damage at one period during the winter, but may lose its resistance quickly when growing conditions occur and therefore be less resistant at another time. Variety B, on the other hand, does not lose its resistance quickly and therefore retains its resistance during these warm periods.

The correlation coefficients between the results of the bulk F_2 and the bulk F_3 tests were as follows: for the progenies r = 0.71; for the parents r = 0.80. The lower correlation coefficient for the progenies than for the parents indicated that non-additive gene effects, such as dominance and/or epistatsis were present. However, as noted previously the relatively high correlation coefficients between the parents and their progeny indicate that the major gene action was additive.

Correlation between Winter Survival and Leaf Damage

In order to determine the feasibility of using leaf damage data as a measure of winter hardiness, correlation coefficients were calculated between the leaf damage data and winter survival data. These are shown in Table 13. Each experiment where leaf damage readings were obtained was correlated with the average of all the data on winter survival. It was thought that this would give the best measure of the variability a breeder might encounter in using leaf damage readings as a measure of winter hardiness. The correlation coefficients indicate that leaf damage ratings give a fairly good indication of the winter hardiness of winter barley varieties. The r-values varied from 0.76 to 0.94 for parental or homozygous material. For heterozygous material, the r-values varied from 0.56 to 0.86. These data indicate that leaf damage readings would provide useful information to the barley breeder so that progress toward cold resistance could be continued even in years when no winterkilling occurs.

Artificial Cold Tests on Bulk F_2 and Parents

A second method of evaluating this material for winter hardiness consisted of freezing in a freezing chamber plants that had been naturally hardened under field conditions. This method had been used rather successfully with winter wheat. The parents and their 153 bulk F_2 progenies were seeded in flats and allowed to harden outside, then they were frozen for 24 hours at temperatures of $-16°$ and $-14°$ C.

The average survival of the 18 winter barley varieties, their bulk F_2 progenies and the mid-parent values of all crosses are shown in Table 14. The varieties which had the highest average survival were Kido, Dicktoo, Shonan, Meimi, Reno, and Kentucky I. These

Table 14. Average percent survival of 18 winter barley varieties, their 153 bulk F$_2$ progenies and the mid-parent values in freezing chamber tests at Lincoln, Nebraska, in the winter season of 1951-52.[1]

Parent of crosses	Dictoo	Meimi	Peking	Shonan	Kido	Kentucky I	Randolph	Marm	Khayyam	Suchow	Sabbaton	Caucasus	Reno	Hokudo	Kura	Black Russian	Derbent	Apsheron	Average of its 17 progenies
Dictoo	*97*	67	64	92	62	88	74	60	66	77	46	53	76	52	66	68	53	34	65
Meimi	96	*94*	68	73	62	67	63	63	63	59	56	72	34	28	70	60	31	25	56
Peking	82	81	*67*	76	50	48	56	69	67	46	65	42	59	56	31	40	54	51	55
Shonan	97	96	82	*97*	64	52	40	77	61	33	43	81	56	51	51	36	19	37	55
Kido	98	97	83	98	*99*	64	67	46	66	69	54	51	50	63	53	20	38	57	55
Kentucky I	91	90	76	91	92	*85*	41	66	61	51	55	52	67	39	60	27	36	48	54
Randolph	86	84	70	86	87	80	*74*	64	49	34	59	43	54	59	48	47	59	44	53
Marm	82	80	67	82	83	76	70	*66*	61	59	59	39	73	55	26	23	31	11	52
Khayyam	85	84	70	85	86	79	74	70	*73*	34	61	49	61	1	25	45	53	28	50
Suchow	66	64	50	66	67	60	54	50	54	*34*	43	51	44	33	48	39	29	21	45
Sabbaton	83	82	68	83	84	77	72	68	71	52	*69*	57	16	34	32	24	26	14	44
Caucasus	55	54	40	55	56	49	44	40	43	24	41	*13*	26	51	11	33	6	13	43
Reno	92	90	77	92	93	86	80	76	80	60	78	50	*86*	25	17	40	12	16	43
Hokudo	86	85	71	86	87	80	74	71	74	54	72	44	81	*75*	23	12	43	25	38
Kura	49	48	34	49	50	43	38	34	37	18	35	7	44	38	*1*	11	9	0	34
Black Russian	51	49	35	51	51	45	39	35	38	19	37	9	45	39	2	*4*	1	5	31
Derbent	57	55	42	57	58	51	45	41	45	25	43	15	51	46	9	10	*16*	24	31
Apsheron	49	47	33	49	50	43	37	33	37	17	35	7	43	37	0	2	8	*0*	27
Average of 17 mid-parent values	77	75	62	77	78	71	66	62	65	47	64	37	72	66	31	33	39	31	

[1]The survival values above the diagonal are those for the bulk F$_2$ progenies; those below the diagonal are the mid-parent values and the italicized values are those for the varieties themselves.

Table 15. The analysis of variance of survival in artificial freezing tests of 18 winter barley varieties and their 153 bulk F_2 progenies grown at Lincoln, Nebraska, in the winter season of 1951-1952.

Source of variation	Degrees of freedom	Mean squares
Replications	2	164,833**
Entries	170	1,472**
Among crosses	152	1,154**
Among lines	17	6,146**
Within lines	135	525
Among parents	17	3,979**
Parents vs. crosses	1	7,246**
Error	340	552

**F-value exceeds 1 percent level of significance.

6 varieties also ranked highest in the field survival tests. With the exception of Reno, the bulk F_2 progenies of these varieties also ranked highest. These data suggest the possibility that the male sterile derivative of Reno was significantly lower in cold resistance than the variety Reno. However, this conclusion was not substantiated in the field winter survival tests. In field tests the progenies of Reno ranked among the higher surviving progenies. The low rank of the Reno progenies in the artificial freezing tests might be explained by assuming that the factor or factors it possesses for resistance to cold tend to be phenotypically recessive or that the genetic factors this variety possesses for high field survival were not revealed by the artificial freezing tests.

The average survival of the parent varieties was 58.4 percent while that of the bulk F_2 progenies was 46.2 percent. The analysis of variance of the results of this test shows this difference to be statistically significant. A summary of the analysis of variance for this test is shown in Table 15. This difference indicates that there was a preponderance of factors phenotypically dominant or partially dominant for cold tenderness. This does not agree with what was observed in the bulk F_2 field survival tests which indicated a tendency

Table 16. Correlation coefficients between the survival in artificial freezing tests and winter survival in field tests of 18 winter barley varieties and their bulk F_2 progenies at Lincoln, Nebraska, Hays, Kansas, and Lafayette, Indiana, in 1951-52.

Winter survival experiments	Average survival in field tests (per cent)	Correlation coefficient*	
		Progeny	Parents*
Lincoln, Nebraska			
Normal seeding rate	69.9	0.60	0.86
Normal seeding rate, protected	79.4	0.61	0.91
One-half normal seeding rate	90.1	0.53	0.84
Hays, Kansas	47.5	0.81	0.86
Lafayette, Indiana	70.8	0.79	0.89
Average of five experiments		0.67	0.95

*All correlation coefficients are significant at the 1 percent level.

for winter hardiness to be partially dominant over winter tenderness. As was pointed out previously, in the tests where severe winterkilling occurred, winter tenderness appeared to be partially dominant. This observation suggests that the genetic factors controlling their reaction in artificial freezing tests are either the same as or behave in a manner similar to those controlling their reaction in severe winter survival field tests.

If the genetic factors controlling survival in artificial freezing tests were the same as those controlling survival in severe field tests, then the results of the two tests should be highly correlated. The survival in artificial freezing tests were correlated with the survival in all the field tests. These correlation coefficients and the average survival values in each field test are shown in Table 16. There appears to be a slight tendency for the survival in the artificial freezing tests to be more closely correlated with the survival in the severe field tests than in moderate field tests. The correlation coefficients for the bulk F_2 progenies are consistently below those for the parent varieties. Since only about 30 seeds were used in each replication, it is possible that this was too small a lot of seed to adequately sample the heterogeneous bulk F_2 progenies. If the lot of seed tested does not provide a good sample of the population, part of the differences between replicates would be genetic and, therefore, would cause high variability in results. This would explain the consistently lower correlation coefficients observed for the F_2 progenies as compared with those observed for the parents. The high correlation coefficient of 0.95 obtained in the parental samples between the average winter survival of all tests and the average survival in the artificial freezing tests indicates that this is a very good technique to use in evaluating winter barley varieties for winter hardiness. A correlation coefficient of 0.89 was obtained for the parental samples between the average winter survival of the parents in the bulk F_3 tests and their survival in the artificial freezing tests. This is further evidence of the reliability of the artificial freezing tests in evaluating the winter hardiness of these winter barley varieties.

The analysis of variance of the artificial freezing tests summarized in Table 15 also shows the among line mean square value to be much higher than the within line mean square. As noted in the earlier part of these studies, this indicates that additive gene effects were of major importance. This analysis further shows that the mean square for error was large, indicating that a high amount of variability occurred in this test. The coefficient of variability was computed to be 49.5 percent. This high variability suggests that in artificial tests it would be advisable to increase the number of replications. However, as pointed out previously the small size of samples from the highly heterogeneous material probably contributed greatly to the variability of the results.

Table 17. Chi-square values for the goodness of fit of non-six row (V) vs. six-row (v) to a 3:1 ratio in 17 F_2 progenies of Khayyam a 2-row variety, crossed with 17 other 6-row winter barley varieties and grown at Lincoln, Nebraska, in the crop year 1951-1952.

Parent of crosses	Black Russian	Kido	Shonan	Randolph	Hokudo	Derbent	Marm	Reno	Kentucky I	Apsheron	Dicktoo	Suchow	Sabbaton	Peking	Kura	Caucasus	Meimi
Khayyam	0.01	0.02	0.03	0.08	0.13	0.16	0.29	0.29	0.36	0.57	0.61	1.24	2.21	2.22	2.89	3.18	13.78*

*Significant at the 1 percent level.

Table 18. Chi-square values for the goodness of fit of colored lemma (B) vs. colorless lemma (b) to a 3:1 ratio in 45 F_2 progenies of three black lemma winter barley varieties crossed with 15 white lemma varieties and grown at Lincoln, Nebraska, in the crop year 1951-1952.[1]

Parent of crosses	Khayyam	Kentucky I	Kura	Marm	Reno	Kido	Sabbaton	Randolph	Hokudo	Suchow	Dicktoo	Peking	Meimi	Apsheron	Shonan
Black Russian	1.30	0.35	2.95	2.67	2.83	2.21	0.56	4.79	21.78	24.67	4.93	6.62	8.31	6.75	29.63
Caucasus	0.63	3.16	0.24	0.74	12.06	15.64	20.19	11.93	5.33	15.16	28.76	34.47	13.25	7.68	53.69
Derbent	2.21	8.91	18.38	40.13	10.47	9.08	13.76	0.64	6.74	4.84	8.33	7.47	36.36	44.08	38.40

[1] A chi-square of 3.84 or larger indicates significance at the 5 percent level of probability; one of 6.64 or larger indicates significance at the 1 percent level.

Relationship between the Segregation of Qualitative Characters and Winter Survival

In this group of crosses it was possible to study the segregations of the simply inherited characters lemma color (B,b), kernel row number (V,v), and male sterility (Ms,ms). These studies were made on the F_2 progenies at Lincoln, Nebraska, after the material had undergone winterkilling. Therefore, it was thought that significant deviations from the monohybrid ratio of 3:1 for these characters would indicate that there was a differential winter survival of the plants possessing the contrasting characters. When this occurred it suggested that a gene or genes controlling winter survival were linked with the particular qualitative gene being studied.

Previous summaries (21, 31) have shown that the factor pair for kernel row number (V,v) is located in linkage group I and that the factor pair for lemma color (B,b) is located in linkage group II. To the knowledge of the authors, it is not known in which linkage group the factor pair for male sterility (Ms,ms) is located. These studies provided an opportunity for determining whether or not the latter factor pair is located in linkage group I or II or neither.

In Table 17 is a summary of the chi-square values obtained for the goodness of fit to a 3:1 ratio for the non-six row vs. six row character in the crosses in which this character segregated. Only one cross, Meimi x Khayyam, had a segregation which deviated significantly from a 3:1 ratio. These data indicate that, with the exception of Meimi, this group of varieties differs very little from each other in the factors they possess for winter survival in linkage group I. Since they include varieties with a winter hardiness level as low as Apsheron, one can conclude that, with the exception of Meimi, this group of varieties is not a good source of factors for winter hardiness located in linkage group I.

The significant deviation from a 3:1 ratio in the cross, Meimi x Khayyam, was due to an excess of 6-row plants. Since Meimi is a 6-row variety and the most winter hardy of the two, these data indicate that Meimi possesses a gene or genes linked with the factor for 6-row (v) in linkage group I which will provide a significantly higher level of winter hardiness than that possessed by Khayyam and probably all other varieties in this study.

Table 18 gives a summary of the chi-square values for goodness of fit to a 3:1 ratio for those crosses which segregated for lemma color (B,b). Thirty-two of the 45 crosses that could be studied gave F_2 segregations which deviated significantly from a 3:1 ratio. This indicates that among this group of varieties there are genes linked with the lemma color factor pair (B,b) which have a significant effect on winter survival. Black Russian, Caucasus, and Derbent were the black lemma varieties and did not segregate when crossed

Table 19. Chi-square values for the goodness of fit of normal fertility (Ms) vs. male sterility (ms) to a 3:1 ratio of 153 F. progenies of 18 winter barley varieties in all possible single crosses and grown at Lincoln, Nebraska, in the crop year 1951-1952.[1]

Parent of crosses	Apsheron	Caucasus	Derbent	Black Russian	Kura	Meimi	Kido	Shonan	Hokudo	Dicktoo	Kentucky I	Randolph	Sabbaton	Suchow	Khayyam	Marm	Peking	Reno
Apsheron		0.05	0.08	3.00	0.00	0.47	0.11	0.87	0.04	2.48	0.42	3.72	0.22	1.19	0.19	2.37	13.61	0.14
Caucasus			1.61	0.52	2.13	0.02	3.69	1.92	1.33	0.03	0.00	2.83	0.51	0.14	0.35	1.77	8.33	6.26
Derbent				1.20	0.34	0.00	0.05	1.45	0.18	0.00	2.02	0.52	4.96	0.19	2.63	0.74	0.12	9.99
Black Russian					0.61	0.21	1.93	1.91	0.44	0.40	0.12	10.66	6.83	3.05	7.10	1.04	0.05	0.64
Kura						0.17	1.81	0.00	9.84	8.03	2.32	0.38	1.64	2.61	0.00	4.72	4.26	1.70
Meimi							0.37	1.52	9.99	0.08	19.51	6.56	0.33	5.66	1.18	7.96	2.21	5.23
Kido								8.94	15.22	0.46	6.48	2.73	18.38	3.56	12.19	5.08	16.67	19.75
Shonan									0.41	7.51	9.78	20.76	5.28	0.13	5.27	26.44	1.33	11.50
Hokudo										0.12	14.06	1.79	1.59	6.70	9.69	6.87	3.16	10.26
Dicktoo											15.25	5.94	1.58	7.02	25.27	5.45	5.90	25.15
Kentucky I												10.59	3.09	4.54	0.09	2.46	12.83	3.92
Randolph													17.22	5.61	13.76	0.17	3.62	14.84
Sabbaton														12.08	0.00	17.54	15.59	31.61
Suchow															13.65	5.21	34.17	4.54
Khayyam																16.05	15.24	19.17
Marm																	19.84	11.95
Peking																		31.76
Reno																		

[1] A chi-square of 3.84 or larger indicates significance at the 5 percent level of probability; one of 6.64 or larger indicates significance at the 1 percent level.

to each other indicating that they possessed the same factors for lemma color.

In the crosses which deviated significantly from a 3:1 ratio for colored vs. white lemma, all had a deficiency of colored lemma plants. This would indicate that Black Russian, Derbent, and Caucasus, all of which are rather low in winter hardiness, do not possess genes located in linkage group II which give appreciable winter hardiness. This was made especially apparent in their crosses with Apsheron, a variety with a low level of winter hardiness. Even Apsheron appeared to possess genes in linkage group II which are superior to those possessed by these three varieties.

Khayyam was the only variety whose crosses with Black Russian, Caucasus, and Derbent all fit 3:1 ratios for the lemma color character. This would indicate that linkage group II of this variety also is a poor source of genes for winter hardiness. Other varieties which may be somewhat similar to Khayyam are Kentucky I, Kura, and Marm. These varieties gave 3:1 ratios with Black Russian and Caucasus, but not with Derbent. Varieties which appeared to possess genes in linkage group II that conditioned higher winter survival than all three black lemma varieties were Hokudo, Suchow, Dicktoo, Meimi, Apsheron and Shonan.

In summary, it is suggested that linkage group II is important for genes for winter hardiness and that Hokudo, Suchow, Dicktoo, Meimi, Apsheron, and Shonan possess factors conditioning winter hardiness in this linkage group.

In Table 19 is a summary of the chi-square values for the goodness of fit of normal male fertility vs. male sterility to a 3:1 ratio of all 153 F_2 progenies. Sixty-seven of these crosses had segregations which deviated significantly from a 3:1 ratio. In all crosses but one, this deviation was due to a shortage of male sterile (ms,ms) plants. Even among the 86 crosses that fit a 3:1 ratio, as determined by the chi-square test, 65 crosses had a shortage of male sterile (ms,ms) plants, indicating that several crosses among this group might not fit a 3:1 ratio if tested more extensively. These data indicate, therefore, that there are genes for winter hardiness located in the same linkage group as the one in which the ms gene is located. This would suggest

Table 20. Chi-square tests for goodness of fit to a 9:3:3:1 ratio and for linkage of kernel row number and for lemma color in F_2 progenies of three winter barley crosses grown at Lincoln, Nebraska, in the crop year 1951-1952.

Crosses	Fit to a 9:3:3:1 ratio	Test for linkage
Black Russian x Khayyam	7.16	5.85*
Caucasus x Khayyam	4.13	0.33
Derbent x Khayyam	3.11	0.74

*Significant at the 5 percent level.

Table 21. Chi-square values for the detection of linkage between the factor pair for male fertility (Ms,ms) and the factor pair for kernel row number (V,v) in 17 F_2 progenies of crosses between Khayyam, a 2-row winter barley variety, and several winter barley varieties grown at Lincoln, Nebraska, in the crop year 1951-1952.

	Black Russian	Kido	Shonan	Randolph	Hokudo	Derbent	Marm	Reno	Kentucky I	Apsheron	Dicktoo	Suchow	Sabbaton	Peking	Kura	Caucasus	Meimi
						Repulsion Phase											
Khayyam	------	------	------	------	------	------	------	------	------	------	------	------	1.14	0.81	------	------	------
						Coupling Phase											
Khayyam	2.94	2.29	2.90	3.44	1.22	0.02	12.35**	0.44	0.03	0.23	0.48	0.07	------	------	0.96	3.35	1.22

**Significant at the 1 percent level.

Table 22. Chi-square values for the detection of linkage between the factors for male fertility (Ms,ms) and the factors for lemma color (B,b) in 45 F_2 progenies of crosses among several winter barley varieties grown at Lincoln, Nebraska, in the crop year 1951-1952.

	Khayyam	Kentucky I	Kura	Marm	Reno	Kido	Sabbaton	Randolph	Hokudo	Suchow	Dicktoo	Peking	Meimi	Apsheron	Shonan
							Repulsion Phase								
Black Russian	2.94	------	3.36	0.12	------	------	0.68	------	2.37	23.09	------	1.53	0.98	------	------
Caucasus	1.06	------	4.87	------	------	------	4.45	------	0.05	2.81	7.75	------	4.08	0.00	1.22
Derbent	6.23	------	1.89	------	------	------	------	0.25	------	1.33	------	3.08	------	------	------
							Coupling Phase								
Black Russian	------	2.16	------	------	0.21	0.28	------	0.05	------	------	------	------	------	0.25	8.73
Caucasus	------	2.40	1.96	0.40	3.10	------	------	1.63	------	------	------	17.27	------	------	------
Derbent	------	1.95	0.34	0.56	0.07	0.77	------	------	5.62	------	2.03	------	4.86	4.00	5.69

[1]A chi-square of 3.84 or larger indicates significance at the 5 percent level of probability; one of 6.64 or larger indicates significance at the 1 percent level.

that a gene or genes for winter tenderness was introduced into the male sterile derivatives of the varieties from the source of the male sterility factor, Barbless, C.I. 5105. This effect was lowest among the progenies of the relatively tender varieties, Apsheron, Caucasus, Derbent, Black Russian and Kura because of the 75 crosses in which these varieties are involved, only 12 showed significant deviations from a 3:1 ratio in their segregations for the male sterility character. In the other 78 crosses, 54 crosses showed significant deficiencies of male sterile plants.

In summary, the data indicate that the linkage group in which the male fertility factor pair (Ms,ms) is located may be quite important for genes that determine winter hardiness.

These data also provided an opportunity for determining whether or not linkage occurred between any of the qualitative characters studied. Three crosses gave an opportunity for studying the inheritance of row number and lemma color. The F_2 of all three crosses fits a 9:3:3:1 ratio; however, in the cross Black Russian x Khayyam, the chi-square test for linkage indicated an association in the inheritance of these two characters. These results are shown in Table 20. A close examination of the data showed that the significant linkage chi-square value was due to an excess of the recombined types and a deficiency of the parental types. This, of course, is contrary to what would occur if the factors were linked. These results are, therefore, considered to be an extreme chance variation and the factors for kernel row number and lemma color are concluded to be inherited independently. This is in agreement with the conclusions of previous workers.

Table 21 gives a summary of the chi-square values obtained from the study of the associations in inheritance of kernel row number and male sterility. The only cross to indicate an association in inheritance or linkage was the cross Marm x Khayyam. An examination of the data again showed that the significant chi-square value was caused by a deficiency of parental combinations and an excess of recombination types. Again this is probably an extreme chance variation and it is concluded that the factor pair for kernel row number (V,v) is inherited independently of the factor pair for male fertility (Ms,ms).

A summary of the chi-square values obtained in the study of the association of the inheritance of lemma color and male sterility are shown in Table 22. Twelve of the 45 crosses indicated that these two factor pairs are associated in their inheritance.

A close examination of segregations shows that in five of the twelve crosses there was a deficiency of the parental combinations and an excess of the recombination phenotypes. Therefore, it appears that something other than linkage caused the association in inheritance between male sterility and lemma color. This was probably

Table 23. A summary of the F_2 segregation of winter barley crosses involving Derbent that segregated for lemma color (B,b) and male sterility (Ms,ms) after being exposed to winterkilling at Lincoln, Nebraska, in 1951-1952.

Crosses	Phenotypic classes					
	Male fertile Colored lemma	Male fertile White lemma	Male sterile Colored lemma	Male sterile White lemma	Total	Chi-square for independence
	(Number of Plants)					
Derbent x Khayyam	173	58	35	26	292	6.23**
Meimi x Derbent	47	52	22	11	132	4.86*
Hokudo x Derbent	91	54	36	9	190	5.62*
Shonan x Derbent	75	53	24	28	180	5.69*
Apsheron x Derbent	21	26	4	13	64	4.00*
Derbent x Peking	110	61	41	13	225	3.08
Derbent x Kura	51	41	18	9	119	1.89
Derbent x Suchow	123	60	48	17	248	1.03
Derbent x Randolph	131	47	37	16	231	0.25
Kido x Derbent	117	72	33	13	235	0.07
Dicktoo x Derbent	55	36	22	8	121	2.03
Marm x Derbent	98	71	25	24	218	0.34
Kentucky I x Derbent	136	72	41	15	264	1.95
Reno x Derbent	133	69	26	13	241	0.56
Sabbaton x Derbent	145	71	29	22	267	0.77
Derbent x Black Russian	106	0	28	0	134	
Caucasus x Derbent	103	0	26	0	129	

*Chi-square value was significant at the 5 percent level of probability.
**Chi-square value was significant at the 1 percent level of probability.

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caused by the fact that both of these factors were observed to be linked to a gene or genes controlling winter hardiness in many crosses. As a result, there tended to be an excess of male-fertile, white lemma plants in most of the crosses. A summary of the segregations observed in the crosses involving Derbent is shown in Table 23. Those for Caucasus and Black Russian do not differ greatly from these. A rather consistent excess of plants of the male fertile, white lemma phenotype indicate that the two genes or groups of genes for high winter survival which appear to be linked with the white lemma factor (b) and the normal fertility factor (Ms) in these crosses together give a higher level of hardiness than when each is alone.

In summary, these data indicate that the male-fertility factor pair is not located in linkage group I nor in linkage group II. Linkage group II and the linkage group in which the male-fertility factor pair is located are important for genes determining the winter hardiness of this group of winter barley varieties.

Association of Male Sterility with Tillering and Plant Height

Number of tillers per plant and average plant height data were taken on one replication of the normal seeding rate treatment and both replications of the one-half seeding rate treatment of the bulk F_2 progenies and parents which were grown at Lincoln, Nebraska in 1951-1952. These notes were obtained to determine whether or not the inheritance of the male sterility factor pair (Ms,ms) was associated with the inheritance of these characters. It was also possible to determine the gene action which occurred in the inheritance of the tillering and plant height characters.

First, the correlation coefficients between the average number of tillers per plant and the average winter survival were calculated to determine whether or not the progenies which had the greatest amount of winterkilling also had the greatest amount of tillering. These were calculated to be 0.45 for the bulk F_2 progenies and 0.35 for the parents. The value for the F_2 progenies was significant at the 1 percent level while that for the parent varieties was not. These values indicate that there was no tendency for the progenies which had the lowest survival to show an increased amount of tillering, in fact there was a slight tendency for those with the highest survival also to have the most tillers.

Table 24 gives a summary of the average number of tillers per plant for the normal and for the male sterile plants of all F_2 progenies and parents. When a comparison is made between the number of tillers per plant of normal and of male sterile plants, the average of the 17 progenies of each variety shows that the male sterile plants had a slightly higher amount of tillering than the normal plants. Table 25 gives the analysis of variance of these data. This analysis indicates that the crosses differed in the amount of tillering; however,

Table 24. Number of tillers per plant produced by the male-fertile and male-sterile winter barley plants of 153 bulk F₂ progenies and 18 parent varieties grown at Lincoln, Nebraska, in the crop year 1951-1952.[1]

Parent of crosses	Reno	Kentucky I	Randolph	Dicktoo	Marm	Shonan	Khayyam	Meimi	Sabbaton	Kido	Hokudo	Kura	Apsheron	Peking	Suchow	Caucasus	Derbent	Black Russian	Average of its 17 progenies
Reno	*2.26*	2.39	2.64	2.13	2.29	2.46	2.71	2.28	2.12	2.33	2.14	2.03	1.97	2.27	2.08	2.01	2.09	1.76	2.23
Kentucky I	2.77	*2.53*	2.17	2.45	2.25	2.31	2.08	2.34	2.16	2.20	2.23	2.20	2.06	2.24	2.10	2.03	2.09	1.99	2.20
Randolph	2.91	2.65	*2.18*	2.33	2.08	2.13	2.23	2.13	2.14	2.49	2.39	2.23	2.25	2.05	2.49	1.96	2.10	1.77	2.20
Dicktoo	2.50	2.43	2.47	*2.29*	2.28	2.46	2.12	2.00	1.89	2.20	1.99	2.31	2.45	1.98	2.04	1.88	2.27	2.01	2.16
Marm	2.56	2.48	2.39	3.16	*2.18*	2.47	2.22	2.22	2.14	2.41	2.34	1.97	2.12	2.18	1.87	1.72	1.72	1.88	2.14
Shonan	2.59	2.64	2.24	2.45	3.39	*1.91*	1.95	2.07	2.26	2.18	2.03	1.93	2.05	2.04	2.01	1.88	1.68	1.79	2.12
Khayyam	3.27	2.22	2.23	2.39	2.84	2.70	*2.56*	2.31	2.17	2.25	2.12	1.77	1.66	2.05	1.98	2.26	1.68	2.15	2.11
Meimi	2.97	2.29	2.29	1.96	2.87	2.37	2.54	*2.18*	2.39	2.21	1.88	2.00	2.04	1.92	2.13	2.09	1.82	1.82	2.10
Sabbaton	2.53	2.36	2.54	2.16	2.47	2.16	2.40	2.80	*2.23*	2.11	2.20	2.02	2.00	2.04	1.83	1.76	1.94	1.84	2.07
Kido	2.80	2.07	2.67	2.20	2.83	2.35	2.95	2.26	2.76	*2.31*	1.83	1.95	1.78	1.87	1.54	1.89	1.84	1.62	2.07
Hokudo	2.35	2.46	2.63	2.52	2.50	2.14	2.28	1.85	2.59	2.70	*1.84*	1.92	1.96	1.82	1.77	1.87	1.64	1.59	2.00
Kura	2.44	2.18	2.58	2.52	2.32	2.10	1.97	2.38	2.52	2.11	2.03	*2.05*	1.95	1.97	2.13	1.45	1.78	1.40	1.98
Apsheron	2.55	2.30	2.15	2.14	2.56	2.10	1.84	2.22	2.08	1.91	2.22	1.14	*2.33*	1.94	1.85	1.66	1.57	1.78	1.96
Peking	3.41	1.98	3.07	2.80	2.65	2.16	2.60	2.38	2.41	2.04	1.92	2.08	2.20	*2.62*	1.84	1.63	1.64	1.62	1.96
Suchow	2.06	2.15	2.46	2.22	1.96	2.02	2.26	2.32	1.79	1.78	1.52	2.17	1.57	1.82	*1.88*	1.66	1.48	1.54	1.89
Caucasus	2.02	1.97	2.07	2.05	2.21	1.87	1.88	2.34	2.21	2.31	2.09	2.42	1.92	1.89	1.83	*1.68*	1.63	1.90	1.86
Derbent	2.56	2.19	2.44	2.47	2.00	1.75	1.85	2.28	2.08	1.98	1.84	1.86	2.38	1.78	1.55	1.88	*1.83*	2.06	1.84
Black Russian	1.60	2.47	2.26	2.52	2.39	1.84	2.00	1.85	1.67	2.03	1.75	1.63	1.80	1.81	1.66	2.37	1.67	*1.79*	1.80
Average of its 17 progenies	2.51	2.31	2.46	2.41	2.53	2.21	2.34	2.34	2.34	2.33	2.18	2.21	2.12	2.28	1.95	2.05	2.01	1.99	

[1]Values above the diagonal are those of the male fertile F₂ plants; those below the diagonal are those of the male sterile F₂ plants; and the italicized values are those of the male fertile parental plants.

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Table 25. The analysis of variance of the number of tillers per plant of the male-fertile and male-sterile plants observed in the F_2 of 153 crosses of winter barley at Lincoln, Nebraska, in the crop year 1951-1952.

Source of variation	Degrees of freedom	Mean squares
Replications	2	3.1584**
Crosses	152	0.5462**
Among lines	17	2.8692**
Within lines	135	0.2536
Error (a)	301	0.2175
Sterility	1	10.5389**
Crosses x sterility	152	0.1657
Error (b)	297	0.1618

**F-value exceeds the one percent level.

the male sterility character affected the tillering of all crosses in the same direction. The average number of tillers per plant for all male fertile or normal plants (Ms,Ms and Ms,ms) in all crosses was 2.05 while that for the male sterile plants (ms,ms) was 2.27. This suggests that the male fertility gene has a physiological effect on tillering or that there are genes linked to the male fertility factor pair which control tillering. As with the winter survival data, the major gene action appears to be additive, because the among line variance was highly significant while the within line variance was not significant.

The correlation coefficient between the average tillering of the parents (mid-parent value) and that of their F_2 progeny for all crosses was 0.47, while that between the average of each variety itself and the average of its 17 progenies for the 18 varieties was 0.60. Both values are highly significant. The relatively low correlation coefficients were probably due in part to the relatively small difference between the parent values, the highest parent, Peking, averaging 2.62 tillers per plant and the lowest parent, Caucasus, averaging 1.68 tillers per plant. Probably combined with this is the fact that tillering is a character that is easily affected by environment.

Table 26 gives a summary of the average plant height of the male-fertile and the male sterile plants in the F_2 progenies of all crosses. These data indicate that the male sterile plants are definitely shorter than the male fertile plants. For all crosses, the average height of the male fertile plants was 32.0 inches, while that of the male sterile plants was 28.1 inches. This suggests that the male fertility factor pair has a physiology effect on plant height or that they are linked with genes which control plant height. The analysis of variance of this character is shown in Table 27 and indicates that this difference of 3.9 inches is statistically significant. However, this analysis also indicates that the crosses differed in the way their plant heights were affected by the male sterility genes or the plant

Table 26. Plant height data of the male fertile and male sterile winter barley plants of 153 F₂ progenies and 18 parent varieties grown at Lincoln, Nebraska, in crop year 1951-1952.[1]

Parent of crosses	Kentucky I	Kura	Marm	Shonan	Randolph	Reno	Dicktoo	Kido	Khayyam	Derbent	Caucasus	Meimi	Apsheron	Black Russian	Hokudo	Suchow	Sabbaton	Peking	Average of its 17 progenies
								(Inches)											
Kentucky I	*36.3*	37.0	36.0	34.0	32.5	36.0	34.3	33.0	34.3	35.7	34.3	35.0	35.0	34.3	33.3	32.3	32.0	31.7	34.2
Kura	32.7	*33.0*	37.0	33.0	37.3	33.3	34.3	37.3	33.0	31.0	29.7	32.0	30.0	30.0	34.3	32.3	33.0	30.3	33.2
Marm	33.3	32.7	*35.0*	34.0	33.3	34.7	33.0	33.3	34.3	33.0	31.3	32.0	35.7	30.3	32.7	31.0	32.0	30.0	33.2
Shonan	30.0	27.3	28.5	*33.0*	32.3	33.0	32.0	32.3	32.0	32.0	33.7	32.0	33.0	33.0	33.0	32.0	32.0	30.3	32.6
Randolph	30.0	31.3	28.3	29.7	*32.0*	34.0	34.7	32.3	33.7	31.3	33.7	34.3	32.0	34.0	31.3	32.3	31.0	29.0	32.9
Reno	32.7	31.0	30.3	28.0	27.3	*33.7*	33.0	32.7	34.7	32.3	32.0	33.0	31.0	32.3	31.3	31.7	31.0	30.0	32.7
Dicktoo	31.0	30.0	29.7	27.7	28.0	30.0	*33.3*	32.7	32.0	30.7	32.7	31.3	33.7	32.7	29.7	31.3	29.3	31.0	32.3
Kido	29.0	31.7	29.7	29.0	27.7	28.0	28.7	*33.0*	33.0	31.3	32.3	33.0	32.7	31.3	29.3	28.7	21.3	30.3	32.2
Khayyam	30.0	27.3	30.7	28.7	27.0	29.0	28.7	29.7	*34.3*	30.7	29.7	33.3	31.7	31.0	31.7	31.0	32.0	28.6	32.2
Derbent	33.0	26.5	29.5	28.3	28.7	29.7	28.7	29.3	27.0	*32.0*	32.0	30.7	29.0	32.3	30.0	30.0	32.0	31.0	31.5
Caucasus	30.7	29.5	29.3	28.7	29.0	27.0	29.3	29.7	26.3	27.3	*30.5*	32.3	29.0	30.7	31.7	30.3	31.0	28.7	31.5
Meimi	28.7	29.7	26.7	27.7	27.3	29.3	25.7	28.7	29.0	26.0	28.3	*30.3*	32.7	31.3	31.0	31.7	29.0	30.3	32.0
Apsheron	30.7	28.0	31.3	28.7	27.3	26.3	29.0	27.7	29.0	27.7	24.7	29.3	*33.0*	29.3	32.0	31.3	29.7	30.3	31.7
Black Russian	30.3	29.0	24.7	29.7	31.0	28.7	29.3	26.7	26.3	26.7	27.0	26.0	27.3	*26.0*	31.7	31.3	32.5	27.7	31.5
Hokudo	24.0	30.3	28.0	27.7	27.0	25.0	27.7	26.0	27.3	27.7	27.3	27.0	29.3	27.0	*29.0*	28.7	30.3	30.0	31.3
Suchow	29.3	31.3	27.3	29.0	29.7	27.7	28.3	26.3	28.7	27.0	27.7	27.7	25.3	28.7	27.0	*29.7*	29.3	27.7	30.8
Sabbaton	29.3	30.0	28.0	29.0	24.7	26.7	25.7	26.0	27.3	30.0	26.3	26.3	26.3	29.5	27.0	24.3	*29.0*	28.3	30.9
Peking	26.7	27.3	27.3	27.7	25.7	22.7	25.3	26.7	23.3	26.7	28.0	25.0	26.7	25.0	26.7	23.3	23.7	*25.5*	29.6
Average of its 17 progenies	30.1	29.7	29.1	28.6	28.2	28.2	28.4	28.3	28.0	28.2	28.0	27.6	27.9	27.8	27.2	27.6	27.1	25.8	

[1]The values above the diagonal are those of the male fertile F₂ progenies; those below the diagonal are those of the male sterile F₂ progenies; the italicized values are those of the normally fertile parental varieties.

Table 27. The analysis of variance of plant height of the male-fertile and male-sterile plants observed in the F_2 generation of 153 crosses of winter barley at Lincoln, Nebraska, in the crop year 1951-1952.

Source of variation	Degrees of freedom		Mean squares
Replications	2		412.20**
Crosses	152		19.50**
Among lines		17	103.63**
Within lines		135	8.90**
Error (a)	304		5.17**
Sterility	1		3470.84**
Crosses x sterility	152		2.87**
Error (b)	292		2.05

**F-value exceeds the 1 percent level of significance.

height genes linked with male fertility. The data in Table 26 show that the greatest reduction in plant height was observed in the cross, Kentucky I x Hokudo, the reduction in height being 9.3 inches. The least reduction in height was observed in the cross, Caucasus x Kura, where the reduction was only 0.2 inch. When the average effect is determined from the average of the 17 progenies of each variety, there is very little difference in the way the varieties respond through their progenies. This would indicate that none of the varieties were able to consistently overcome the plant height reduction effect of the male sterility genes or the plant height reducing genes linked to the male sterility gene.

The plant height of each variety correlated very well with the average plant height of their 17 progenies, the correlation coefficient being 0.84. A correlation coefficient of 0.65 was obtained between the mid-parent plant height and the height of the F_2 progeny. This indicates that non-additive gene action and/or environment were affecting the expression of plant height in these crosses. This conclusion is substantiated by the analysis of variance for this character where the within line variance was found to be statistically significant. Nevertheless, as with the other characters studied, the additive gene effects as measured by the among line variance was much larger than the non-additive gene effects which were measured by the within line variance.

A slight positive correlation was observed between plant height and winter survival. The correlation coefficient observed in the F_2 progenies was 0.30 and was statistically significant at the 0.01 percent level, while that for the parent varieties was 0.20 and was not significant.

SUMMARY

Winter survival data were obtained from replicated tests on 153 bulk F_2 and bulk F_3 progenies and parents of all possible single crosses among 18 winter barley varieties. These varieties had been selected on the basis of their performance in regional winter hardi-

ness field trials. They were chosen as representing the most hardy varieties which have been collected by the U.S.D.A. in the various winter barley growing areas of the world.

The F_2 data were obtained in the crop year 1951-1952 from a test at Hays, Kansas, a test at Lafayette, Indiana, and three tests at Lincoln, Nebraska. The F_3 data were obtained at North Platte and Lincoln, Nebraska, in the crop years 1953-1954 and 1954-1955. Estimates of leaf damage from cold periods which occurred during the winter were obtained at Lincoln, Nebraska, at three different dates in the 1951-1952 crop year, two different dates in the 1953-1954 crop year, and at one date during the 1954-1955 crop year. Survival data from artificial freezing tests were obtained on the bulk F_2 progenies and parents when grown in greenhouse flats and allowed to harden naturally out of doors.

The winter survival data indicated that all the varieties possessed different gene combinations for winter hardiness. Phenotypic expression of winter hardiness varied in all gradations from the possibility of complete dominance for high winter hardiness to the possibility of complete dominance for winter tenderness or low winter survival. Peking, Marm, Caucasus, and Kura appeared to possess a preponderance of factors which expressed winter hardiness as being phenotypically dominant while Meimi appeared to possess a preponderance of factors which expressed winter tenderness as being phenotypically dominant.

Dominance relationships appeared to vary depending on the severity of the test. Under severe killing or low winter survival, winter tenderness was usually dominant, while under low killing or high winter survival, high winter hardiness appeared to be dominant.

The major gene effects controlling winter survival in this group of winter barley varieties appear to be additive. A comparison of the among line variance and the within line variance showed the former to be 28 and 44 times as large, respectively, as the latter in the F_2 and F_3 generations.

Correlations between the average survival in individual tests and the average of all tests indicated that an individual test of two replications gave a fairly reliable evaluation of the winter hardiness of this group of varieties of winter barley. The correlation coefficients varied from 0.76 to 0.94.

The analysis of the leaf damage data indicated that the varieties differed in the gene combinations each possessed in their expression of this character. The expression of this character varied from resistance to leaf damage being dominant to susceptibility being dominant. However, dominance appeared to be incomplete in most crosses. Kentucky I appears to possess factors for leaf damage whereby resistance to leaf damage was usually expressed as being partially dominant to completely dominant. *Kido, on the other hand,*

appeared to possess factors for leaf damage whereby susceptibility to leaf damage was expressed as being partially dominant to completely dominant.

A few varieties and progenies ranked significantly different in their resistance to leaf damage at different times during the winter. This suggested that the varieties may have differed in the rate at which they gained and lost their resistance to leaf damage.

Very good correlations were obtained between the results of the individual tests measuring leaf damage and the average of all the winter survival tests. The correlation coefficients varied from 0.76 to 0.94 for the parent varieties and 0.72 to 0.90 for the F_2 and F_3 progenies. These data indicate that leaf damage data would be very valuable to the plant breeder in evaluating the winter hardiness of winter barley varieties in years when no differential winterkilling occurred.

Survival in artificial freezing tests correlated very well with the results of field survival tests. The correlation coefficients were as follows: for the parental varieties in the F_2 and F_3 tests, $r = 0.95$ and 0.89, respectively; and for the bulk F_2 progenies, $r = 0.67$. Samples consisting of only 30 seeds were used for each replication and probably were inadequate for representing the highly heterogeneous F_2 progenies. This probably accounts for the much lower correlation coefficient observed for the F_2 progenies, as compared to those observed for the parental varieties. Nevertheless, these data indicate that artificial freezing tests would be very reliable in evaluating the winter hardiness of winter barley varieties. The rather high correlations observed between survival in artificial freezing tests and survival in field tests indicate that resistance to cold temperatures appears to be the major factor in determining winter survival.

These investigations provided an opportunity to study F_2 segregations of the simply inherited qualitative characters, kernel row number (V,v), lemma color (B,b), and male fertility (Ms,ms). These studies were made after winterkilling occurred, therefore, significant deviations from 3:1 ratios for these characters were presumed to indicate that a gene or genes controlling winter survival were linked with the factor pair being studied. This would result in differential survival of the two phenotypes and cause deviations from a 3:1 ratio to occur.

The factor pair for kernel row number (V,v), which is located in linkage group I, was found to fit a 3:1 ratio in 16 out of 17 crosses but did not fit a 3:1 ratio in the cross Meimi x Khayyam. It was concluded that Meimi was the only variety which appeared to possess a gene or genes in linkage group I for an appreciable amount of winter hardiness.

Thirty-two of the forty-five crosses segregating for lemma color (B,b), which is located in linkage group II, deviated significantly

from a 3:1 ratio. All thirty-two showed a deficiency of plants with colored lemmas. It was concluded that Black Russian, Derbent and Caucasus, the black lemma varieties, and Khayyam, and probably Kentucky I, Kura, and Marm did not possess factors located in linkage group II which gave an appreciable amount of winter hardiness.

The male fertility factor pair (Ms,ms) was concluded to be located in a linkage group other than linkage groups I and II. The linkage group in which the male fertility factor pair is located appeared to be an important center for genes determining winter survival since 66 of 153 crosses had a significant shortage of male sterile plants. Furthermore, 65 of the remaining crosses had a shortage of male-sterile plants, although the shortages were not significant as measured by the chi-square test. Since these shortages occurred in crosses where the male sterile parent was the more hardy parent, as well as where it was the more tender parent, it was concluded that a gene or genes for winter tenderness was introduced into many varieties with the male sterile factor pair.

The male sterility (ms,ms) genes were observed to be associated with a slight increase in tillering and a substantial decrease in plant height, the decrease averaging 3.9 inches. The F_2 progenies differed in the amount their plant heights were reduced, the range in reduction being from 0.2 to 9.3 inches. Additive gene action was of primary importance in controlling tillering and plant height.

LITERATURE CITED

1. Aamodt, O. S. and Platt, A. W. Resistance of wild oats and some cereal varieties to freezing temperatures. Scient. Agr. 14:645-650. 1934.

2. Anderson, A. and Kiesselbach, T. A. Studies on the technic of control hardiness tests with winter wheat. Jour. Amer. Soc. Agron. 26:44-50. 1934.

3. Andrews, J. E. Controlled low temperature tests of sprouted seeds as a measure of cold hardiness of winter wheat varieties. Can. Jour. Pl. Sci. 38:1-7. 1958.

4. Ausemus, E. R. and Bamberg, R. H. Breeding hard red winter wheats for the northern great plains area. Jour. Amer. Soc. Agron. 39:198-206. 1947.

5. Barley winterhardiness nursery 1958. United States Department of Agriculture. CR 33-58 July, 1958.

6. Carpenter, R. W. Inheritance of winterhardiness, growth habit, and earliness in crosses between Early Blackhull, Minhardi, and Hope wheats. Unpublished M.S. thesis, University of Nebraska. 1939.

7. Cochran, W. G. and Cox, G. M. Experimental designs. John Wiley and Sons, Inc. New York. 1950.

8. Coffman, F. A. Results from uniform winterhardiness nurseries of oats grown from 1942 to 1946. Jour. Amer. Soc. Agron. 39:1027-1035. 1947.

9. Hayes, H. K. and Aamodt, O. S. Inheritance of winter hardiness and growth habit in crosses of Marquis with Minhardi and Minturki wheats. Jour. Agr. Res. 35:223-236. 1927.

10. Hill, D. D. and Salmon, S. C. The resistance of certain varieties of winter wheat to artificially produced low temperatures. Jour. Agr. Res. 35:933-937. 1927.

11. Kiesselbach, T. A. and Anderson, A. Breeding winter wheat for resistance to stinking smut, *Tilletia levis* and *T. tritici*. Nebr. Agr. Exp. Res. Bul. 51. 22 pp. 1930.

12. Kiesselbach, T. A. and Ratcliff, J. A. Oat investigations. Nebr. Agr. Exp. Res. Bul. 160. 48 pp. 1917.

13. Laude, H. H. Cold resistance of winter wheat, rye, barley, and oats in transition from dormancy to active growth. Jour. Agr. Res. 54:899-917. 1937.

14. Martin, J. F. The cold resistance of Pacific coast spring wheat at various stages of growth as determined by artificial refrigeration. Jour. Amer. Soc. Agron. 24:871-880. 1932.

15. Martin, J. H. Comparative studies of winter hardiness in wheat. Jour. Agr. Res. 35:493-535. 1927.

16. Mather, K. and Andersson, G. The determination of winterhardiness in oats. Jour. Agr. Sci. 24:627-635. 1934.

17. Peltier, G. L. and Kiesselbach, T. A. The comparative cold resistance of spring small grains. Jour. Amer. Soc. Agron. 26:681-687. 1934.

18. Poehlman, J. M. Breeding winter barley for hardiness and disease resistance. Econ. Bot. 6:176-184. 1952.

19. Quisenberry, K. S. Inheritance of winter hardiness, growth habit, and stem-rust reaction in crosses between Minhardi winter and H-44 spring wheats. U.S.D.A. Tech. Bul. 218. 45 pp. 1931.

20. Quisenberry, K. S. and Clark, J. A. Breeding hard red winter wheats for winter hardiness and high yield. U.S.D.A. Tech. Bul. 136. 28 pp. 1929.

21. Robertson, D. W., Weibe, G. A., and Shands, R. G. A summary of linkage studies in barley. Supplement II, 1947-1953. Agron. Jour. 47:418-425. 1955.

22. Rosen, H. R., Weitman, L. M., McClelland, C. K. Winter injury as related to fall and winter growth and crown-rust infection in oat varieties and their hybrids. Ark. Agr. Exp. Sta. Bul. 418. 17 pp. 1942.

23. Rosenquist, C. E. Winterhardiness in the first generation of several wheat crosses. Jour. Amer. Soc. Agron. 25:528-533. 1933.

24. Salmon, S. C. Resistance of varieties of winter wheat and rye

to low temperature in relation to winter hardiness and adaptation. Kans. Agr. Exp. Tech. Bul. 35. 66 pp. 1933.

25. Smith, L. Cytology and genetics of barley. Bot. Rev. 17:173-174. 1951.

26. Sprague, G. F. and Tatum, L. A. General vs. specific combining ability in single crosses of corn. Jour. Amer. Soc. Agron. 34:923-932. 1942.

27. Suneson, C. A. A male-sterile character in barley. A new tool for the plant breeder. Jour. Hered. 31:213-214. 1940.

28. Suneson, C. A. and Peltier, G. L. Cold resistance adjustments of field-hardened winter wheats as determined by artificial freezing. Jour. Amer. Soc. Agron. 26:50-58. 1934.

29. Suneson, C. A. and Peltier, G. L. Effect of stage of seedling development upon the cold resistance of winter wheats. Jour. Amer. Soc. Agron. 26:687-692. 1934.

30. Weibel, R. O. and Quisenberry, K. S. Field versus controlled freezing as a measure of cold resistance of winter wheat varieties. Jour. Amer. Soc. Agron. 33:336-343. 1941.

31. Wiebe, G. A. and Reid, David A. Comparative winter hardiness of barley varieties. U.S.D.A. Tech. Bul. 1176. 20 pp. 1958.

32. Woodward, R. W. Linkage in barley. Agron Jour. 49:28-32. 1957.

33. Worzella, W. W. Inheritance of cold resistance in winter wheat, with preliminary studies on the technic of artificial freezing tests. Jour. Agr. Res. 50:625-635. 1935.

34. Worzella, W. W. and Cutler, G. H. Factors affecting cold resistance in winter wheat. Jour. Amer. Soc. Agron. 33:221-230. 1941.

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