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Studies on the association between grain yield and
crown-rust reaction loci in several genetic
backgrounds of Avena sativa

by

Robert John Jondle

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INTRODUCTION

As a new system for controlling crown rust disease (caused by Puccinia coronata Cda. var. avenae Frazier and Ledingham) of oats (Avena sativa and A. byzantina), multiline cultivars have been developed and released from the Iowa Agriculture and Home Economics Experiment Station (Frey and Browning, 1971; Frey, Browning, and Grindeland, 1971a, 1971b). The multiline cultivars (one early in maturity and the other midseason) are composed of selected mixtures of isolines. An isolate was developed by backcrossing a newly found gene which conditioned resistance to the crown rust fungus into a recurrent parent (early or midseason background); thus the isolines had a common genetic background and they differed from one another by only alleles at a crown rust reaction locus and closely linked chromosomal segments. These isolines in the two series were routinely tested to insure conformity to the recurrent parent in height, maturity, grain yield, test weight, and appearance. Isolines with crown rust resistance genes from four sources, (a) C.I. 8079, an A. sterilis line from Israel, (b) C.I. 7232, a synthetic tetraploid, (c) C. I. 7171, an A. sativa line from Argentina, and (d) C.I. 7146, an A. sativa line from Brazil, had significant positive or negative grain-yield deviations when tested in rust-free environments (Frey and Browning, 1971). These authors suggested it was likely that linkage existed between loci for crown rust reaction and those for

yield expression.

Crown rust resistance genes are easily identified; therefore, they might be useful as marker genes for transferring associated grain-yield factors into different genetic backgrounds. In my study, four pairs of isolines, some of which showed associated yield differences, were chosen. Each isoline was crossed (and backcrossed) with three cultivars: Lodi, O'Brien, and Goodfield, using the rust resistance from the isoline as the marker gene. The study was designed to test whether or not the grain-yield increase (or decrease) associated with the crown rust resistance gene in an isoline could be transferred along with the crown rust resistance marker gene into these three genetic backgrounds. The data also were used to investigate type of gene action for the yield factors.

REVIEW OF LITERATURE

Numerous examples of associations between qualitatively and quantitatively inherited traits have been reported. For wheat, Middleton and Hebert (1950) reported the qualitatively inherited trait, purple straw color, was associated with the quantitatively inherited trait, kernel weight. Wiebe (1952) used barley isolines to show an association between orange lemma and certain malting quality characteristics. In another barley study, using lines isogenic except for the short segments marked by genes for smooth awn and orange lemma, Fasoulas and Allard (1962) found significant genetic variability for seven of eight quantitative¹ characters measured. A substantial part (average of 32 percent) of the genetic variance was caused by nonallelic interactions (epistasis).

Associations between qualitative and quantitative traits could result from: (1) a pleiotropic effect of the qualitative gene, (2) epistasis, or (3) linkage between the qualitative gene and other loci which affect the quantitative trait. An example of a pleiotropic effect in wheat involves the gene for awns (Suneson et al., 1948; McNeal et al., 1969). Atkins and Norris (1955) compared 10 pairs of awned versus awnless wheats and found higher grain yield and test weights for awned isolines. In soybeans, nodulating isolines were superior in

¹The words qualitative and quantitative will be used to denote qualitatively inherited and quantitatively inherited, respectively.

nitrogen fixation to nonnodulating isolines (Sears and Lynch, 1951; Weber, 1966a,b). Lee (1964), working with cotton, attributed pleiotropic effects of the pilose allele, H_2 , in decreasing the lint length. In barley, Gaul et al. (1968) discussed the pleiotropic effect of the erectoides mutant 16 on length of culm, spike internodes, awn, and seed.

Another possible explanation for the association between qualitative and quantitative traits is epistasis (the interaction between loci). In lines that are nearly isogenic for the qualitative trait, epistatic effects on a quantitative trait could result from either (1) the qualitative gene interacting with the genetic background, or (2) loci linked to the qualitative gene interacting with the genetic background. Modifiers and suppressors can be present in the genetic background which differentially affect the expression of the qualitative gene and/or its associated effect on the quantitative trait. For example, Gaul and Grunewaldt (1971) found that the effect of a barley erectoides mutant on culm and spike-internode length varied with the genetic background into which it was placed. He concluded that a great number of genes were able to modify the gene action of a mutated locus.

An association between a qualitative and a quantitative trait due to linkage of two loci is illustrated by associations between crown-rust resistance genes and inferior or superior grain yields found for isolines of oats under rust-free conditions (Frey and Browning, 1971). The isolines produced with

a crown-rust resistance allele from Avena strigosa L. had an associated ten percent reduction in grain yield, while other isolines with a crown-rust resistance allele from A. sterilis had associated four to six percent increased grain yield. To account for these cases, Frey and Browning (1971) concluded that linkage existed between a "yield" locus (loci) and a crown-rust reaction locus. Using these same oat isolines, Frey (1972) found significant differences in stability indexes between the recurrent parent and comparable isolines. Campbell and Frey (1972), working with interspecific oat crosses (A. sativa x A. sterilis) found high groat-protein percentage was associated with the A. sterilis traits of jointed awn, dark seed color, abscission spikelet separation, and shattering.

Examples of associations between qualitative and quantitative traits, possibly caused by linkage effects, are found in other crops also. In wheat, a high protein gene from Atlas 66 was found to be closely associated with adult leaf-rust resistance (Haunold et al., 1962; Johnson et al., 1963). High protein also appeared to be associated with low adult resistance (or tolerance) to stem rust (Johnson et al., 1968), whereas a gene for glume blotching was associated with increased grain protein (Swaminathan et al., 1969). Tandon et al. (1970) discovered linkage between the dominant (R) allele for red grain color and high protein content. In a study by Sun and Shands (1968), the stem-rust resistance genes from the wheat line C.I. 12633 were associated with low kernel weight, while

stem-rust resistance genes from Wis. 255 were not.

In barley, Day and Dickson (1957), using the marker gene method, found the allele for 2-row expression (linkage group I) was associated with high protein. No associations between marker genes and protein percentages were found in the other four linkage groups studied. In the cross of O.A.C. 21 by Mars, the rough-awn class of segregates had a mean diastatic activity significantly higher than that of the smooth-awn class (Day, Down, and Frey, 1955).

Another marker-gene study used barley isolines formed by backcrossing the single long-haired rachilla marker gene from the donor parent Lion into the recurrent parent Atlas (Suneson et al., 1952). The awn smoothness locus (Rr) was found to be in the same linkage group (V) as the rachilla-hair length locus (Ss) and with recombination values ranging from 28.1 to 42.7 percent. At the end of the backcrossing (Lion x Atlas¹⁰), all four types of homozygous lines (RRSS, RRss, rrSS, and rrss) were available for yield testing. In all comparisons the two semismooth-awned composites (rrSS and rrss) showed significant yield advantages over Atlas while the rachilla-hair length locus showed no association with yield. This implied either a pleiotropic effect of the semismooth-awn locus or linkage of this locus with other yield loci. In a later paper, Everson and Schaller (1955) found some rough-awned lines that had the high yield factors. Since crossing over appeared to have occurred between the awn and yield loci, they concluded that

linkage was involved. This study also showed that large genetic-environmental interactions occurred with the gene(s) for increased yield. Suneson and Stevens (1957) found the beneficial effect of the linked yield factors was activated by both cold and short days. Another qualitative trait, hooded, was also backcrossed into Atlas (Suneson and Stevens, 1957). Hooded Atlas yielded 18 to 25 percent less than Atlas 46 at low elevation tests, while it was consistently higher yielding than Atlas 46 in high elevation tests.

Wiebe et al. (1963), using barley isolines for virescent (vv) and green (VV), calculated the genetic length of the segment transferred from the donor parent to be 5.3 crossover units. The vv isolines were higher yielding than the VV ones. In another study, four backcross-derived isogenic lines of Atlas barley differing in the length of the lemma awn, full- (AABB), half- (AAbb), and quarter-awned (aaBB), and awnless (aabb), were tested by Qualset et al. (1965). The A and B genes conditioning awn development were independent and their associated linkage blocks within the isolines were calculated to be about 5.2 crossover units in length. Differences between the genotypes were found which were not related to awn development, and these were presumed to be due to either linkage with "quantitative" factors or to pleiotropic effects of the genes governing awn development. The biggest difference was with the quantitative character, kernel number per spike, where half- and quarter-awned isolines had higher kernel number than full-

awned and awnless. It was proposed that under moisture stress the depressing effect would not be as great on half-awned types, allowing higher kernel number for half- and quarter-awned types. Schaller et al. (1972) presented similar data suggesting a pleiotropic or linkage effect being present in the isolines.

Nine isolines of cotton were developed by backcrossing alleles at different loci to the recurrent parent Texas Marker-1 (Kohel and Richmond, 1971). Productivity of quantitative characters was determined for each isolate. Significant variability of strains within each isolate suggested linkage with other genes affecting the quantitative traits measured. Harding and Allard (1965), using isolines in lima beans, found a linkage block next to the color (Cc) locus which affected seed size. Duvick (1966), working with corn, reports a linkage between the fertility restoring (Rf₁) locus and yield factors.

Numerous other studies have failed to show associations between qualitative and quantitative traits. By comparing wheat isolines, differing for rust reaction alleles and chromosomal segments linked to them, Suneson et al. (1941) found the isolines did not differ in yield when in a rust-free environment. Similarly, other studies with nearly isogenic lines (Caldwell et al., 1958; Atkins and Finney, 1957; Atkins et al., 1966; and Johnson and Schlehuber, 1969) found no differences between comparable wheat isolines for quanti-

tative traits, implying that associations between qualitative and quantitative traits are not universal. In oats, Tiyawalee (1972) investigated whether high groat-protein percentages were inherited partly through genes at major loci, by using the marker-gene technique. Sixteen low-protein oat isolines (17.1 to 21.8 percent), each with a unique crown rust resistance gene, were crossed to three wild oat strains (A. sterilis) that had high groat-protein percentage (25.1 to 28.9 percent) and were susceptible to crown rust. Within each of 45 crosses, groups of homozygous resistant and susceptible F_3 -derived lines were tested for groat protein. In general, few associations were found between the qualitative trait of disease resistance and groat protein percentage.

As stated by Thoday (1961):

For quantitative traits, the gene variation arises from a number of loci, and the contribution of any locus to phenotypic variance is sufficiently small relative to that of the other loci--plus environmental causes and accidents of development, make the effects of one locus difficult to handle independently.... Now it is clear that there is nothing in principle, though it may be difficult or laborious in practice, to prevent us from handling the genes concerned with quantitative variables by more or less classical genetic methods.

In a recent article by Law (1967), intervarietal substitutions were used in wheat to locate factors controlling quantitative traits. The 7B chromosome of the cultivar Hope was found to differ from that of Chinese Spring for four quantitative factors: height, grain weight, grain number, and tiller number. The approximate locations on the 7B chromosome for

the loci affecting three of these factors were found by their association with four genetic markers on the chromosome. These results indicate the potential for finding loci affecting quantitatively inherited traits and then utilizing this knowledge in improving the trait in commercial cultivars.

PROCEDURES

Theoretical Basis for Study

Atkins and Mangelsdorf (1942) proposed the marker-gene method for tracing the inheritance of quantitatively inherited traits. With this method, a pair of nearly isogenic lines are formed which are genetically identical except for alleles at the marker gene locus and closely linked chromosomal segments. The isolines are developed by carrying a single identifiable locus (marker locus) in the heterozygous state through a number of backcrossing or selfing generations. After eight to ten generations, almost all loci other than the marker locus have returned to the homozygous condition. By increasing the number of generations of backcrossing the opportunity for crossing over increases, resulting in a smaller length of chromosomal segment (from the original nonrecurrent parent) being linked with the marker gene. When the last generation of backcrossing is complete, lines heterozygous for the marker gene are selfed, producing two types of nearly isogenic lines homozygous for the two alleles, respectively, at the marker locus. If these isolines are experimentally tested, and the homozygous lines with one allele differ in productivity of a quantitative trait from the homozygous lines for a second allele, a genetic association is evident between the marker locus and loci affecting the quantitative trait. As stated earlier, the genetic association may be caused by (1) pleiotropism,

(2) epistasis, or (3) linkage to other quantitative genes.

The oat isolines, developed at Iowa Agriculture and Home Economics Experiment Station for use in multiline cultivars, were produced via backcrossing genes into two recurrent parents. Frey and Browning (1971) found certain crown rust resistant isolines had significantly different yields than their susceptible recurrent parents under rust-free conditions. Crosses between these isolines and three common oat cultivars were used to develop the materials for this study.

Burton (1966) proposed using "near-isogenic populations" (a method previously used in barley by Day, Down, and Frey, 1955) instead of isogenic lines to reduce the amount of time needed to test for associations between qualitative and quantitative traits. Adequate near-isogenic populations could be produced with fewer backcrosses than it would take to produce isolines and they may be more representative of the original cross. Differences between marker alleles could still be measured since the population approach provides a random genetic background for both alleles. Adequate numbers of lines within each population are needed to insure, on the average, equivalent genetic backgrounds for the populations. Tiyawalee (1972) used such "isopopulations" to test for associations between the marker loci for reaction to crown rust and the quantitative trait, groat-protein percentage. He created two isopopulations of oat lines from each cross of a low protein-rust resistant parent with a high protein-rust

susceptible parent. The isopopulations from a cross consisted of two groups of random F_3 -derived lines. In one group all lines carried the resistance allele in the homozygous and homogeneous state and, in the second, all lines carried the recessive allele similarly. With an adequate number of lines in each group, the mean genetic background for both groups should be equal.

In my study, generally three pairs of isopopulations were developed from each combination of parental lines: (1) F_2 -derived, (2) Bc_1F_2 -derived, and (3) Bc_2F_2 -derived. Each pair of isopopulations consists of (1) a homozygous crown-rust resistant isopopulation and (2) a homozygous crown-rust susceptible isopopulation. A significant difference in mean yield between the two isopopulations of a pair would indicate an association between the marker locus and a locus (loci) for yield. If no yield difference occurred between the two groups, no genetic association was assumed to occur in that background.

Materials

The materials for my study were derived from 24 crosses of hexaploid oats (Avena sativa), produced by crossing three oat cultivars with four pairs of nearly isogenic lines. These four pairs of "isolines" were produced by the backcross method where both isolines of a pair have the same donor parent (source of crown-rust resistance), but one isolate had C.I. 8044 (early maturity) as its recurrent parent while the

other had C.I. 7555 (midseason). Each isoline was produced by bulking Bc_5F_3 progenies and theoretically was identical to its recurrent parent except for alleles at the crown-rust reaction locus and closely linked chromosomal segments. Of these eight (four pairs) isolines, six had previously shown either a positive or negative association between the rust resistance marker gene (plus linked chromosomal areas) and grain yield in rust-free environments (Frey and Browning, 1971).

The four original sources of the crown-rust resistance genes that were incorporated into these four pairs of isolines are shown in Table 1. Each crown rust resistance source was backcrossed into both the early and midseason recurrent parents, forming two isolines for each resistance source. The early recurrent parent, C.I. 8044, was derived from the cross Clintland x Garry-5 (Frey, Browning, and Grindeland, 1971a). C.I. 7555 was derived from the cross Hajira x Banner x Victoria 3 x Victory x Hajira 4 x Roxton 5 x ⁸Clintland (Frey, Browning, and Grindeland, 1971b).

The four sources of crown rust resistance that were incorporated into these eight isolines came from different areas of the world. The first, C.I. 8079 (or Wahl #8), was collected in Israel by Dr. I. Wahl. The following crosses were made to incorporate this gene into the early (X434II) and midseason (X270I) genetic backgrounds:

X434II = Clintland x Garry 2 x C.I. 8079 3 x ⁵C.I. 8044

X270I = C.I. 7555⁶ x C.I. 8079

Table 1. Sources of resistance, recurrent parents, and accession numbers of isolines used in crosses

Source of resistance	Early series	Midseason series
C.I. 8079 (Wahl #8)	X434II	X270I
C.I. 7171 (P.I. 185783)	X541	X447
C.I. 7232 (Saia)	X550I	X117
C.I. 7146 (Ascencao)	X469II	X423
Recurrent parents of the isolines	C.I. 8044 (C237-89III)	C.I. 7555 (C649)

The second source of rust resistance, C.I. 7171 (P.I. 185783), has adult-plant resistance (Simons, 1967) and was introduced from Argentina.

X541 = C.I. 7171 x C.I. 7154 2 x Bonkee 3 x ⁴C.I. 8044

X447 = C.I. 7171 x C.I. 7154 2 x Bonkee 3 x ⁴C.I. 7555

C.I. 7232 has a more complicated history. A diploid oat (Avena strigosa, C.D. 3820) with crown rust resistance was crossed with tetraploid A. abyssinica (C.D. 4549), and from this a fertile tetraploid, Aberdeen 101 (C.I. 7232) resulted (Zillinsky et al., 1959). C.I. 7232 is a black-seeded early line.

X550I = C.I. 8044⁵ x B312 (Zillinsky's strain of C.I. 7232)

X117 = C.I. 7232 x Burnett 2 x Clintland 3 x Cherokee 4 x
Clintland 5 x ⁶C.I. 7555

The midseason line X117 is the bulk progeny from a single

Bc₁₀F₅ plant that had crown-rust resistance and yellow seeds.

The last source of resistance genes was C.I. 7146 (Ascencao), which was introduced from Brazil. Crown rust resistance was obtained from this source by the following crosses:

X469II = C.I. 8044⁶ x Ascencao (V)

X423 = C.I. 7555⁶ x Ascencao

Six of the eight isolines in Table 1 had previously shown associations between the rust resistance and yield deviations under rust-free conditions (Frey and Browning, 1971). The two isolines with Wahl 8 as the donor parent both had a greater yielding ability than their respective recurrent parents. Testing over a three-year period (and four locations per year), X434II averaged 6.7 percent higher yield than C.I. 8044, while X270I averaged 4.6 percent higher than C.I. 7555. For the two isolines with C.I. 7171 as the donor parent, X541 had a mean superiority of 7.7 percent, while X447 had no yield superiority over its recurrent parent. The isolines derived with C.I. 7232 as the donor parent both had yield reductions associated with the rust resistance locus: X550I had an 11.0 percent reduction in yield when compared to C.I. 8044 and X117 yielded 9.6 percent less than C.I. 7555. For the two isolines derived from the Ascencao donor parent, X469II had no difference in yield from its recurrent parent, while X423 averaged 4.0 percent higher in yield.

In this study, each of these isolines were crossed (and

backcrossed) to three adapted cultivars to test whether the yield associations could be transferred along with the rust resistance into these three genetic backgrounds. The three Corn Belt cultivars I used were Lodi (C.I. 7561), O'Brien (C.I. 8174), and Goodfield (C.I. 7266). Lodi is late in maturity and tall. Goodfield and O'Brien are medium in maturity, and short and tall, respectively. The pedigrees for Lodi, O'Brien and Goodfield are:

Lodi = Hawkeye x Victoria 2 x Garry 3 x Richland x Bond

O'Brien = Victoria 2 x Hajira x Banner 3 x Victory x

Hajira 4 x Roxton 5 x Clintland

Goodfield = Hawkeye x Victoria 2 x Garry 3 x Clintland

Six of the original 24 crosses (i.e., eight isolines crossed to three cultivars) were discontinued before my study was completed because in crosses involving X469II and X117 I encountered unpredicted difficulties in the rust testing. Ultimately, no crown rust race was found which could differentiate the rust resistance of X469II from the recurrent parent. Singh (1971) later found resistance to crown rust races 264B, 290, and 326 carried by X469II broke down under high temperature (27°C) and high nitrogen conditions. It is possible that this instability contributed to my inability to detect the X469II resistance in crosses.

In the three crosses with X117, no homozygous resistant F_2 -derived families were found, even though one-fourth of the F_2 -derived families should have been homozygous resistant. The

rust resistance had been lost between the F_1 and F_2 . Later studies by Dherawattana (1971) showed that X117 has 42 chromosomes plus a pair of small fragments. This fragment pair carries the crown-rust resistance gene derived from C.I. 7232. The resistant F_1 hybrids were monosomic for the fragment. The transmission of the univalent fragment (with the resistance gene) was found to be 22 percent through the egg and only 1.1 percent through the pollen. With this transmission rate, only about two homozygous resistant F_2 plants could be expected out of 1000. Very likely, this accounted for my inability to find homozygous resistant F_2 -derived lines.

Development of Isopopulations

In the spring of 1969, the 18 crosses among the six isolines (described in Table 2) and three cultivars were made. The isolines were used as males in the crosses.

F_1 seeds were planted in 10-cm pots (one per pot) and each seedling was tested with an appropriate crown rust race to insure it came from a crossed seed. In June 1969, the resistant F_1 plants were used as females and backcrossed with the cultivars being used as the recurrent parents. In fall 1969, the Bc_1F_1 seeds were planted similarly in 10-cm pots and the seedlings were tested for rust resistance. The resistant Bc_1F_1 seedlings derived from isolines X434II and X270I were again backcrossed to provide Bc_2F_1 seeds. In addition to producing crossed seeds on F_1 and Bc_1F_1 plants, I also harvested F_2 and

Table 2. Isolines or cultivars of oats crossed, original resistance sources, crown rust races used to identify marker genes, and grain yields of isolines in percent of recurrent parent

Lines	Source of resistance	Crown rust race used	Isoline grain yield in % of recurrent parent
A. Isolines			
X434II	C.I. 8079 (Wahl 8)	264B	106.7
X270I	C.I. 8079 (Wahl 8)	264B	104.6
X541	C.I. 7171 (P.I. 185783)	264A	107.7
X447	C.I. 7171 (P.I. 185783)	264A	101.1
X550I	C.I. 7232 (Saia)	264A	88.8
X423	C.I. 7146 (Ascencao)	326	105.9
B. Cultivars			
Lodi	None		
O'Brien	None		
Goodfield	None		

Bc₁F₂ from them. Bc₂F₁ were selfed only.

In fall 1969, the F₂ seeds from each cross were space planted in a greenhouse bed. The F₃ seeds from each F₂ plant were bulked to produce an F₂-derived line. In spring 1970, 30 seeds of each F₂-derived line were planted in a hill in the field for seed increase. Hills were sown 75 cm apart

in rows 75 cm apart. The Bc_1F_2 and Bc_2F_2 seeds were space planted 30 cm apart in rows 75 cm apart in the field in 1970 also. Bc_1F_2 and Bc_2F_2 plants were harvested and threshed separately to produce Bc_1F_2 - and Bc_2F_2 -derived lines, respectively.

In the fall 1970, the F_2 -, Bc_1F_2 -, and Bc_2F_2 -derived lines from the 18 cross combinations were tested in the greenhouse for reaction to the appropriate races of crown rust. To produce seedlings for the rust tests, two hills, each with six seeds, were planted from a derived line. The seeds were sown in a sterilized mixture of sand, soil, and peat in a ratio of 1:2:1 placed in steel flats, each of which accommodated 54 hills spaced 5 cm apart in perpendicular directions. Usually a flat contained 25 derived lines (50 hills) plus the two parents of the cross from which the derived lines segregated. When the seedlings in a flat were in the one- and two-leaf stage, they were inoculated by spraying the leaves with an atomized suspension of urediospores and Mobilsol (an isoparaffinic oil which is a nontoxic medium for urediospores). After the oil had dried, the plants were sprayed with distilled water and placed in a moist chamber. Sixteen to twenty hours later, the flats were placed either in a growth chamber kept at 20°C or on a greenhouse bench kept at 20° to 30°C.

Approximately ten days after inoculation the seedlings were classified for rust reaction using the scale developed by Murphy (1935). Seedlings classified as type 0, 1, or 2

were considered resistant, while types 3 and 4 were considered susceptible. Derived lines with all susceptible or all resistant seedlings were saved for use in the isopopulations, and derived lines containing a mixture of resistant and susceptible seedlings were discarded.

The lines derived from isolines X541 and X447 had an adult-plant rust resistance reaction which required field testing. In the summers of 1970 and 1971, F_2 - and Bc_1F_2 -derived lines from these isolines were tested for adult-plant resistance in the field with crown-rust race 264A. Thirty seeds from each derived line were planted in a hill and the hills were spaced 75 cm apart in rows 75 cm apart. A rust epiphytotic of race 264A was initiated by inoculating all hills in every fourth row, which contained a susceptible spreader cultivar. During the last two weeks of May, plants of the susceptible spreader were inoculated by hypodermic injections with a suspension of crown-rust race 264A urediospores in a 0.5% solution of Tween-20. In both years, adequate rust epiphytotics were obtained to give differential readings between the check cultivars, and also between the derived lines. Generally, the rust reaction readings were taken twice during the period of the last week of June to the first week of July. Lines with all susceptible plants or all resistant plants were recorded as susceptible and resistant F_2 -derived lines, and remnant seed of these lines were used in the 1972 yield experiments. Resistant and susceptible isopopulations

were composed of resistant and susceptible F_2 -derived lines, respectively. The F_2 -derived lines were randomly selected within each isopopulation.

In 1972, ten experiments were conducted on these isopopulations (see Table 3).

Table 3. 1972 experiments

Experiment number	Plot type	Isopopulations derived from crosses with this isoline
69	Microplots	X423
70		X550I
71		X434II
72		X541
73		X270I
74		X447
76	4-row plots	X434II
77		X541
78		X270I
79		X447

Microplots (hill plots) as described by Frey (1965) were used for experiments 69 through 74. For these, 30 oat seeds were planted in each hill with a hand jab-planter. Hills were spaced 30 cm apart in perpendicular directions with two rows of border hills around the outer edge of each experiment. These six experiments were planted in randomized complete block designs each with three blocks per replicate. Each intra-replicate block had resistant and susceptible isopopulations

from the cross of one resistance source and one of the cultivars: Lodi, O'Brien, or Goodfield. For experiments 69 and 70, two locations each with six replicates were planted, while experiments 71 through 74 have five replicates at each location.

For experiments 76 through 79, I used plots each consisting of four rows 3 m long and with a 30 cm spacing between rows. The seeding rate was one seed per cm of row. The plot rows are trimmed to a length of 240 cm prior to harvest. The four 4-row plot experiments were planted in randomized complete block designs with three blocks per replicate, and each block containing resistant and susceptible isopopulations from the cross of one resistance source and one of the cultivars: Lodi, O'Brien, or Goodfield. Two locations, each with two replicates, were used for each 4-row plot experiment.

The two locations used for all ten experiments were: (1) the Field Research Center, Ames, Iowa and (2) the Northern Iowa Experimental Farm, Kanawha, Iowa. These locations are representative of central and northcentral, respectively. The F_2 - and Bc_1F_2 -derived isopopulations were in the F_5 generation, whereas the Bc_2F_2 -derived isopopulations were in the F_4 generation at the time of testing. At Ames, the hill plot experiments were planted on April 8 and 9 and the 4-row plots on April 9 and 10. At Kanawha, both the hill plot and 4-row plot experiments were planted on April 18 and 19. To evaluate the entries under rust-free environments, all experiments were sprayed once a week throughout the disease season

with the fungicide maneb. Heading date was recorded at Ames on two replicates of each experimental entry when 50 percent of the panicles were completely emerged from the boots.

Height was measured in cm from ground level to the panicle tips, and was taken approximately two weeks before harvest on two replications of each experiment. Grain yield, measured in grams per plot, was obtained for each entry in all replicates and weight per volume (kilograms per volume) was measured on all 4-row plots.

During the 1970, 1971, and 1972 seasons, 4-row plots were also conducted on both sets of isolines used as donors of rust-resistance genes and their recurrent parents, for a total of eight rust-free environments. In 1970, data were obtained from five environments representing northwestern (Sutherland, Iowa), northcentral (Kanawha, having both high and low soil fertility environments), central (Ames), and eastern (Independence) Iowa. The single environment used in 1971 was at the Northwestern Iowa Experimental Farm, Sutherland, Iowa. In 1972, both high and low fertility environments were located at the Northcentral Iowa Experimental Farm, Kanawha, Iowa.

RESULTS

The coefficients of variation (CV) for grain yield and test weight in the experiments conducted in 1972 are shown in Table 4. Frey (1965) found that CV's for oat grain yields in Iowa ranged from 7.0 to 9.0 percent for four-row plots and from 15 to 25 percent for microplots. CV's for test weight averaged 3.3 percent. The 1972 CV's were within acceptable limits.

Grain Yield

Experiments on parental lines

The data from the eight tests conducted during 1970, 1971, and 1972 to verify the yield differences among the two sets of isolines and their recurrent parents, were used in a combined analysis of variance (Table 5). The genotype x environment (experiment) interaction mean square was nonsignificant; therefore, the error mean square was used to test differences in grain yield means of the isolines and their recurrent parent. Highly significant variation occurred among means of environments and means of isolines.

The grain yield trends shown over the eight environments (Table 6) and in 1972 (Table 7) were consistent with previous data (Frey and Browning, 1971), but generally, the percentage difference between a derived isoline and its recurrent parent was lower than previously reported. Since grain yield differences found in the two 1972 environments were consistent with

Table 4. Coefficients of variation for grain yield and test weight for 1972 experiments

Donor parent	Experiment number	<u>Coefficients of variation</u>	
		Grain yield	Test weight
<u>Four-row plot</u>			
X434II	76	10.0	3.3
X541	77	6.8	4.2
X270I	78	7.9	2.8
X447	79	7.0	2.8
<u>Microplot</u>			
X423	69	16.3	
X550I	70	16.5	
X434II	71	16.3	
X541	72	17.3	
X270I	73	17.6	
X447	74	18.5	

previous reports, the mechanism (i.e., genetic, environmental, and genetic x environmental interaction) causing these differences was assumed to be operative in these environments, and, therefore, yield differences among the isopopulations (i.e., resistant and susceptible) developed from crosses of the isolines with Lodi, O'Brien, and Goodfield should have been expressed in the 1972 environments if the same mechanism was

Table 5. Mean squares from combined analysis of variance on grain yields of eight isolines and their recurrent parents collected in 1970-72

Source of variation	Degrees of freedom	Mean squares
Rep/environments	40	13,612**
Genotypes	9	57,857**
Environments	7	690,978**
G x E	63	1,966
Error	360	1,948
Total	479	

CV = 8.1%

**Significant at the 1% level.

associated with the rust resistance loci in these different genetic backgrounds.

1972 isopopulation experiments

The combined analysis of variance (two replications at each of two locations) for the isopopulations derived from crossing Lodi, O'Brien and Goodfield with X⁴J⁴II and tested in four-row plots (experiment 76) is shown in Table 8.

The error mean square (with 284 degrees of freedom) was used to calculate F values for each source of variation. The analysis indicates that the mean grain yield of the resistant isopopulations differed significantly from that for the

Table 6. Mean differences in grain yield (in grams per plot and in percent of recurrent parent) between the recurrent parent and the isolines used as parents when tested in eight environments

Isoline (I)	Recurrent parent (RP)	Difference	
		g/plot (I - RP)	% of RP
<u>Early series</u>			
X434 II	C.I. 8044	+25.6**	+ 4.9 (+6.7 ^a)
X541		+14.0	+ 2.7 (+7.7 ^a)
X550I		-58.0**	-11.0
X469II		- 2.1	- 0.4
<u>Midseason series</u>			
X270I	C.I. 7555	+13.6	+ 2.4 (+4.6 ^a)
X447		+ 6.6	+ 1.2 (+1.1 ^a)
X117		-35.2**	- 6.3 (-9.6 ^a)
X423		+24.9**	+ 4.4

^aPercentage difference in grain yield found by Frey and Browning (1971) during years 1967 through 1969.

**Significant at the 1% level.

Table 7. Mean differences in grain yield (in grams per plot and in percent of recurrent parent) between the recurrent parent and the isolines used as parents in 1972 over two environments

Isoline (I)	Recurrent parent (RP)	Difference	
		g/plot (I - RP)	% of RP
<u>Early series</u>			
X434II	C.I. 8044	+66.1*	+13.4 (+6.7 ^a)
X541		+10.6	+ 2.0 (+7.7 ^a)
<u>Midseason series</u>			
X270I	C.I. 7555	+37.8	+ 6.7 (+4.6 ^a)
X447		-25.0	- 4.1 (+1.1 ^a)

^aPercent difference in grain yield found by Frey and Browning (1971).

*Significant at the 5% level.

**Significant at the 1% level.

susceptible isopopulations. Furthermore, the mean square for recurrent parent x (R vs S) was nonsignificant which shows that the yield differential was similar for all genetic backgrounds. The adjusted mean¹ of the resistant isopopulations equalled 615.0 grams per plot, whereas the adjusted mean of the susceptible isopopulations was 600.4 g/plot. The difference

¹Mean values for experiments 69 through 79 were adjusted to correct for unequal numbers encountered within recurrent parents and within backcross levels.

Table 8. Mean squares from the analysis of variance of grain yield for isopopulations derived from crosses with X434II and tested in four-row plots (experiment 76)

Source of variation ^a	Degrees of freedom	Mean squares
Locations (Loc)	1	52,626.1**
Rep/Loc	2	34,183.7**
Entries (E)	142	13,109.2**
Res vs susc (R vs S)	1	26,895.7**
Among Rec parents (RP)	2	143,077.9**
(R vs S) x RP	2	9,246.9
Gen/RP	6	18,102.5**
(R vs S) x Gen/RP	6	9,115.6*
Entries residual	125	10,933.3**
Loc x Entries	142	4,387.1
Loc x (R vs S)	1	7,209.9
Loc x RP	2	34,779.1**
Loc x (R vs S) x RP	2	4,529.1
Loc x Gen/RP	6	10,586.1*
Loc x (R vs S) x Gen/RP	6	1,530.3
Loc x E residual	125	3,715.6
Error	284	3,712.2

^aRes vs susc - resistant isopopulations versus susceptible isopopulations; RP - recurrent parents: Lodi (C.I. 7561), O'Brien (C.I. 8174), and Goodfield (C.I. 7266); Gen - among generations (F_2 -, Bc_1F_2 -, and Bc_2F_2 -derived isopopulations).

*Significant at the 5% level.

**Significant at the 1% level.

was 14.6 or the resistant isopopulations yielded 2.4 percent more grain than did the susceptible ones. The (R vs S) x Gen/RP interaction mean square was significant, indicating the yield differential was not constant between generations within each recurrent parent. As expected, both the Loc and RP mean squares were highly significant.

The combined analysis of variance for isopopulations derived from crosses of Lodi, O'Brien, and Goodfield with X270I is shown in Table 9. As with the X434II crosses, the mean yield of the rust resistant populations of lines yielded significantly more than the susceptible ones, and the interaction of rust reaction x recurrent parent was not significant. The adjusted mean of the resistant isopopulations was 610.8 g while the susceptible adjusted mean was 589.7 g. The difference in yield was 21.1 g or the resistant populations yielded 3.6 percent more than the susceptible ones. The resistant versus susceptible source of variation did not interact with any other variables in this experiment.

Both isolines, X434II and X270I, had originally received crown rust resistance genes from the same source, C.I. 8079. The resistant isopopulations developed from crosses with these two isolines had significant increases in grain yield and in relatively the same percent difference (2.4% and 3.6% over the susceptible isopopulation means). These results imply that the grain yield factor(s) has been transferred along with the crown rust resistance from the donor parent into the genetic

Table 9. Mean squares from the analysis of variance of grain yield for isopopulations derived from crosses with X270I (experiment 78) and tested in four-row plots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	51,187.8**
Rep/Loc	2	118,416.6**
Entries	148	8,010.6**
R vs S	1	62,002.5**
RP	2	182,281.8**
(R vs S) x RP	2	231.8
Gen/RP	6	11,796.1**
(R vs S) x Gen/RP	6	4,369.5
Entries residual	131	5,049.9**
Loc x entries	148	3,296.6**
Loc x (R vs S)	1	396.1
Loc x RP	2	45,478.5**
Loc x (R vs S) x RP	2	434.2
Loc x Gen/RP	6	10,789.3**
Loc x (R vs S) x Gen/RP	6	1,050.1
Loc x E residual	131	2,478.2
Error	296	2,226.3

^aSee Table 8 for explanation.

**Significant at the 1% level.

background of all three recurrent cultivars, Lodi, O'Brien, and Goodfield.

The fluctuations of the resistant and susceptible isopopulation means are shown in Tables 10 and 11. Both the donor parents and recurrent parent means were obtained from progenies

Table 10. Mean grain yields of the resistant and susceptible isopopulations for each generation, the donor parent (X434II), and the recurrent parents tested in experiment 76 in four-row plots

Material		Yield (g/plot)		
Donor parent (X434II)		581	563	510
F ₂ -derived:	Res	562	583	644
	Sus	565	597	600
Bc ₁ F ₂ -derived:	Res	580	623	666
	Sus	580	629	623
Bc ₂ F ₂ -derived:	Res	583	657	636
	Sus	568	612	631
Recurrent parents		567	605	653
		(Goodfield)	(O'Brien)	(Lodi)
LSD (.05) = 30.7 g				

of the actual parent of plants used to make the crosses from which the F₂-derived isopopulations were produced. The first and second backcrosses were made to random plants selected from the respective recurrent parent (no remnant seeds were saved from these parents). Each experiment contains three estimates of grain yield for the donor parent, since the same donor parent was present in each of three blocks of an experiment. It is interesting to note that in certain instances the actual donor and recurrent parents selected for the first crosses differed significantly from the mean of the "pure line" cultivar from which they came. For example, in experiment 76,

Table 11. Mean grain yields of the resistant and susceptible isopopulations for each generation, the donor parent (X270I), and the recurrent parents tested in experiment 78 in four-row plots

Material	Yield (g/plot)		
Donor parent (X270I)	597	610	563
F ₂ -derived: Res	577	628	642
Sus	553	590	612
Bc ₁ F ₂ -derived: Res	594	619	599
Sus	561	628	589
Bc ₂ F ₂ -derived: Res	562	653	624
Sus	550	615	609
Recurrent parents	498 (Goodfield)	582 (O'Brien)	635 (Lodi)
LSD (.05) = 23.0 g			

the mean of the specific X434II donor parents used in crosses with Lodi was significantly lower in grain yield than that of the X434II isoline. Another example occurred in experiment 78 where the mean of Goodfield lines actually used as parents was significantly lower in grain yield than that of the Goodfield cultivar. These differences may indicate the presence of variability for yield within a "pure line" oat cultivar. Differences within "pure line" cultivars have been found in oats by Arias and Frey (1973) and may be attributed to cumulative mutations and/or outcrossing.

The mean differences between resistant and susceptible isopopulations fluctuated over backcross levels, but whenever

there was a significant difference in the means, the resistant isopopulation mean was higher. This indicates that the grain yield increase associated with the crown rust resistance gene from C.I. 8079 was present and generally could be transferred into the different genetic backgrounds.

The other four-row plot experiments involved isopopulations developed from crosses with the two isolines having the adult-plant rust resistance from C.I. 7171. Over 12 environments, Frey and Browning (1971) found that isolate X541 had a significant grain yield increase of 7.7% over its recurrent parent. The combined analysis for the grain yield data I collected on isopopulations developed from crosses of X541 with Lodi, O'Brien, and Goodfield is shown in Table 12. The resistant versus susceptible mean was significant at the 1% level. The mean grain yield of the resistant isopopulations was 599.8 g while the susceptible mean was 585.0 g, giving a difference of 14.8 g or 102.5% of the susceptible mean. This increase agrees with that found by Frey and Browning (1971) although it is lower in magnitude. Grain yield means of resistant and susceptible isopopulations are shown in Table 13. Using the $LSD (.05) = 19.6$ g, the only significant differences were in Bc_1 level of Goodfield and F_2 of O'Brien. It appears that a detectable grain yield difference which is associated with the rust resistance from C.I. 7171 in isolate X541 can be transferred into these different genetic backgrounds.

The analysis of variance for experiment 79 (Table 14)

Table 12. Mean squares from the analysis of variance of grain yield for isopopulations derived from crosses with X541 (experiment 77) and tested in four-row plots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	56,218.8**
Rep/Loc	2	41,876.2**
Entries	80	17,146.4**
R vs S	1	14,126.9**
RP	2	385,071.7**
(R vs S) x RP	2	2,139.0
Gen/RP	2	4,200.6
(R vs S) x Gen/RP	2	6,552.5*
Entries residual	71	7,910.6**
Loc x entries	80	3,307.2**
Loc x (R vs S)	1	724.9
Loc x RP	2	40,105.7**
Loc x (R vs S) x RP	2	5,059.6*
Loc x Gen/RP	2	2,340.1
Loc x (R vs S) x Gen/RP	2	2,776.1
Loc x entries residual	71	2,299.9*
Error	160	1,581.9

^aSee Table 8 for explanation.

*Significant at the 5% level.

**Significant at the 1% level.

contains isopopulations derived from crosses with X447. The R vs S mean square was not significant. This is in agreement with data from Frey and Browning (1971). The mean of the resistant isopopulations was 606.8 g while the susceptible mean

Table 13. Mean grain yields of the resistant and susceptible isopopulations for each generation, the donor parent (X541), and the recurrent parents tested in experiment 77 in four-row plots

Material	Yield (g/plot)		
Donor parent (X541)	528	584	539
F ₂ -derived: Res	531	608	652
Sus	530	584	634
Bc ₁ F ₂ -derived: Res	542	-	657
Sus	508	-	669
Recurrent parents	524	608	667
	(Goodfield)	(O'Brien)	(Lodi)
LSD (.05) = 19.6 g			

was 608.0 g, a difference of 1.2 g, with the resistant mean being 99.8% of the susceptible mean. Res vs sus did interact with Gen/RP and Loc. Susceptible isopopulations were significantly higher in grain yield at the F₂ and Bc₁ levels for recurrent parents Lodi and O'Brien, respectively (Table 15), while resistant isopopulations were significantly higher yielding at the Bc₁ level of Goodfield. For each recurrent parent, the isopopulations were significantly different at one generation but not at the other. This caused a significant (R vs S) x Gen/RP interaction. The significant Loc x (R vs S) was caused by susceptible isopopulations being significantly higher yielding in 2 out of 6 generations for location 1, while resistant isopopulations were significantly higher in 2 out of 6

Table 14. Mean squares from the analysis of variance of grain yield on isopopulations derived from crosses with X447 (experiment 79) and tested in four-row plots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	6,550.3
Rep/Loc	2	33,100.9**
Entries	95	8,393.2**
R vs S	1	128.9
RP	2	211,565.4**
(R vs S) x RP	2	5,319.5
Gen/RP	3	8,925.9**
(R vs S) x Gen/RP	3	6,940.8*
Entries residual	84	3,760.2**
Loc x entries	95	2,449.4*
Loc x (R vs S)	1	7,785.9*
Loc x RP	2	7,589.9*
Loc x (R vs S) x RP	2	3,546.5
Loc x Gen/RP	3	4,380.8
Loc x (R vs S) x Gen/RP	3	1,948.5
Loc x entries residual	84	2,186.2
Error	190	1,807.9

^aSee Table 8 for explanation.

*Significant at the 5% level.

**Significant at the 1% level.

generations at location 2. For experiment 79, no consistent grain yield differences between resistant and susceptible isopopulations could be detected.

In general, the 1972 four-row plot experiments gave

Table 15. Mean grain yields of the resistant and susceptible isopopulations for each generation, the donor parent (X447), and the recurrent parents tested in experiment 79 in four-row plots

Material	Yield (g/plot)		
Donor parent (X447)	599	574	600
F ₂ -derived: Res	580	613	634
Sus	578	601	658
Bc ₁ F ₂ -derived: Res	562	598	653
Sus	535	625	650
Recurrent parents	505 (Goodfield)	592 (O'Brien)	629 (Lodi)
LSD (.05) = 21.0			

similar results to those found in previous years (Frey and Browning, 1971) and Table 6. A summary of all four-row plot data on these four isolines and the isopopulations developed from them is given in Table 16.

The data from Table 16 over 7 years and 22 environments presents fairly conclusive evidence in favor of the hypothesis that grain yield factors are associated with the crown rust reaction loci. The 1972 experiments, although in only two environments, did follow previous trends and indicated that these yield differences could be transferred into different genetic backgrounds.

Table 16. Grain yield differences (in percent) found in four-row plots between isoline (I) and its recurrent parent (RP) or between resistant (R) and susceptible (S) isopopulations

Original isoline involved	1966 through 1969, ^a (I - RP) 12 env.	1970-72 (I - RP) 8 env.	<u>1972 - 2 environments</u>	
			Checks (I - RP)	Isopopu- lations (R - S)
X434II	+6.7*	+4.9**	+13.4*	+2.4**
X270I	+4.6*	+2.4	+6.7	+3.6**
X541	+7.7*	+2.7	+2.0	+2.5**
X447	+1.1	+1.2	-4.1	-0.2

^aFrey and Browning (1971).

*Significant at the 5% level.

**Significant at the 1% level.

Microplot experiments

Previous to 1972, microplot experiments had not been used to compare the yields of the isolines I used as rust resistance sources and their recurrent parents. The original grain yield differences associated with the crown-rust loci had been observed by using four-row plots. Four of the microplot experiments (experiments 71, 73, 72, and 74) I conducted in 1972 contained resistant and susceptible isopopulations from crosses involving the same parents as those tested in the four-row plots. Identical lines were not tested in each of the two

Table 17. Number of replications, isolines used in crosses to form isopopulations, and the original source of disease resistance for microplot experiments conducted in 1972

Experiment number	Number of reps	Isopopulations derived from crosses with this isolate	Original source of disease resistance
71	10	X434II	C.I. 8079
73	10	X270I	C.I. 8079
72	10	X541	C.I. 7171
74	10	X447	C.I. 7171
69	12	X423	C.I. 7146
70	12	X550I	C.I. 7232

plot types, but the random samples of resistant and susceptible derived lines were from common "pools". Therefore, unless the micro- and four-row plots represent different environments, one would expect similar trends and results.

Microplot experiments 71 and 73 had isopopulations derived from crosses of Lodi, O'Brien, and Goodfield with X434II and X270I, respectively. For experiment 71 (Table 18), the R vs S mean square was not significant, the means of the resistant and susceptible isopopulations being 33.1 and 33.2 g/plot, for a difference of 0.1 g. The R vs S interacted with recurrent parents (RP) and generations within recurrent parents (Gen/RP). The (R vs S) x RP interaction can be explained from the trends

Table 18. Mean squares from the analysis of variance of grain yield on isopopulations derived from crosses with X434II (experiment 71) and tested in microplots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	6,396.0**
Rep/Loc	8	287.7**
Entries	110	257.8**
R vs S	1	.1
RP	2	4,080.9**
(R vs S) x RP	2	462.1**
Gen/RP	6	124.3**
(R vs S) x Gen/RP	6	104.1**
Entries residual	93	192.4**
Loc X entries	110	40.5*
Loc x (R vs S)	1	2.7
Loc x RP	2	370.7**
Loc x (R vs S) x RP	2	48.6
Loc x Gen/RP	6	110.6**
Loc x (R vs S) x Gen/RP	6	22.9
Loc x entries residual	93	30.2
Error	880	29.4

^aSee Table 8 for explanation.

*Significant at the 5% level.

**Significant at the 1% level.

shown in Table 19. The means of the susceptible isopopulations were higher than the resistant means with the recurrent parent Lodi, whereas the opposite was true for isopopulations with Goodfield as the recurrent parent. No difference between

Table 19. Mean grain yields of the resistant and susceptible isopopulations for each generation, the donor parent (X434II), and the recurrent parents tested in experiment 71 in microplots

Material		Yield (g/plot)		
Donor parent (X434II)		29.7	30.8	25.6
F ₂ -derived:	Res	31.2	31.5	35.3
	Sus	28.2	33.2	36.6
Bc ₁ F ₂ -derived:	Res	30.1	35.6	36.6
	Sus	28.4	33.7	37.4
Bc ₂ F ₂ -derived:	Res	30.0	35.4	32.6
	Sus	28.6	34.5	37.9
Recurrent parents		30.4 (Goodfield)	34.7 (O'Brien)	37.5 (Lodi)
LSD (.05) = 1.9 g				

resistant and susceptible isopopulations was found with the recurrent parent O'Brien. The (R vs S) x Gen/RP resulted from the irregular pattern in grain yield differences over generations from F₂ toward the recurrent parent.

For experiment 73 (Table 20), the mean square for R vs S again was nonsignificant, with the mean of the resistant isopopulations being 32.8 while the susceptible mean was 32.2. The difference of 0.5 g for a 1.7% in favor of the resistant mean. Obviously, the mean difference was in the same direction as I found in four-row plots and Frey and Browning (1971) reported, but it was not statistically significant in the microplot experiment. R vs S interacted with generations within

Table 20. Mean squares from the analysis of variance of grain yield on isopopulations derived from crosses with X270I (experiment 73) and tested in microplots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	717.9**
Rep/Loc	8	245.9**
Entries	113	156.0**
R vs S	1	86.8
RP	2	969.2**
(R vs S) x RP	2	86.0
Gen/RP	6	339.0**
(R vs S) x Gen/RP	6	128.6**
Entries residual	96	131.5**
Loc x entries	113 1	66.9**
Loc x (R vs S)	1	286.4**
Loc x RP	2	96.5*
Loc x (R vs S) x RP	2	37.7
Loc x Gen/RP	6	333.1**
Loc x (R vs S) x Gen/RP	6	54.3
Loc x entries residual	96	48.7**
Error	904	32.8

^aSee Table 8 for explanation.

*Significant at the 5% level.

**Significant at the 1% level.

recurrent parents, and with locations. The (R vs S) x Gen/RP interaction is depicted in Table 21 by the irregular differences between resistant and susceptible isopopulations within a given recurrent parent as you advance from F_2 to Bc_1 to Bc_2 .

Table 21. Mean grain yields of the resistant and susceptible isopopulations for each generation, the donor parent (X270I), and the recurrent parents tested in experiment 73 in microplots

Material	Yield (g/plot)		
Donor parent (X270I)	38.1	34.3	31.4
F ₂ -derived: Res	32.7	31.7	37.7
Sus	30.5	35.0	34.9
Bc ₁ F ₂ -derived: Res	30.2	32.4	31.1
Sus	28.4	32.4	32.2
Bc ₂ F ₂ -derived: Res	31.1	34.8	33.1
Sus	31.0	33.0	32.6
Recurrent parents	25.8 (Goodfield)	29.8 (O'Brien)	34.6 (Lodi)
LSD (.05) = 2.0 g			

The three recurrent parents had large differences between resistant and susceptible isopopulations in the F₂-derived level, but these differences were reduced at the Bc₁ and Bc₂ levels. In separating the two locations to look at the (R vs S) x Loc interaction, no difference in grain yield means (R vs S) was found at location 1 (Ames), but location 2 (Kanawha) had the resistant isopopulations significantly higher than the susceptible mean. The resistant mean at location 1 was 33.1 g, while the susceptible mean was 33.5 g, a difference of .4 g or 98.7% of the susceptible mean. For location 2, the resistant mean was 32.5 g while the susceptible mean was 30.9 g for a significant difference of 1.6 g or 105.0% of the susceptible

mean.

Whenever a significant difference was found in location 2, the resistant mean was higher. In location 1, no general trend was found and the resistant isopopulations appeared to be equal to the susceptible isopopulations. No significant (R vs S) x Loc interaction occurred in experiment 78 with similar isopopulations in four-row plots. The difference in the micro-environment of a microplot versus a four-row plot may account for this difference. The data from location 2 are consistent with previous data on four-row plots (Frey and Browning, 1971) while no trends could be found with data from location 1.

Microplot experiments 72 (Table 22) and 74 (Table 24) had isopopulations derived from crosses with isolines X541 and X447, respectively. Both of these isolines obtained their disease resistance from C.I. 7171. The R vs S mean square for both of these experiments was nonsignificant. For experiment 72, R vs S did not interact with any of the other variables, while (R vs S) x RP and Loc x (R vs S) were both significant in experiment 74. The overall mean for the resistant isopopulations was 33.0 g while the susceptible mean was 32.3 g — a 2.2% advantage for the resistant mean. The (R vs S) x RP interaction resulted from the susceptible isopopulations having higher grain yield with Lodi as the recurrent parent, while resistant isopopulations were superior yielding with Goodfield as the recurrent parent.

Since the Loc x (R vs S) mean square for experiment 74

Table 22. Mean squares from the analysis of variance of grain yield for isopopulations derived from crosses with X541 (experiment 72) and tested in microplots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	229.2**
Rep/Loc	8	119.4**
Entries	70	246.9**
R vs S	1	108.9
RP	2	1,240.5**
(R vs S) x RP	2	38.9
Gen/RP	3	311.3**
R vs S x Gen/RP	3	83.6
Entries residual	59	277.7**
Loc x entries	70	48.4**
Loc x (R vs S)	1	119.4
Loc x RP	2	48.3
Loc x (R vs S) x RP	2	13.4
Loc x Gen/RP	3	63.7
Loc x (R vs S) x Gen/RP	3	78.9
Loc x entries residual	59	46.1*
Error	560	32.0

^aSee Table 8 for explanation.

*Significant at the 5% level.

**Significant at the 1% level.

was significant, the two locations were separated to examine the reason for the interaction. The mean of the resistant isopopulations for Loc 1 was 37.1 g versus 34.7 g for that of the susceptible isopopulations which was a significant differ-

Table 23. Mean grain yields of the resistant and susceptible isopopulations for each generation, the donor parent (X541), and the recurrent parents tested in experiment 72 in microplots

Material	Yield (g/plot)		
Donor parent (X541)	28.0	30.8	26.3
F ₂ -derived: Res	29.4	32.7	35.3
Sus	27.9	35.0	33.8
Bc ₁ F ₂ -derived: Res	32.4	32.8	35.7
Sus	31.6	30.9	34.6
Recurrent parents	30.5 (Goodfield)	33.8 (O'Brien)	35.9 (Lodi)
LSD (.05) = 2.0 g			

ence (.01 level) of 2.4 g or a 6.9% advantage for resistant mean. For location 2 the resistant mean was 29.4 g and the susceptible mean was 30.2 g for nonsignificant difference of .8. This interaction of the isopopulations with locations 1 and 2 actually follows a general trend that Frey and Browning (1971) found for X447, the isoline from which experiment 74 isopopulations were derived. They found the mean yield of X447 to be 1.1% higher than its recurrent parent, but in individual environments, the difference fluctuated from 10.5% less to 8.7% more than the recurrent parent. Interestingly, this 8.7% increase came from the central Iowa location, which was location 1 in my 1972 experiment.

Experiment 69 tested isopopulations developed from crosses

Table 24. Mean squares from the analysis of grain yield on isopopulations derived from crosses with X447 (experiment 74) and tested in microplots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	6,622.5**
Rep/Loc	8	108.3**
Entries	70	218.6**
R vs S	1	104.0
RP	2	2,899.9**
(R vs S) x RP	2	301.6**
Gen/RP	3	461.7**
(R vs S) x Gen/RP	3	39.4
Entries residual	59	123.6**
Loc x (R vs S)	70	70.5**
Loc x (R vs S)	1	460.1**
Loc x RP	2	297.4**
Loc x (R vs S) x RP	2	16.5
Loc x Gen/RP	3	273.4**
Loc x (R vs S) x Gen/RP	3	18.7
Loc x entries residual	59	50.3
Error	560	36.9

^aSee Table 8 for explanation.

*Significant at the 5% level.

**Significant at the 1% level.

with X423, which had previously shown higher grain yield than its recurrent parent. The R vs S mean square (Table 26) was significant. The adjusted mean of the resistant isopopulations was 35.5 g versus 34.8 g for the susceptible mean--for a

Table 25. Mean grain yields of the resistant and susceptible isopopulations for each generation, the donor parent (X447), and the recurrent parents tested in experiment 74 in microplots

Material	Yield (g/plot)		
Donor parent (X447)	38.3	31.3	33.5
F ₂ -derived: Res	32.9	31.8	38.4
Sus	29.2	32.1	39.7
Bc ₁ F ₂ -derived: Res	30.3	32.3	33.7
Sus	28.2	30.3	35.5
Recurrent parents	26.8 (Goodfield)	29.7 (O'Brien)	36.2 (Lodi)

LSD (.05) = 2.2 g

difference of .7 g or 102.1% of the susceptible mean. The (R vs S) x RP interaction was significant and Table 27 shows that resistant isopopulations were significantly higher yielding with recurrent parents O'Brien and Goodfield, but susceptible isopopulations were higher yielding with Lodi as the recurrent parent. One hypothesis could be that the yield factors associated with the crown rust resistance were repressed or nonfunctional in the Lodi genetic background while the yield factor was functional in the O'Brien and Goodfield backgrounds.

Microplot experiment number 70 was conducted on isopopulations derived from crosses of Lodi, O'Brien, and Goodfield with isoline X550I. This isoline had previously shown a lower

Table 26. Mean squares from the analysis of variance of grain yield for isopopulations derived from crosses with X423 (experiment 69) and tested in microplots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	7,421.1**
Rep/Loc	10	226.9**
Entries	111	284.9**
R vs S	1	165.9*
RP	2	3,809.8**
(R vs S) x RP	2	441.9**
Gen/RP	3	407.8**
(R vs S) x Gen/RP	3	24.7
Entries residual	100	216.5**
Loc x entries	111	51.9**
Loc x (R vs S)	1	98.3
Loc x RP	2	8.9
Loc x (R vs S) x RP	2	59.2
Loc x Gen/RP	3	294.7**
Loc x (R vs S) x Gen/RP	3	52.0
Loc x entries residual	100	44.9*
Error	1110	32.9

^aSee Table 8 for explanation.

*Significant at the 5% level.

**Significant at the 1% level.

yielding ability than its recurrent parent. As shown in Table 28 there was a significant R vs S mean square in this experiment. The grain yield mean for the resistant isopopulations was 32.9 g while the susceptible isopopulation mean was 34.4,

Table 27. Mean grain yields of the resistant and susceptible isopopulations for each generation, the donor parent (X423), and the recurrent parents tested in experiment 69 in microplots

Material		Yield (g/plot)		
Donor parent (X423)		37.2	38.2	35.3
F ₂ -derived:	Res	32.7	37.0	38.6
	Sus	31.3	34.7	39.9
Bc ₁ F ₂ -derived:	Res	33.3	36.1	35.1
	Sus	30.8	34.9	37.0
Recurrent parents		29.7 (Goodfield)	32.9 (O'Brien)	33.7 (Lodi)
LSD (.05) = 1.5 g				

a 1.5 g difference or 95.7% of the susceptible mean. The (R vs S) x RP interaction is clarified in Table 29 where it is shown that the resistant isopopulation means were significantly lower for both generations with Goodfield as the recurrent parent, while only for the F₂ when Lodi was a parent and in no generation when O'Brien was a parent. The lower yield associated with the rust resistance locus from X550I appears to have been transferred into the Lodi and Goodfield backgrounds.

In general, the microplot experimental data were in agreement with previous data on four-row plots but were less definitive than the four-row plot data. Data from X270I, X541, and the isopopulations derived from these isolines, all indicated

Table 28. Mean squares from the analysis of variance of grain yield for isopopulations derived from crosses with X550I (experiment 70) and tested in microplots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	1,119.7**
Rep/Loc	10	137.5**
Entries	110	254.1**
R vs S	1	695.5**
RP	2	2,823.2**
(R vs S) x RP	2	663.4**
Gen/RP	3	1,240.4**
(R vs S) x Gen/RP	3	54.4
Entries residual	99	165.6**
Loc x entries	110	45.2**
Loc x R vs S	1	1.2
Loc x RP	2	.4
Loc x (R vs S) x RP	2	15.3
Loc x Gen/RP	3	142.5**
Loc x (R vs S) x Gen/RP	3	95.7*
Loc x entries residual	99	42.6**
Error	1100	30.4

^aSee Table 8 for explanation.

*Significant at the 5% level.

**Significant at the 1% level.

the resistant isolines and isopopulations were higher yielding than their susceptible counterparts (even though the microplot experiments were not significant at the 5% level). The microplot information on X423 generally agreed with previous

Table 29. Mean grain yields of the resistant and susceptible isopopulations for each generation, the donor parent (X550I), and the recurrent parents tested in experiment 70 in microplots

Material	Yield (g/plot)		
Donor parent (X550I)	25.1	24.0	21.7
F ₂ -derived: Res	28.3	33.6	33.9
Sus	32.8	32.5	36.2
Bc ₁ F ₂ -derived: Res	32.9	30.5	38.1
Sus	36.5	30.1	38.1
Recurrent parents	28.2	38.4	37.8
	(Goodfield)	(O'Brien)	(Lodi)

LSD (.05) = 1.5 g

information on four-row plots (Frey and Browning, 1971), since with two of the three recurrent parents, the resistant isopopulations were significantly higher in yield than were the susceptible isopopulations. Data on X447 from microplots, four-row plots, and Frey and Browning (1971) all show no difference in grain yield between resistant and susceptible genotypes, but there is a general tendency for a significant interaction of (R vs S) x Loc to occur when the resistance gene was derived from X447. Susceptible isopopulations derived from X550I were significantly higher yielding than resistant ones when tested in microplots.

Five of the six microplot experiments supported previous data, while experiment 71 (X434II) did not. No difference in

yielding ability was found between resistant and susceptible isolines derived from X434II when tested in microplots while resistant isolines and isopopulations were superior in yield when tested in four-row plots. Possible explanations for the microplots being less definitive (and for the inconsistency found with X434II data from microplots versus four-row plots) are (1) fewer number of lines within certain isopopulations in microplot experiments, or (2) microplots provided an environment which was different from four-row plot environment.

Test Weight

Measurements of test weight (grain weight per volume) were taken on all plots of all entries in the four-row plot experiments (numbers 76 through 79). During the period 1966 through 1969, nonsignificant, but slight, differences in test weight were found between the isolines and their recurrent parents (Frey and Browning, 1971). A combined analysis of variance on the test weight data for the eight isolines and their recurrent parents over eight environments (1970-1972) showed that these genotypes differed significantly for this trait (Table 30). These ten genotypes could be separated into two groups of five: one group having shorter, earlier maturity genotypes (C.I. 8044 and isoline derivatives from this) and the second group containing taller, midseason maturity genotypes (C.I. 7555 and its isoline derivatives). Test weight differences would be expected between these two groups and

Table 30. Mean squares from combined analysis of variance on test weights of the eight isolines and their recurrent parents during 1970, 1971, and 1972

Source	Degrees of freedom	Mean squares
Rep/environments	40	.25
Genotypes	9	7.65**
Environments	7	5.76**
G x E	63	1.44**
Error	360	.12
Total	479	

**Significant at the 1% level.

may be a major factor in the highly significant genotype mean square.

The genotype x environment interaction was significant, with three of the eight environments having a nonsignificant genotype effect (no difference between genotypes). The mean test weights for all isolines and their recurrent parents are shown in Table 31. While none of the mean differences in Table 31 were significant, they all were negative. Over all 22 environments, X434II averaged 0.6 kg/hl lower in test weight than C.I. 8044, while X270I averaged 0.8 kg/hl lower than C.I. 7555. Both X434II and X270I had the same rust resistance gene from source C.I. 8079. X541 averaged 0.3 kg/hl lower in test weight while X447 averaged 0.5 kg/hl lower.

Table 31. Mean differences in test weights (kg/hl) between isolines and recurrent parents when tested in four-row plot experiments

Isoline (I)	Recurrent parent (RP)	Mean difference (I - RP)		
		1966- 1969 ^a	1970- 1972 ^b	1972 checks ^c
X434II	C.I. 8044	-0.6	-0.5	-1.2
X270I	C.I. 7555	-0.6	-1.1	-0.9
X541	C.I. 8044	-0.4	-0.0	-0.3
X447	C.I. 7555	-0.3	-0.9	-0.3

^aFrey and Browning (1971); 12 environments.

^b8 environments.

^c2 environments, checks from the 1972 experiments: 76 through 79.

1972 experiments on isopopulations

The analyses of variance on test weights for experiments 76 and 78 are given in Tables 32 and 33, respectively. For experiment 78, the R vs S mean square was significant at the 5% level and did not interact with any of the other variables. The resistant mean was 48.0 kg/hl while the susceptible mean was 47.7--a 0.3 kg/hl difference or 100.6% of the susceptible mean. Of the 18 test weight comparisons between resistant and susceptible isopopulations on Tables 34 and 35, only three were significantly different. For experiment 76 the test weight means of the resistant and susceptible isopopulations

Table 32. Mean squares from the analysis of variance of test weight for isopopulations derived from crosses with X434II (experiment 76) and tested in four-row plots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	437.04**
Rep/Loc	2	40.87**
Entries	142	3.12**
R vs S	1	.72
RP	2	93.01**
(R vs S) x RP	2	1.32*
Gen/RP	6	6.00**
(R vs S) x Gen/RP	6	1.15**
Entries residual	125	1.69**
Loc x entries	142	.61**
Loc x (R vs S)	1	1.39
Loc x RP	2	6.29**
Loc x (R vs S) x RP	2	1.38*
Loc x Gen/RP	6	.91*
Loc x (R vs S) x Gen/RP	6	.12
Loc x entries residual	125	.52*
Error	284	.36

^aSee Table 8 for explanation.

*Significant at the 5% level.

**Significant at the 1% level.

were both 46.7 kg/hl.

Experiments 77 and 79 contained isopopulations developed from crosses with isolines X541 and X447, respectively, both of which had their sources of crown rust resistance from

Table 33. Mean squares from the analysis of variance of test weight for isopopulations derived from crosses with X270I (experiment 78) and tested in four-row plots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	204.79**
Rep/Loc	2	56.41**
Entries	148	1.48**
R vs S	1	1.20*
RP	2	29.94**
(R vs S) x RP	2	.69
Gen/RP	6	6.84**
(R vs S) x Gen/RP	6	.42
Entries residual	131	.86**
Loc x entries	148	.27
Loc x (R vs S)	1	.01
Loc x RP	2	4.27**
Loc x (R vs S) x RP	2	.14
Loc x Gen/RP	6	.23
Loc x (R vs S) x Gen/RP	6	.21
Loc x entries residual	131	.22
Error	296	.26

^aSee Table 8 for explanation.

*Significant at the 5% level.

**Significant at the 1% level.

C.I. 7171. Their analyses of variance (Tables 36 and 37) indicate nonsignificant R vs S mean squares but significant (R vs S) x RP interactions. For experiment 77, the susceptible isopopulations had a mean superiority in test weight of 0.4

Table 34. Mean test weight values of the resistant and susceptible isopopulations for each generation, the donor parent (X434II), and the recurrent parents tested in experiment 76 in four-row plots

Material	Test weight (kg/hl)		
Donor parent (X434II)	47.9	49.7	47.7
F ₂ -derived: Res	48.2	47.9	45.9
Sus	46.1	47.7	46.1
Bc ₁ F ₂ -derived: Res	48.2	47.9	43.8
Sus	47.4	47.4	44.4
Bc ₂ F ₂ -derived: Res	47.4	47.9	43.8
Sus	47.7	48.2	43.8
Recurrent parents	47.2 (Goodfield)	47.9 (O'Brien)	43.0 (Lodi)
LSD (.05) = 0.8 kg/hl			

kg/hl over the resistant ones. In experiment 79 the resistant isopopulations were higher in test weight by only 0.2 kg/hl. In experiment 77, the susceptible isopopulations had a significantly higher test weight at the Bc₁F₂ level with Lodi as the recurrent parent, but significant differences were not obtained between isopopulations for the other two recurrent parents. In experiment 79 the susceptible isopopulation test weight mean was significantly higher than the resistant mean in both generations when O'Brien was a parent but no other significant differences were observed. The cause(s) of the R vs S source interacting with only one recurrent parent is not known. Perhaps, there was a variable epistatic effect

Table 35. Mean test weight values of the resistant and susceptible isopopulations for each generation, the donor parent (X270I), and the recurrent parents tested in experiment 78 in four-row plots

Material	Test weight (kg/hl)		
Donor parent (X270I)	46.1	45.9	47.2
F ₂ -derived: Res	47.9	46.9	46.7
Sus	47.9	46.9	46.1
Bc ₁ F ₂ -derived: Res	49.2	47.7	47.4
Sus	49.0	48.2	47.7
Bc ₂ F ₂ -derived: Res	49.7	48.7	46.9
Sus	49.2	48.7	45.7
Recurrent parents	50.9 (Goodfield)	49.0 (O'Brien)	45.2 (Lodi)
LSD (.05) = 0.8 kg/hl			

resulting from the different genetic backgrounds from the three recurrent parents.

In general, the test weight results from experiments 76 through 79 were similar to previous data from Frey and Brown-
ing (1971). The only significant R vs S mean square for test weight was found between resistant and susceptible isopopulations derived from X270I.

Heading Data and Height

Analyses were performed on data for heading date and height and the adjusted means for these traits are presented in Table 40. The presence of large heading date or height

Table 36. Mean squares from the analysis of variance of test weight for isopopulations derived from crosses with X541 (experiment 77) and tested in four-row plots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	178.43**
Rep/Loc	2	35.80**
Entries	80	2.00**
R vs S	1	1.36
RP	2	29.20**
(R vs S) x RP	2	3.38**
Gen/RP	2	1.32
(R vs S) x Gen/RP	2	.28
Entries residual	71	1.27**
Loc x entries	80	.32
Loc x (R vs S)	1	.01
Loc x RP	2	.15
Loc x (R vs S) x RP	2	.47
Loc x Gen/RP	2	.94
Loc x (R vs S) x Gen/RP	2	.31
Loc x entries residual	71	.31
Error	160	.59

^aSee Table 8 for explanation.

**Significant at 1% level.

differences between resistant and susceptible isopopulations could be important in the interpretation of the experiments where significant and/or sizable grain yield differences occurred. For experiment 76, the resistant isopopulations, on the average, had a significant increase in grain yield

Table 37. Mean squares from the analysis of variance of test weight for isopopulations derived from crosses with X447 (experiment 79) and tested in four-row plots

Source of variation ^a	Degrees of freedom	Mean squares
Loc	1	346.10**
Rep/Loc	2	10.14**
Entries	95	1.09**
R vs S	1	.33
RP	2	10.48**
(R vs S) x RP	2	3.75**
Gen/RP	3	3.34**
(R vs S) x Gen/RP	3	.42
Entries residual	84	.76**
Loc x entries	95	.32
Loc x (R vs S)	1	.02
Loc x RP	2	2.99**
Loc x (R vs S) x RP	2	.40
Loc x Gen/RP	3	.33
Loc x (R vs S) x Gen/RP	3	.19
Loc x entries residual	84	.26
Error	190	.27

^aSee Table 8 for explanation.

**Significant at the 1% level.

(+14.6 g) but earlier heading date (.36 days) and shorter plant height (1 cm). Generally, genotypes with earlier heading date and shorter height tend to be lower yielding during a good oat growing season, such as occurred in 1972. In other words, the reduction in heading date and height would not be

Table 38. Mean test weight values of the resistant and susceptible isopopulations for each generation, the donor parent (X541), and the recurrent parents tested in experiment 77 in four-row plots

Material	Test weight (kg/hl)		
Donor parent (X541)	48.5	46.3	47.9
F ₂ -derived: Res	49.0	46.6	45.4
Sus	48.5	46.6	46.3
Bc ₁ F ₂ -derived: Res	49.2	--	45.9
Sus	49.0	--	47.7
Recurrent parents	49.0 (Goodfield)	49.0 (O'Brien)	44.9 (Lodi)

LSD (.05) = 1.1 kg/hl

expected to accompany the yield increase found in this experiment in 1972. Similarly in experiment 77, the resistant isopopulations had a significantly shorter height (2.08 cm).

The resistant isopopulations in experiment 78, on the average, were .38 days later in maturity. In experiment 70, the resistant isopopulations were significantly lower yielding and also had a significantly earlier heading date (.76 days) and shorter height (1.34 cm).

In conclusion, the heading date and height differences, most likely, could not have been major factors in contributing to significant yield differences between resistant and susceptible isopopulations.

Table 39. Mean test weight values of the resistant and susceptible isopopulations for each generation, the donor parent (X447), and the recurrent parents tested in experiment 79 in four-row plots

Material	Test weight (kg/hl)		
Donor parent (X447)	45.4	44.9	45.9
F ₂ -derived: Res	47.2	46.3	46.9
Sus	47.4	47.4	46.2
Bc ₁ F ₂ -derived: Res	49.0	46.7	46.3
Sus	48.5	47.9	46.1
Recurrent parents	49.2 (Goodfield)	48.7 (O'Brien)	45.7 (Lodi)
LSD (.05) = 0.8 kg/hl			

Comparisons between Pairs of Random Sib Lines

In setting up my experiments, it was not always possible to have equal numbers of resistant and susceptible lines in two isopopulations from one source (e.g., X434II x Lodi), so the analyses of variance on the grain yield and test weight data from an experiment were computed using a model that corrected the mean squares for unequal numbers within classes. However, to investigate segregation patterns for grain yield and possible evidence of crossovers between loci for yield and those for reaction to crown rust, I needed to make comparisons between pairs of random sib lines originated from common F₁, Bc₁F₁, or Bc₂F₁ plants.

Therefore, for the five experiments in which a significant

Table 40. Differences between adjusted means of resistant and susceptible isopopulations for all experiments

Experiment number	Yield (g)	Heading date (days)	Height (cm)
<u>Four-row plots</u>			
76	+14.6**	-.36*	-1.00*
77	+14.8**	ns ^a	-2.08**
78	+21.1**	+.38*	ns
79	ns	-.46**	-2.36**
<u>Microplot</u>			
69	+ .73*	ns	ns
70	- 1.49**	-.76**	-1.34*
71	ns	ns	ns
72	ns	ns	ns
73	ns	ns	+1.72**
74	ns	-.80**	ns

^ans = nonsignificant.

*Significant at the 5% level.

**Significant at the 1% level.

mean square occurred for the resistant vs susceptible (R vs S) source, entries (F_2 -derived lines) were categorized according to the exact F_1 , Bc_1F_1 , or Bc_2F_1 from which they originated. Next, random pairs (i.e., one susceptible and one resistant) of F_2 , Bc_1F_2 , and Bc_2F_2 -derived lines were selected from each category. For example, in the crosses involving Lodi and X434II, I had four F_1 's of the single cross, four F_1 's of the Bc_1 , and three F_1 's of the Bc_2 . I was able to obtain two, three, one, and two pairs (i.e., one susceptible and one resistant) of F_2 -derived lines, respectively, from the four F_1 's of the original cross, one, one, two, and three pairs, respectively, from the four Bc_1F_1 's and three, two, and one pairs, respectively, from the three Bc_2F_1 's. The pairs of lines from one F_1 (or Bc_1F_1 or Bc_2F_1) were used to compute mean grain yields and frequency distributions for one set of isopopulations. Because equal numbers of resistant and susceptible F_2 -derived lines were chosen from each F_1 family, a direct comparison was possible between the resistant and susceptible isopopulation means of each set without adjustment according to a statistical assumption and, also, this arrangement permitted the estimation of segregation patterns, if any existed.

The grain yield comparisons between the resistant and susceptible isopopulations for each cross combination in experiments 76, 77, 78, 69, and 70 are summarized in Table 41. In experiments 76, 77, and 78, higher grain yields were consistently associated with the resistant isopopulations. In these three experiments, 57 of 76 pairs of isopopulations from common

Table 41. Summary of grain yield comparisons between paired resistant (R) and susceptible (S) isopopulations containing F_2 -, Bc_1F_2 -, and Bc_2F_2 -derived families

Experiment number	Recurrent parent	Number of pairs of isopopu- lations	Number of isopopu- lations with R-S > 0	Number of R-S significant (t.05)	
				>0	<0
<u>Four-row plots</u>					
76 (X434II)	Lodi	11	9	4	0
	O'Brien	12	8	1	0
	Goodfield	10	8	1	0
	Total	33	25	6	0
78 (X270I)	Lodi	8	6	1	0
	O'Brien	10	8	5	1
	Goodfield	13	9	2	0
	Total	31	23	8	1
77 (X541)	Lodi	4	3	2	1
	O'Brien	3	2	0	0
	Goodfield	5	4	0	1
	Total	12	9	2	2
<u>Microplots</u>					
69 (X423)	Lodi	10	4	0	1
	O'Brien	7	6	1	0
	Goodfield	9	5	2	2
	Total	26	15	3	3
70 (X550I)	Lodi	7	2	2	2
	O'Brien	8	4	1	0
	Goodfield	8	1	0	1
	Total	23	7	3	3

F_1 's had the resistant isopopulation with the higher grain yield, and in 16 of the 57 comparisons the mean of resistant lines was significantly (5% level) higher in yield than its susceptible counterpart. In experiment 69, slightly over half of the comparisons (i.e., 15 of 26) had the resistant isopopulation with a higher grain yield than the susceptible one. The interaction of recurrent parent by rust reaction class, with respect to yield, was evident in this experiment. With O'Brien as the recurrent parent, the resistant isopopulations had higher grain yields than their susceptible counterparts in six of seven comparisons, whereas with the other two recurrent parents, Lodi and Goodfield, the resistant isopopulations were superior in half of the comparisons. For experiment 70 (with X550I as donor parent), as expected, the mean grain yield of the susceptible isopopulation was larger in 16 of 23 comparisons. The results given in Table 41 support the conclusions obtained from the analyses of variance of these five experiments, when corrections of means were made because of unequal numbers of lines in the susceptible and resistance classes. Therefore, conclusions drawn for the statistical adjustments for unequal numbers within isopopulation classes evidently were appropriate.

Grain Yield Segregation Patterns

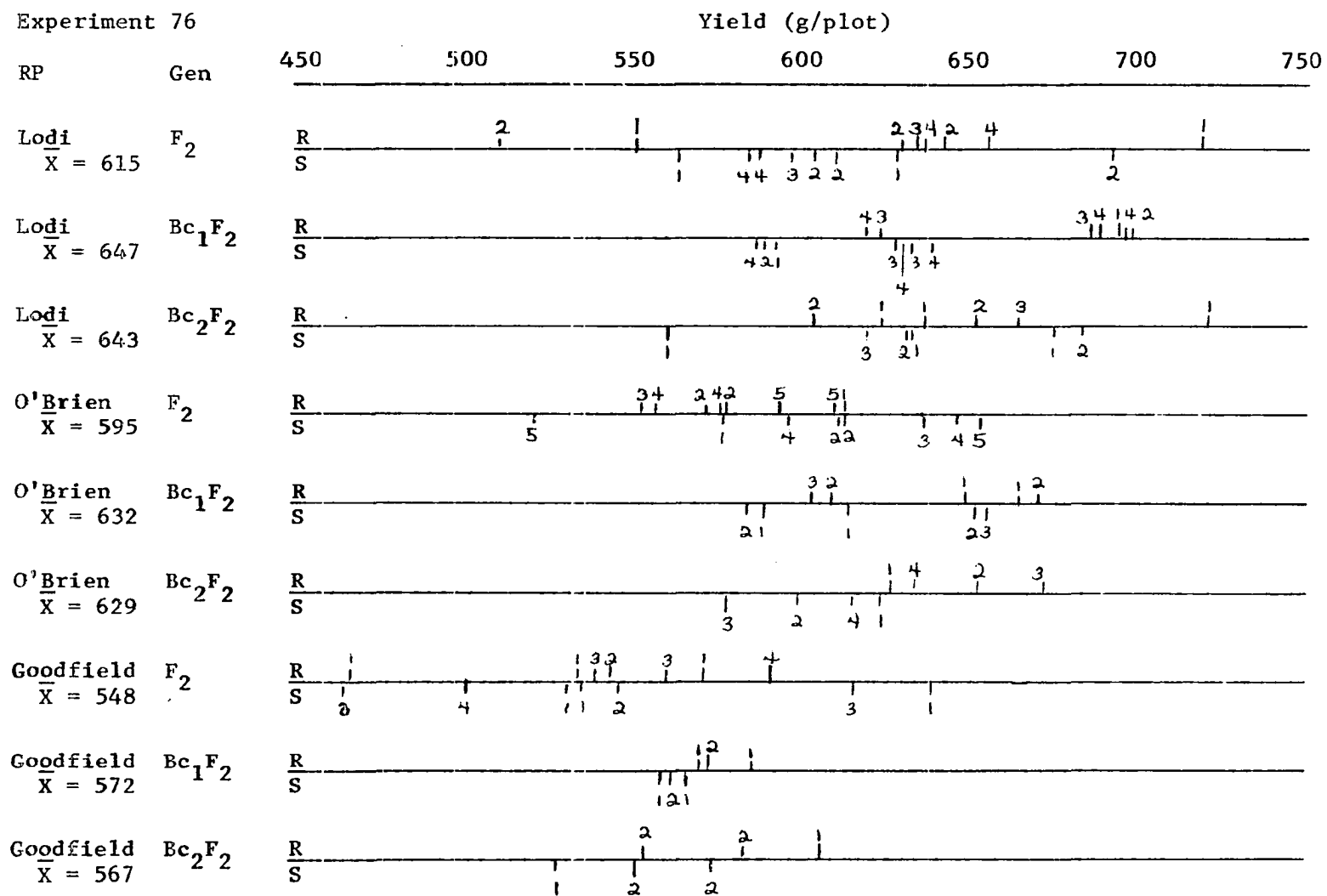
To test for segregation patterns for the grain yield of F_2 -, Bc_1F_2 -, Bc_2F_2 -derived lines, and perhaps, to find evidence

of crossing over between grain-yield and rust-reaction loci, I constructed graphs to show the mean yields of resistant and susceptible lines from the same F_1 families. So that all F_1 families from a given mating could be charted on the same graph, I adjusted all F_1 family means to a common level. For example, if the mean grain yield of all lines in F_1 family "A" was 15 g lower than the overall mean of all F_1 families from the same cross-generation (e.g., the F_2 of X434II x Lodi), 15 g were added to the yield of each line derived from F_1 plant "A". Graphs of experiments 76, 77, 78, 69, and 70 (where significant grain yield differences occurs between resistant and susceptible isopopulations) were inspected for possible evidence of segregation patterns for grain yield.

Figure 1 contains adjusted grain yield means for F_2 -derived lines in experiment 76 (with X434II as the donor parent). Separate graphs are presented for each recurrent parent-generation combination (i.e., Lodi- F_2 ; Lodi-Bc₁ F_2 , etc.). Adjusted grain yield means of resistant F_2 -derived lines are shown above the horizontal line and adjusted means of susceptible counterparts are below this line. Within each recurrent parent-generation combination, all F_2 -derived lines originating from the same F_1 plant have the same code number. For example, in the Lodi- F_2 combination the two pairs of resistant and susceptible F_2 -derived lines with code number "1" were derived from the same F_1 plant. Each generation was graphed separately in Figure 1.

Figure 1. Adjusted grain yield means of F_2 -derived lines within each recurrent parent-generation combination in experiment 76 (donor parent = X434II) in four-row plots (within each recurrent parent-generation combination, all F_2 -derived lines from the same F_1 plant have the same code number)

Experiment 76



The average amount of recurrent parent germplasm is expected to increase from 50% to 75% to 87.5%, when proceeding from F_2 -derived to Bc_1F_2 -derived to Bc_2F_2 -derived lines. Yield differences between F_2 -derived lines originating from different F_1 plants (but within the same generation) were "neutralized" by adjusting all line means to the overall mean of that generation. Of course, genetic variation among F_2 -derived lines within an F_1 family could have been due to yield genes associated with the rust reaction locus and (or) the samples of background genes that they contained. Backcrossing reduced the amount of this genetic variation for yield because the background from which samples of genes would be drawn would become more homogeneous (i.e., like the recurrent parents) and therefore the Bc_2F_2 graphs should have given more precise information on segregation patterns. The amount of genetic variation between pairs of F_2 -derived lines within an F_1 family should decrease as the number of backcrosses increases, because, on the average, a larger percentage of the germplasm would trace to the recurrent parent. Unfortunately, the Bc_2F_2 generations in the 1972 experiments contained smaller numbers of lines than the F_2 and Bc_1F_2 generations, e.g., there were 16 F_2 -derived and eight Bc_2F_2 -derived lines with O'Brien as the recurrent parent, and 14 F_2 -derived and six Bc_2F_2 -derived lines with Goodfield, so the numbers of lines within the Bc_2F_2 generations were generally too small to establish definite segregation classes for grain yield.

Experiment 76 (Figure 1) represented the best of the five experiments for visually detecting segregation patterns for grain yield. In the F_2 generation with Lodi as the recurrent parent, a majority of the adjusted means for the resistant lines were between 630 and 655 g, whereas the susceptible lines tended to bunch between 580 and 610 g. Similarly, in the Lodi-Bc₁F₂, a majority of the resistant lines occurred between 690 and 705 g and susceptible ones in the range of 630 to 645 g. These discrete classes are suggestive of a segregation pattern expected when alleles with major effect are segregating at one locus or at a group of linked loci. Less discrete groupings were found in the Bc₂F₂ with Lodi as the recurrent parent. In the generations with O'Brien as the recurrent parent, F_2 and Bc₁F₂ resistant lines generally were equal or lower in grain yield than their susceptible counterparts, whereas in the Bc₂F₂ with this recurrent parent, the resistant lines were consistently higher in grain yield than were the susceptible lines. With Goodfield as the recurrent parent no discrete classes or differences between resistant and susceptible lines were detected. Generally, I found no discrete class differences in grain yield between resistant and susceptible F_2 -derived lines in similar graphs drawn for experiments 77, 78, 69, and 70. In other words, both resistant and susceptible lines had relatively continuous frequency distributions. Two important conclusions were reached by inspecting the graphs of experiments 76, 77, 78, 69, and 70. First,

certain susceptible lines had grain yields comparable to the highest yielding resistant lines and, likewise, certain resistant lines had grain yields comparable to the lowest yielding susceptible lines. These results implied, but did not prove, that the yield advantages Frey and Browning (1971) found associated with certain crown-rust resistance genes may be separable from the resistance genes and possibly transferable to susceptible lines. Therefore, I concluded that crossing over may have occurred between the yield locus (loci) and the rust reaction loci in my experiments. My second conclusion from these graphs resulted from the discrete classes found in Figure 1. These discrete classes indicated to me the possibility that a simple (one or two gene) model may describe the segregation patterns of grain yield for my experiment.

On the assumption that crossing over may have occurred between the grain yield and crown rust reaction loci in crosses involving X434II, I attempted to calculate crude estimates of crossover percentages. My model assumed additive gene action and a single grain yield locus (designated Aa). Using these assumptions, within the homozygous resistant and susceptible isopopulations three classes of grain yield segregates would be expected, two homozygous (AA and aa) and one heterozygous (Aa). With random selection of F_2 -derived lines and additive gene action, the mean of the heterozygote class would be expected to equal the mean of all resistant and susceptible lines within a given generation, and the mean

of each homozygous class would deviate from the generation mean by one-half of the difference between the donor isolate and its original recurrent parent (i.e., the difference between X434II and C.I. 8044, respectively). For example, the yield of X434II was 524 g and that of C.I. 8044 was 476 g for a difference of 48 g and the grain yield mean of all lines within F₂ generation of X434II x Lodi was 615 g. Therefore the expected mean of the AA (with two alleles for high grain yield) and aa homozygotes would be 639 g and 591 g, respectively. The expected yield range for the heterozygous state of alleles at the yield locus (loci) would be from 603 to 627 g (i.e., the mean, 615 g \pm 12 g which is one-fourth of the differential between X434II and C.I. 8044). F₂-derived lines from the X434II x Lodi cross with yields above 627 g were considered in class AA (i.e., homozygous for high yield) and those below 603 g in class aa (i.e., homozygous for low yield). No heterozygosity of alleles at rust reaction loci was represented in the oat lines I used because only homozygous resistant or susceptible ones were used, so if a heterozygote was detected for yield, one of the gametes that was contributed to this line had to be a crossover. Using this same technique yield ranges were constructed for all generations within each recurrent parent for the five experiments (i.e., experiments 76, 77, 78, 69, and 70) where significant associations were demonstrated between grain yields and reactions to crown rust.

Returning now to experiment 76 (X434II x Lodi), resistant

F_2 -derived lines with mean yield above 627 were classed as non-crossovers, resistant lines between 603 g and 627 g as single crossover heterozygotes, and lines below 603 g as double crossovers. Likewise, yields of susceptible lines above 627 were classified as double crossovers, those between 627 g and 603 g were single crossovers, and those below 603 g were considered noncrossovers. To obtain the crossover percentages, the total number of crossovers of both resistant and susceptible lines were divided by the total number of gametes (i.e., twice the total number of lines) represented in the generation being analyzed. For example, in the Lodi x X434II cross, four double crossovers plus two single crossovers were detected in 16 lines for a total of $4(2) + 2 = 10$ crossovers, and the estimated crossover percentage of $10/32$ or 31 percent.

Crossover percentages obtained by using the procedure described above are presented in Table 42 for experiments 76, 77, 78, 69, and 70. The values are presented on the basis of generations for each parental combination and as means across generations and on a donor-parent basis. Obviously, the crossover values are very sporadic, ranging from a low of 8 to a high of 69 percent. Since the parental state of linkage in X434II, X541, X270I, and X423 was coupling (i.e., high yield and rust resistant), the repulsion phase of linkage (i.e., crossovers) would be expected to increase with repeated backcrossing, but obviously, there was no trend for this increase to occur in any of the parental combinations. Also, it would

Table 42. Percent crossing over between the rust reaction loci and a hypothesized single yield factor locus calculated from an additive gene action model for grain yield

Experi- ment	Donor	Recurrent parent	Generation			Weighted mean
			F ₂	BC ₁	BC ₂	
76	X434II	Lodi	31	21	50	33
		O'Brien	69	20	25	44
		Goodfield	50	50	33	46
						40
77	X541	Lodi	36	50	--	39
		O'Brien	50	--	--	50
		Goodfield	58	35	--	50
						47
78	X270I	Lodi	38	50	38	42
		O'Brien	14	63	22	28
		Goodfield	39	39	31	38
						35
69	X423	Lodi	59	48	--	53
		O'Brien	38	38	--	38
		Goodfield	47	25	--	40
						44
70	X550I	Lodi	40	69	--	48
		O'Brien	58	56	--	57
		Goodfield	8	42	--	17
						43

be expected that the three recurrent parents crossed to one donor should show similar crossover percentages. Possibly, the three crossover percentage estimates associated with any donor parent could be considered homogenous in all cases except for that of X550I, where the values ranged from 17 to

57 percent. Undoubtedly, much of the sporadic nature of the crossover percentage estimates was due to (a) the low number of F_2 -derived lines upon which the estimates were based and (b) the even lower number of gametes sampled in making the successive backcross generations.

The mean crossover percentages for the five donor parents ranged from 35 for X270I to 47 for X541. Note that the values for X434II and X270I (both of which carry the same crown rust resistance allele) were similar, i.e., 35 and 40 percent, respectively. All of the crossover percentages for the five donor sources seem unreasonably high in light of the past experience with them. The associations between rust-resistance alleles and those for yield deviations were carried through a minimum of five backcross generations when the isolines used as donors in my study were developed, and this tenacity of association would suggest lower crossover distances between the loci involved. Probably, my estimates are inflated by inadequate sampling of the "background germplasm", which would tend to overestimate the crossover percentages. In other words, some resistant noncrossover lines could be intermediate yielding because of a low-yield background, and these would be classed as single crossovers. A similar error could occur in the opposite direction for susceptible noncrossovers with a high-yield background. Since small numbers were present within each recurrent parent-generation combination, the misclassification of one or two lines could greatly inflate

the crossover percentages. Therefore, the actual crossover percentages may be considerably smaller than those shown in Table 42.

The crown rust resistance gene extracted from C.I. 8079 and present in X434II (experiment 76) and X270I (experiment 78) had crossover percentages consistently lower than 50 percent. Also, Figure 1 depicts rather discrete segregation patterns when X434II was used as the donor parent for grain yield. Combining all evidence I concluded that the resistance gene from C.I. 8079 probably is linked to a single yield locus (or block of loci acting as a single unit for crossover purposes). In no other case would the model permit the detection of any simple segregation pattern, but since segregation between rust reaction type and grain yield did occur, I would conclude linkage probably exists between each of these other crown rust resistance alleles and the associated loci for grain yield.

DISCUSSION

A major objective of most plant breeding projects involving field crops is to increase the yielding capacity of cultivars while retaining other traits of the cultivars in a desirable state. When grain yield was found to be associated with certain crown-rust reaction loci in oats (Frey and Browning, 1971), the obvious question was: Can these grain yield associations be transferred with the crown-rust resistance alleles (via backcrossing) and maintained in other genetic backgrounds? In several cases, these associations involved average grain yield increases (over many environments) of four to seven percent. According to Browning et al. (1964), past improvement for grain yield of oats in Iowa was approximately 15 percent, accomplished over a period of 30 years. Another association in oats between qualitatively and quantitatively inherited traits was observed by Campbell and Frey (1972). They found that several seed traits (awn expression, seed color, and lemma hairiness) were associated with groat-protein percentage. The potential for incorporating the grain yield improvements into cultivars by backcrossing to transfer a crown-rust marker gene is what prompted this study.

There are several points about my experimental techniques that are critical to the validity and usefulness of the conclusions I can draw from this study. First were the sample

sizes of F_2 -derived lines within the individual isopopulations sufficiently large. Adequate numbers of random F_2 -derived lines were needed in a pair of isopopulations to insure that the mean genetic backgrounds of the resistant and susceptible counterparts were equivalent. The sample sizes of the isopopulations of a pair usually varied, and furthermore, there were variable sample sizes between experiments. For example, there were from two to ten entries among isopopulations in the different backcross levels, from eight to 28 entries among isopopulations within recurrent parents, and 35 to 75 entries among isopopulations within experiments. Even though all entries were chosen at random, these pairs of isopopulations with a low number of entries may not have had equivalent genetic backgrounds due to small sample sizes. In total, however, the trends of mean yields for resistant versus susceptible classes usually confirmed the expectations based on previous experience; therefore, overall for any given experiment, the number of entries within a pair of isopopulations did not seem to be a serious source of error.

A second point for consideration is the fact that all my data were collected in one growing season. Experiments grown in 1971 had to be discarded due to hail damage late in the season. Normally, data collected in only one season would be considered inadequate to measure grain yield differentials. However, I did split each of the ten experiments between two test sites (i.e., Ames and Kanawha, Iowa) which should have

represented somewhat different environments. The mean grain yield of all four-row plot entries was 10 g (2%) higher at Ames than at Kanawha, while mean yield of microplots was 0.8 g (3%) higher at Kanawha. More importantly, the yield differences expressed between the donor isolines and their recurrent parents in my experiments in 1972 paralleled the results for these isolines over the five previous years (Table 16). I concluded, therefore, that the mechanisms that caused the yield differentials between isolines in the previous five years (i.e., 1967 through 1971) also were operative in the environments where I grew my experiments in 1972, and, even though I sampled only one season, it probably was adequate to test the hypothesis of my study.

A third point that requires explanation is the fact that the F_1 and Bc_1F_1 plants were used as females in crosses with recurrent parents (susceptible to crown rust) to obtain the subsequent backcross level. When using the resistant parent as the female, selfed seed would not be separable from F_1 seed by rust tests of seedlings from them. In the initial series of crosses, where the susceptible recurrent parents were used as females and all F_1 plants were rust tested, of more than 400 " F_1 " seeds, only two were selfs. So on the assumption that this low proportion of selfs also would be representative of the backcrosses, there were probably no serious errors in my results due to inability to separate selfs from crosses in the Bc_1F_1 and Bc_2F_1 classes. The susceptible recurrent

parents were used as males in these latter crosses because they were better sources of pollen.

A final crucial point involves the neutrality of crown rust resistance alleles in the absence of attack by the crown rust pathogen. All experiments in 1972 were sprayed periodically to insure rust-free environments. Since the isopopulations carry the crown rust locus in the homozygous state, there would be no heterotic effect resulting from this locus. Each crown rust resistance allele could possibly have a pleiotropic effect on crown rust reaction and grain yield under rust-free conditions, but based on grain yield segregation patterns and estimated crossing over percentages between the resistance allele and yield alleles in this study, it would seem logical to conclude linkage is probably involved rather than pleiotropism.

Yield differentials between resistant and susceptible isopopulations were found when both microplots and four-row plots were used as experimental units, and further, these data corroborated previous results. True, the microplot results were less definitive in showing the grain-yield associations. Prior to 1972, no microplot experiments were conducted for the purpose of comparing the isolines with their recurrent parents. The obvious reason for using microplots is that they require fewer seeds (30 seeds) than do four-row plots (1200 seeds), and the microplot experiments are less expensive to conduct. In the case of my study, microplot experiments were used be-

cause, for many useful oat lines (i.e., they were either homozygous resistant or susceptible), there were not enough seeds to sow an experiment with four-row plots. There are at least two possible explanations for the four-row plots being more definitive than the microplots: (1) the sample size of plants used for estimating grain yield in a microplot was 30, whereas in four-row plots the harvested sample was 500 plants (only 2.5 m of each of the two center rows were harvested), and larger samples generally give more precise estimates of a parameter, (2) F_2 -derived lines in microplots were directly in competition with other genotypes growing in adjacent plots, while genotypes grown in four-row plots had two nonharvested border rows to eliminate potential competition effects between genotypes. The 1972 coefficients of variation for the microplot experiments were approximately twice the size of the four-row plot CV's. Therefore, to compensate for the larger relative error involved, approximately 16 microplot replicates would be comparable to four replicates of the four-row plots. My 1972 microplot experiments had 10 (numbers 71 through 74) and 12 replicates (numbers 69 and 70). In experiment 71 (where no grain yield difference between resistant and susceptible isopopulations was found), increasing the number of microplot replicates would probably have had little effect on the conclusions reached. The effect of increasing the replication number in the other five microplot experiments is not known, but presumably the grain yield trends would have

remained in the same direction.

A second possible explanation for the four-row plots being more definitive than microplots involves microenvironmental differences (i.e., competition effects). Competition between different genotypes is expected to be minimal in four-row plot experiments since the two border rows are not harvested for grain yield evaluation. In microplot experiments, competition effects are present since one genotype will have eight different genotypes surrounding it. Jensen and Federer (1964), looking at single-row plots of wheat, found competitive effects associated with height resulted in the taller genotypes averaging 7.3 bushels per acre higher yield than shorter genotypes. In my isopopulation experiments, the initial crosses of donor by recurrent parent were considered fairly wide for such characters as grain yield, height, and heading date; therefore, segregates within an experimental block could have had relatively large differences for these traits. For example, within the Lodi experimental block in microplot experiment 69, entries ranged from 105 cm to 126 cm for height, and from June 17 to June 28 for heading date. The competition effects present in the microplot experiments either may have reduced or accentuated the grain yield differences previously found between resistant and susceptible isopopulations in four-row plots.

The use of a disease-resistance marker gene would be ideal for my study. Individual crown-rust reaction loci in

oats are easily identified in both the greenhouse and field environments by inoculating plants with a specific race (or races). The presence of crown-rust resistance alleles can be verified during a backcrossing procedure and, when tested under rust-free environments, the rust-reaction locus is expected to be neutral relative to its effect on grain yield or other traits. Marker genes that have a large pleiotropic effect on the trait being studied would be less desirable in detecting major genes for this trait. The crown rust reaction of a genotype can be tested rapidly on small samples (12-15 seedlings) and I tested thousands of F_2 -derived lines before selecting those that were used in the resistant and susceptible isopopulations.

Originally, we assumed that the early and midseason isolines developed by extracting crown-rust resistance genes from the same source (Table 1) would carry the same resistance genes. Singh (1971) ran a series of crown rust disease resistance tests on the eight isolines I used as donor parents and found that the early and midseason isolines with resistance from the same source did not always carry the same resistance gene. The only pair of isolines that had the same resistance gene transferred into both were isolines X434II and X270I derived from C.I. 8079 (Wahl 8). The adult plant resistance from C.I. 7171 (P.I. 185783) was inherited quantitatively (Singh, 1971) and, therefore, different sets of resistance genes could have been transferred to the isolines

X541 and X447. This may explain why a grain yield increase was associated with the resistance allele in X541 and not in X447. The Saia resistance source (Table 1) contributed one crown-rust resistance gene to X117 and a different one to X550I. Similarly, Ascencao carries two crown-rust resistance genes, one of which, Pc-2, was transferred to the early isolate, X469II, and the other, Pc-14, which was transferred to isolate X423.

Each of my donor isolines was produced by bulking either Bc_5F_3 or Bc_6F_3 progenies, and therefore, they should have been very nearly isogenic to the recurrent parent for the crown-rust locus involved. Hanson (1959a,b) determined the average length of chromosome segment that would remain linked intact to a locus with different levels of backcrossing. The average length of linked chromosomal area on each side of the marker gene would be 15.8 centimorgans after six backcrosses (one centimorgan equals the map distance corresponding to a recombination frequency of 1 percent). Falconer (1964), quoting Bartlett and Haldane (1935), approximated the mean length of chromosome introduced with a marker gene to be $100/t$ centimorgans on each side of the marker gene, where t equals the number of backcrosses. With this equation the intact chromosome segment would equal 16.6 centimorgans on each side of the marker gene, so even after six backcrosses there likely would be a sizable amount (approximately 35-40 crossover units) of chromatin linked to the marker gene.

An important conclusion from my study was that a locus with major effect on grain yield which is closely associated with a marker gene can be transferred into different genetic backgrounds via backcrossing. Based on this prospect, an attempt to use crown-rust marker genes to locate major genes for groat-protein percentage in oats was conducted by Tiyawalee (1972). Only two associations were found in his study which involved 16 marker genes and three A. sterilis lines with high groat-protein percentage. While future attempts in using marker genes to locate major loci for quantitatively inherited traits may be successful, present data are not sufficient to predict success or failure in specific cases. Major loci for quantitative traits may be found, but a relatively close linkage to a marker locus would need to be present for the backcrossing technique to be highly effective in transferring the marker gene into another genetic background.

When it was originally assumed that a pair of isolines (i.e., an early and a midseason) with crown-rust resistance from the same donor carried the same resistance allele, the presence of an associated yield deviation in one isolate but not in the other was assumed to indicate either (a) the yield allele showing epistatic gene action or (b) the previous occurrence of a crossover between the rust reaction and yield loci. However, when Singh (1971) showed that the two isolines derived from one source sometimes carried rust-resistance genes at different loci, neither of these explanations was necessary

to explain the results Frey and Browning (1971) reported. My experimental results, of course, tend to argue that certain of the yield alleles from the isolines do show epistatic gene action, since certain grain yield associations were transferred consistently into the three recurrent genetic backgrounds, while other yield associations were not. For example, in the four-row plots, the grain yield increase associated with the allele in X270I that confers resistance to crown rust race 264B was manifest consistently in the genotypic backgrounds of all three recurrent parents (Table 11), whereas the yield increase associated with the race 264B reaction allele in X434II appeared to be manifest in only two of the three recurrent parents (Table 10). Yield association increases or decreases also were successfully transferred from X541, X423, and X550I into the genotypic backgrounds of one or more recurrent parents when the crown rust-resistance alleles were transferred. These cases where a grain yield deviation remained associated with a specific rust resistance allele in one genotypic background but not in another could be interpreted as evidence for epistatic gene action by the yield alleles.

If the grain yield alleles reacted epistatically, it could have two undesirable results: (1) locating such favorable yield alleles would be difficult because detection of them would depend upon the genotypic background into which they were transferred and (2) utilizing such favorable alleles

would be useful in only certain genotypic backgrounds. In other words, with epistatic gene action, even if found, there would be no guarantee that an allele would be expressed in the genotypic background to which it was transferred.

Tables 10, 11, 13, 27, and 29 have adjusted means of the resistant and susceptible isopopulations for the five experiments where significant grain yield differences occurred between resistant and susceptible isopopulations. These tables show the effect of backcrossing the specific crown rust alleles into the three recurrent parents. Generally, an epistatic rather than additive type of gene action was found. In Table 10 (experiment 76, with X434II as the donor parent) no significant grain yield differences (at the 5% level) between resistant and susceptible isopopulations were present with Goodfield as the recurrent parent, while the Bc_2F_2 generation of O'Brien, and the F_2 and Bc_1F_2 generations of Lodi had significant grain yield differences. The yield increase associated with the crown rust resistance allele was expressed as the recurrent parent. This same resistance allele was present in X270I (Table 11, experiment 78), but in this case additive gene action appeared more prevalent, with eight of the nine comparisons having the resistant isopopulation grain yield means substantially higher (10 g or more) than the susceptible one. In five of these nine comparisons the resistant isopopulation was significantly higher in grain yield than their susceptible counterparts. For experiment 77 (Table 13)

epistasis was probably involved since grain yield advantages were not consistently transferred into the three recurrent parents. With X423 as the donor parent (experiment 69, Table 27) resistant isopopulations derived from Goodfield and O'Brien were consistently higher than the susceptible counterparts, but with Lodi as the recurrent parent the susceptible isopopulations were higher in grain yield for both generations. Likewise, an epistatic type of gene action was concluded with X550I as the donor parent (Table 29), with the susceptible isopopulation being significantly higher yielding than the resistant counterparts in both generations for Goodfield and the F_2 generation for Lodi, while no grain yield differences between resistant and susceptible isopopulations were present for O'Brien derivatives. Therefore, it was concluded that in four of these five experiments an epistatic type of gene action was operative, with only experiment 78 (X270I) indicating an additive type of gene action.

The results of my study also bear upon the use of exotic germplasm in plant breeding programs. The original lines used as donors of disease-resistance alleles (i.e., C.I. 8079, C.I. 7171, etc.) were generally very exotic (C.I. 8079 was a collection from the weedy species A. sterilis) and yet major alleles for grain yield in Iowa were found in these exotic sources. It is only incidental that the yield alleles were associated with disease-resistance genes in the exotic lines. Certainly, these results illustrate that exotic and seemingly

unadapted lines can carry genes with a large beneficial effect when they are transferred into adapted genotypes. Backcrossing certainly would appear to be the best method for transferring the small chromosomal segment that carries the desirable gene(s) from an unadapted into an adapted genotype.

Where linkage exists between a rust reaction locus and a grain yield deviation, information is needed to answer two questions: (1) what is the crossover percentage between the rust reaction and grain yield loci, and (2) is the grain yield deviation due to a single yield locus or a block of yield loci that can dissociate from one another. For a linkage between crown rust reaction and grain yield loci to be useful in practical plant breeding programs the crossover percentages would need to be lower in magnitude than those I found (Table 42). Further studies utilizing nearly isogenic lines, rather than isopopulations could provide more precise estimates of a crossover percentage. Specifically, the most accurate estimates of crossover percentages would be obtained by crossing an isogenic line that possesses the rust resistance allele and associated yield deviation to the recurrent parent. The segregates from such a cross would have equivalent genetic backgrounds, and therefore, any grain yield differences found between resistant and susceptible segregates would be directly attributable to the rust resistance allele and the linked yield locus (loci). Segregates that deviated from the expected yield-rust resistance patterns would be crossovers, and the

result would be an accurate estimate of crossing over between the resistance and grain yield loci.

It is unfortunate that the grain yield increases associated with the individual crown rust loci were governed by an epistatic type of gene action. With additive gene action rust resistance alleles at several loci which had favorable yield associations could be transferred into the same genetic background with the expectation that the cumulative yield increase would be the sum of their increases. For example, combining the 6.7, 7.7, and 5.9 percent grain yield increases associated with resistance alleles from isolines X434II, X541, and X423, respectively, could theoretically give a total yield boost of 20 percent, if all of these rust reaction alleles were placed in the same genotype. If this 20 percent increase in grain yield could be obtained, it would be more than equivalent to the yield improvement accomplished for oats in Iowa over a period of 30 years (Browning et al., 1964). Since seemingly the yield genes with which I was working showed an epistatic type of gene action, it would be difficult to attain this 20 percent yield boost by combining resistance alleles and their associated yield increases into a single cultivar.

SUMMARY

Grain yield data summarized over six years indicate certain nearly isogenic oat cultivars (Avena sativa ssp.) contain specific crown rust reaction loci which are associated with grain yield deviations when tested in rust-free environments. In my study an attempt was made to incorporate each of these grain yield associations separately into each of three different genetic backgrounds via backcrossing using the specific crown rust resistance alleles as marker genes. Resistant and susceptible isopopulations of F_2 -, Bc_1F_2 -, and Bc_2F_2 -derived lines were the experimental units to test the null hypothesis of no association between grain yield and crown rust resistance.

Eight isolines of oats, each having a unique crown rust resistance gene, were crossed to three susceptible recurrent parents. Populations of homozygous resistant and susceptible F_2 -, Bc_1F_2 - and Bc_2F_2 -derived lines were selected from each parental combination of donor and recurrent parents. These groups of resistant and susceptible lines provided resistant and susceptible isopopulations. Measurements were taken on grain yield, test weight, heading date, and plant height. From a regression analysis of the data collected on these traits, t-tests were conducted to test whether resistant and susceptible isopopulations derived from the same parental combination had similar or deviant productivity.

Significant grain yield differences between resistant and

susceptible isopopulations were found in five of ten experiments. Although some significant differences were found for the characters test weight, heading date, and plant height, none were considered large enough to have a major effect on yield. Both the microplot and the four-row plot data on grain yield paralleled previous results although the 1972 grain yield differences were lower in magnitude. Generally, the microplot experiments gave less definitive results when compared to four-row plots. My study found the grain yield associated with specific crown rust loci can be transferred into certain recurrent parents via the backcrossing technique. The expression of each grain yield association was influenced by the genetic background of the recurrent parents used, implying an epistatic type of gene action. Grain yield segregation patterns indicated linkage, rather than pleiotropism, was probably involved in the association between grain yield and rust resistance in the isolines X434II, X541, X270I, X423, and X550I.

LITERATURE CITED

- Arias, J. and Frey, K. J. 1973. Grain yield mutations induced by ethyl methanesulfonate treatment of oat seeds. *Radiation Botany* 13: 73-85.
- Atkins, I. M. and K. F. Finney. 1957. Quality characteristics of two pairs of isogenic lines of wheat. *Agron. J.* 49: 351-353.
- Atkins, I. M. and P. C. Mangelsdorf. 1942. The isolation of isogenic lines as a means of measuring the effects of awns and other characters in small grains. *J. of Amer. Soc. Agron.* 34: 667-668.
- Atkins, I. M. and M. J. Norris. 1955. The influence of awns on yield and certain morphological characters of wheat. *Agron. J.* 47: 218-220.
- Atkins, I. M., M. de Stephano, O. Merkle and R. Kilpatrick. 1966. Influence on grain yields and yield components of leaf rust of wheat and crown rust of oats as measured by isogenic resistant and susceptible lines. *Texas Agr. Exp. Sta. Bull.* 1053. 10 p.
- Bartlett, M. S. and J. B. Haldane. 1935. The theory of inbreeding with forced heterozygosis. *J. Genetics* 31: 327-340.
- Breeze, E. L. and K. Mather. 1957. The organization of polygenic activity within a chromosome in *Drosophila*. *Heredity* 11: 373-395.
- Briggs, F. N. 1935. The backcross method in plant breeding. *J. of Amer. Soc. Agron.* 27: 971-973.
- Briggs, F. N. 1938. The use of the backcross in crop improvement. *Amer. Nat.* 72: 285-292.
- Briggs, F. N. and R. W. Allard. 1953. The current status of the backcross method. *Agron. J.* 45: 131-138.
- Browning, J. A. and K. J. Frey. 1969. Multiline cultivars as a means of disease control. *Ann. Rev. Phytopath.* 7: 355-382.
- Browning, J. A., K. J. Frey, and R. L. Grindeland. 1964. Breeding multiline oat varieties for Iowa. *Iowa Farm Sci.* 18(8): 5-8.
- Burton, G. W. 1966. Plant breeding - Prospects for the future. pp. 391-407. *In* *Plant Breeding*. Iowa State Univ. Press, Ames, Iowa.

- Caldwell, R. M., J. F. Schafer, L. E. Compton, and F. L. Patterson. 1958. Tolerance to cereal leaf rusts. *Science* 128: 714-715.
- Campbell, A. R. and K. J. Frey. 1972. Associations between groats-protein percentage in certain plant and seed traits in interspecific oat crosses. *Euphytica* 21: 352-362.
- Culbertson, J. A. and T. Kommedahl. 1956. The effect of seed coat color upon agronomic and chemical characters and seed injury in flax. *Agron. J.* 48: 25-28.
- Day, A. D. and A. D. Dickson. 1957. Association between nitrogen percentage and certain morphological characteristics in barley. *Agron. J.* 49: 244-245.
- Day, A. D., E. E. Down, and K. J. Frey. 1955. Association between diastatic power and certain visible characteristics and heritability of diastatic power in barley. *Agron. J.* 47: 163-165.
- Dherawattana, A. 1971. Crown rust resistance and cytology of a hexaploid oat with 2 fragments derived from intraspecific hybridization. Unpublished M.S. thesis. Library, Iowa State University, Ames, Iowa.
- Duvick, D. N. 1966. Discussion. p. 183. *In* Plant breeding. Iowa State Univ. Press, Ames, Iowa.
- Everson, E. H. and C. W. Schaller. 1955. The genetics of yield differences associated with awn barbing in the barley hybrid (Lion x Atlas¹⁰) x Atlas. *Agron. J.* 47: 276-280.
- Falconer, D. S. 1964. Introduction to quantitative genetics. The Ronald Press Co., New York.
- Fasoulas, A. C. and R. W. Allard. 1962. Nonallelic gene interactions in the inheritance of quantitative characters in barley. *Genetics* 47: 899-907.
- Fleishmann, G., R. McKenzie, and W. A. Shipton. 1971. Inheritance of crown rust resistance in Avena sterilis L. from Israel. *Crop Sci.* 11: 451-453.
- Frey, K. J. 1965. The utility of hill plots in oat research. *Euphytica* 14: 196-208.
- Frey, K. J. 1972. Stability indexes for isolines of oats (Avena sativa L.). *Crop Sci.* 12: 809-812.
- Frey, K. J. and J. A. Browning. 1971. Association between genetic factors for crown rust resistance and yield in oats. *Crop Sci.* 11: 757-760.

- Frey, K. J., J. A. Browning, and R. L. Grindeland. 1967. Oat variety performance-1963-67. Iowa Coop Ext. Serv. (Publ.) Ag 10-8.
- Frey, K. J., J. A. Browning, and R. L. Grindeland. 1970. New multiline oats - designed to break the chain of crown rust. Iowa Farm Sci. 24(8): 3-6.
- Frey, K. J., J. A. Browning, and R. L. Grindeland. 1971a. Registration of Multiline E68, Multiline E69, and Multiline E70 oat cultivars. Crop Sci. 11: 939.
- Frey, K. J., J. A. Browning, and R. L. Grindeland. 1971b. Registration of Multiline M68, Multiline M69, and Multiline M70 oat cultivars. Crop Sci. 11: 940.
- Frey, K. J., J. A. Browning, and R. L. Grindeland. 1971c. Implementation of oat multiline cultivar breeding. pp. 159-169. Proc. IAEA/FAO Panel on mutation breeding for disease resistance. IAEA/FAO Joint Pub. No. 412-417. Vienna, Austria.
- Gaul, H. and J. Grunewaldt. 1971. Independent variation of culm length and spike-internode length of a barley erectoides mutant in a changed genetic background. Proc. of Second Intern. Barley Genetics Symp. pp. 106-118.
- Gaul, H., J. Grunewaldt, and C. Hesemann. 1968. Variation of character expression of barley mutants in a changed genetic background. pp. 77-95. Mutations in Plant Breeding II, IAEA, Vienna.
- Hanson, W. D. 1959a. The breakup of initial linkage blocks under selected mating systems. Genetics 44: 857-868.
- Hanson, W. D. 1959b. Early generation analysis of lengths of heterozygous chromosome segments around a locus held heterozygous with backcrossing or selfing. Genetics 44: 833-837.
- Harding, I. and R. W. Allard. 1965. Genetic variability in highly inbred isogenic lines of the lima bean. Crop Sci. 5: 203-206.
- Haunold, A., V. A. Johnson, and J. W. Schmidt. 1962. Genetic measurements of protein in the grain of Triticum aestivum L. Agron. J. 54: 203-206.
- Jensen, N. F. and Federer, W. T. 1964. Adjacent row competition in wheat. Crop Sci. 4: 641-645.

- Johnson, J. W. and A. M. Schlehuber. 1969. Association between greenbug resistance of wheat and several quantitative characters. *Agron. Abstr.* 1969: 10.
- Johnson, V. A., J. W. Schmidt, D. J. Mattern, and A. Haunold. 1963. Agronomic and quality characteristics of high protein F₂-derived families from a soft red winter-hard red winter wheat cross. *Crop Sci.* 3: 7-10.
- Johnson, V. A., D. A. Whited, P. J. Mattern, and J. W. Schmidt. 1968. Wheat can be improved as human food. *Nebraska University College of Agriculture and Home Economics Quarterly: Farm, Ranch, and Home.*
- Kohel, R. J. and T. R. Richmond. 1971. Isolines in cotton: effects of nine dominant genes. *Crop Sci.* 11: 387-389.
- Law, C. N. 1967. The location of genetic factors controlling a number of quantitative characters in wheat. *Genetics* 56: 445-461.
- Lee, J. A. 1964. Effects of the pilose allele, H₂, on a long staple upland cotton. *Crop Sci.* 4: 442-443.
- McNeal, F. H., D. E. Baldridge, and M. A. Berg. 1969. Agronomic and quality characteristics of awned and awnleted populations of spring wheat. *Crop Sci.* 9: 333-335.
- Middleton, T. and T. Hebert. 1950. Purple straw color in relation to kernel weight in wheat. *Agron. J.* 42: 520.
- Murphy, H. C. 1935. Physiologic specialization in Puccinia coronata avenae. U.S. Dept. of Ag. Tech. Bull. 433.
- Qualset, C. O., C. W. Schaller, and J. C. Williams. 1965. Performance of isogenic lines of barley as influenced by awn length, linkage blocks, and environment. *Crop Sci.* 5: 489-494.
- Riddle, O. C. and G. A. Baker. 1944. Biases encountered in large scale yield tests. *Hilgardia* 16: 1-14.
- Sadanaga, K. and M. D. Simons. 1960. Transfer of crown rust resistance of diploid and tetraploid species of hexaploid oats. *Agron. J.* 52: 285-288.
- Sadanaga, K., H. C. Murphy, and R. Grindeland. 1960. Inheritance of stem resistance of C.I. 7232, a derived tetraploid oat. *Phytopathology* 50: 779-781.
- Schaller, C. W., C. O. Qualset, and J. N. Rutger. 1972. Isogenic analysis of the effects of the awn on productivity of barley. *Crop Sci.* 12: 531-535.

- Sears, O. H. and D. L. Lynch. 1951. Importance of inoculation. *Soybean Digest* 11: 15-17.
- Simons, M. D. 1967. Crown rust resistance of the oat strain, P.I. 174544. *Crop Sci.* 7: 475-477.
- Simons, M. D., I. Wahl, and A. D. deSilva. 1962. Strains of noncultivated *Avena* spp. resistant to important races of the crown rust fungus. *Phytopathology* 52: 585-586.
- Singh, B. P. 1971. Characterization in isogenic lines of oat crown rust resistance genes from four sources. Unpublished Ph.D. dissertation. Library, Iowa State University, Ames, Iowa.
- Spickett, S. G. and J. M. Thoday. 1966. Regular responses to selection. *Genet. Res.* 7: 96-121.
- Sun, P.L.F. and H. L. Shands. 1968. The inheritance of kernel weight in relation to rust reactions of several spring wheat crosses. *Univ. of Wisconsin 1968 Agron. Abst.*
- Suneson, C. A. and H. Stevens. 1957. An evaluation of smooth-awned and hooded Atlas barley. *Agron. J.* 49: 50-52.
- Suneson, C. A., B. B. Bayles, and C. C. Fifield. 1948. Effects of awns on yield and market quality of wheat. *USDA Circ.* 783.
- Suneson, C. A., O. C. Riddle, and F. N. Briggs. 1941. Yields of varieties of wheat derived by backcrossing. *Agron. J.* 33: 835-840.
- Suneson, C. A., C. W. Schaller, and E. H. Everson. 1952. An association affecting yield in barley. *Agron. J.* 44: 584-586.
- Swaminathan, M. S., A. Austin, A. K. Kaul, and M. S. Naik. 1969. Genetic and agronomic enrichment of the quantity and quality in cereals and pulses. pp. 71-86. *In* New approaches to breeding for improved plant protein. FAO/IAEA, Vienna, Austria.
- Tandon, J. P., S. S. Dhillon, and A. K. Goswami. 1970. An association between locus for grain colour and protein content in wheat (*Triticum aestivum*). *Canadian J. of Genetics and Cytology* 12: 28-36.

- Theis, T., H. C. Murphy, M. D. Simons, L. Calpouzos, M. D. McVey, and F. M. Porter. 1961. Oat varieties with adult-plant field resistance to race 264 of the crown rust fungus. *Phytopathology* 51: 303-305.
- Thoday, J. M. 1961. Location of polygenes. *Nature* 191: 368-370.
- Tiyawalee, D. 1972. Studies on linkage between protein and crown-rust reaction loci in crosses of Avena sativa x A. sterilis. Unpublished Ph.D. dissertation. Library, Iowa State University, Ames, Iowa.
- Weber, C. R. 1966a. Nodulating and nonnodulating soybean isolines: I. Agronomic and chemical attributes. *Agron. J.* 58: 43-46.
- Weber, C. R. 1966b. Nodulating and nonnodulating soybean isolines: II. Response to applied nitrogen and modified soil conditions. *Agron. J.* 58: 47-49.
- Wiebe, G. A. 1952. Isogenic analysis in barley. *Abst. Amer. Soc. Agron., Cincinnati, Ohio.*
- Wiebe, G. A., F. C. Petr, and H. Stevens. 1963. Interplant competition between barley genotypes. In W. D. Hanson and H. F. Robinson, eds. *Statistical genetics and plant breeding*. Nat. Acad. Sci.-Nat. Res. Coun. Publ. 982: 546-555.
- Zillinsky, F. J., K. Sadanaga, M. D. Simons, and H. C. Murphy. 1959. Rust-resistant tetraploid derivatives from crosses between Avena abyssinica and A. strigosa. *Agron. J.* 51: 343-345.

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