# RESISTANCE OF BARLEY TO CEREAL LEAF BEETLE
# (OULEMA MELANOPUS L.)

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# ABSTRACT

## RESISTANCE OF BARLEY TO CEREAL LEAF BEETLE (OULEMA MELANOPUS L.)

by Sang Ki Hahn

The cereal leaf beetle (Oulema melanopus L.), a new insect pest, was first identified in North America at Galien, Michigan in 1962, and since then has shown a great potential to damage the small grains.

Shortly after the identification of the cereal leaf beetle in 1962, the search for and identification of host resistance of barley was initiated. On the basis of the field and laboratory screening results, eight parental lines were selected to make a diallel cross set in order to investigate the genetic basis of resistance. In addition, a back-cross with Larker$^2$X CI 6671 was made.

The laboratory larval test for resistance was conducted for the $F_1$ from the six parental diallel cross set and the field test was carried out for the $F_2$ progenies of the eight parental diallel cross and of the back-cross.

The resistance to cereal leaf beetle in barley appears to be recessive. The resistance mechanism associated with cereal leaf beetle in barley seems to be both due to nonpreference of the barley plant by feeding larvae and differential egg laying.

The most resistant combination from the eight parental diallel cross was CI 6671 X CI 6469. Transgressive inheritance was found in the cross of the two lines which indicates the possibility of obtaining higher resistance.

# RESISTANCE OF BARLEY TO CEREAL LEAF BEETLE (*OULEMA MELANOPUS* L.)

By

Sang Ki Hahn

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# INTRODUCTION

The cereal leaf beetle, Oulema melanopus L., a newly introduced insect pest, has shown a great potential to damage small grain production in the United States. This insect was first identified in North America at Galien, Michigan in 1962 and since then, has spread throughout most of Michigan, Indiana, and Ohio (2, 3).

Both adults and larvae of the beetle greatly damage the small grains, with the greatest damage to oats followed by barley and wheat.

Shortly after the identification of this insect, an extensive screening program was initiated to search for host plant resistance in the small grains. World collections of small grains have been tested both in the field nursery and in the laboratory by the United States Department of Agriculture, Michigan State University and Purdue University. Highly resistant wheat strains were found but only some moderately resistant barley strains were obtained.

There have been no studies on the genetics of resistance to this new insect pest in barley. This study is an attempt to find the genetic basis of resistance of the barley plant to the cereal leaf beetle.

# REVIEW OF LITERATURE

The cereal leaf beetle has been a pest of small grains in Europe for many years, occurring throughout the humid and subhumid areas of the entire Western Paleoarctic region including Norway, Central Siberia, North Africa, the entire Mediterranean Basin and the Canary and Madeira Islands (cf. 2, 3).

The biology regarding the life cycle, seasonal appearance and habits of the cereal leaf beetle has been discussed by Ruppel (11) and Castro, Ruppel and Gomulinski (2).

Gallun and Ruppel (4) reported the field screening results of adult and larval feeding damage in Michigan in 1962-1963 for small grains including wheat, oats and barley. The wheats with highly pubescent leaves were largely avoided for oviposition. Gallun, Everson, Ruppel and Craddock (5) continued the field studies to evaluate host plant resistance of cereal crops in 1963-1964. They reported the results of larval feeding damage for 16,095 wheat, 5,423 oat and 8,634 barley strains totaling 30,152 of which, approximately 12 percent of the wheats, 4 percent of oats and less than 1 percent of the barleys had zero to a trace of feeding and rated as resistant. The report of the continued studies in 1964-1965 were made by Schillinger, Gallun, Everson, Smith and Cradock (12). No oats or barley entries were found to possess as high a level of resistance as wheat but some were less preferred as hosts. After four years of successive field tests under various conditions, Schillinger, Smith and Cradock (15) selected many of the highly resistant lines of wheat and only a few of spring barley. Among the several resistant spring barley lines, two of them, CI 6671 and CI 6469, have shown the most resistance with 15 to 40 percent of foliage damage. No winter barley lines were found with more resistance than the spring types.

Resistance is a relative aspect which arises from the relationships between insect and plant. Beck (1) divided the relationships into two principal aspects: (i) host selection by the insect; and (ii) resistance to the insect by the plant. Painter (10) defined the resistance of plant to insect as "the relative amount of heritable qualities possessed by a plant which influence the utlimate degree of damage done by the insect." Recently Beck (1) employed a slightly different definition that "plant resistance is the collective heritable characteristics by which a plant species, race, clone, or individual may reduce the probability of successful utilization of that plant as a host by an insect species." Painter (9,10) divided plant resistance mechanisms into three main categories: (i) preference and nonpreference: in which a plant displays a degree of resistance by exerting an adverse effect on an insects behavior; (ii) antibiosis: in which a plant is resistant by exerting an adverse influence on the growth and survival of the insect; and (iii) tolerance: in which a plant is capable of supporting an insect population without loss of vigor and without reduction of crop yield. While, Beck (1) dropped the tolerance from Painter's three main categories and classified the mechanisms into just "non-preference and antibiosis," because tolerance is an important agronomic plant characteristic and it implies a biological relationship between insect and plant that is quite different from resistance in the strict sense.

According to Gallun and Ruppel (4) and Schillinger (14), plant resistance of wheat to the cereal leaf beetle is primarily associated with nonpreference for oviposition by the adult due to the hairness of the leaf surface. Schillinger (14), working with wheat, has shown that all highly resistant Triticum dicoccum accessions were pubescent but pubescent leaf surface per se, is not the sole factor in determining resistance. However, a barley with pubescence like that in wheat is not known and resistance in barley involves a different mechanism from that of pubescence (15).

Schillinger, Gallun, Everson, Smith and Craddock (12) pointed out that resistance to the cereal leaf beetle in small grains seems to be complicated by the stage of physiological development, type of vegetative growth and disease susceptibility of the plant. Wilson and Shade (16) showed that preference for oviposition differed with the advances of growth stages of the host plant.

Schillinger, Gallun, Everson, Smith and Craddock (12) reported that when pubescent winter wheats were grown in the spring nursery, the resistance was dissipated. Schillinger (13) stated that winter wheat varieties which appeared immune to beetle attack in a fall-planted field nursery were susceptible when tested as non-vernalized seedlings in the laboratory. He also stated that the resistance was greatly influenced by environmental variations and by instability of the adult beetle population under field nursery conditions.

Gallun, Ruppel and Everson (6) pointed out that damage from adult feeding is very little compared to that from larval feeding in the spring unless the number of beetles is extremely high. Everson, Gallun, Schillinger, Smith and Craddock (3) also reported that the most severe feeding damage in the field is influenced by the larval stage.

Schillinger (14), working with wheat, has shown that the resistance reaction in the field nursery was highly consistent with the resistance to larval damage in the laboratory. Thus, the larval test clarified and substantiated the leaf damage ratings of resistant reactions to the cereal leaf beetle that were obtained in the field nursery.

Gallun, Ruppel and Everson (6) stated that larval preference will influence the amount of damage per plant because larvae tend to migrate from leaf to leaf, seeking a preferred food, and the resulting feeding on any one plant could be slight.

Everson, Gallun, Schillinger, Smith and Craddock (3) proposed that the primary center of resistant germ plasm of wheat seemed to be the large continuous area of Asia, Asia Minor and Eurasia.

# MATERIALS AND METHODS

Shortly after the identification of the cereal leaf beetle in 1962, the search for and identification of host resistance of barley was initiated. These tests have been conducted cooperatively by entomologists, plant geneticists, and agronomists of Michigan State University, Purdue University and the United States Department of Agriculture. On the basis of the field and laboratory screening results, eight parental lines were selected to make a diallel cross set. They are given in Table 1.

Among the eight lines, CI 6469 and CI 6671 were used as resistant parents and 411-1, CI 10001 and CI 10968 were used as susceptible ones.

The materials for study consisted of 28 $F_1$ and $F_2$ plants from all possible crosses of eight barley lines. Crosses were made in the growth chamber during the summer of 1965. Part of the $F_1$ seeds from each combination were grown in a growth chamber to obtain $F_2$ seeds for field examination. The remaining $F_1$ seeds of each combination were saved for laboratory tests. In addition a back-cross with $\text{Larker}^2$ X CI 6671 was made in the field and the $F_2$ progenies from each $F_1$ plant were run in a field test.

TABLE 1.--Parents used for the diallel cross.

| Parental Number | Parent | Source | Growth Habit | Resistance to Beetle | Characters |
|---|---|---|---|---|---|
| 1 | 411-1 | Mich. Sel. | Winter | Susceptible | Late in maturity, 6 row, rough awn |
| 2 | CI 938 | Abyssinia | Spring | Moderate | Early, 2 row, rough awn |
| 3 | CI 1031 | Australia | Spring | Moderate | Late, 2 row, rough awn |
| 4 | CI 5057 | Algeria | Spring | Moderate | Early, 6 row, naked, hooded awn |
| 5 | CI 6469 | Poland | Spring | Resistant | Intermediate, 6 row smooth awn |
| 6 | CI 6671 | Iran | Spring | Most Resistant | Most early, 6 row, rough awn |
| 7 | CI 10001 | Canada | Spring | Susceptible | Early, 6 row, smooth awn |
| 8 | CI 10968 | U. S. A. | Spring | Susceptible | Late, 6 row, rough awn |

For the laboratory larval test for resistance, the procedures employed by Schillinger (13, 14) were used. Two $F_1$ barley seedlings were grown in 3½-inch plastic pots containing potting soil. Washed sand was poured on top of the potting soil to allow better detection of the larvae. When the first seedling leaf was fully developed in about a week after sowing, the larval test was made. Late first or early second-instar larvae weighing between 0.9 and 1.1 mg. were used for the test. Two larvae per seedling were confined to the plants by a glass globe embedded in the sand and sealed on the top with four layers of cheesecloth. The test plants with larvae were placed in a growth chamber set at 80 F. for 16 hours of light and at 68 F. for 8 hours of darkness.

The field nursery was set up at Galien, Michigan. The $F_2$ progenies were sown in four-foot rows spaced one-foot apart between rows, using two replications. The border around the block was sown to susceptible Clintland 64 oats to verify the uniformity of the beetle infestations. Natural infestation was relied upon but the combination of a smaller than expected beetle population and an unfortunate insecticide drift from an aerial application to a neighboring oat field limited the resistance evaluations to one site. Fortunately, a high population of beetles infested the alternate nursery. The $F_2$ progenies from the diallel cross and back-cross were sown on April

14, 1966. About 40 seeds for each entry were drilled, using a funnel seeder, into each four-foot row, the rows being spaced one-foot apart.

Evaluations of larval feeding damage were made twice, on June 13 prior to heading and on June 21 after heading. Each progeny was evaluated for larval feeding damage based on the amount of leaf surface consumed.

Ratings of zero to 10 were used. A zero rating designated no larval feeding, "1" = 10 percent feeding, "2" = 20 percent, "3" = 30 percent and so on up to "10" designating 100 percent larval feeding damage, respectively. This scoring system for larval feeding damage was used in both laboratory and field tests. In both laboratory and field tests only larval feeding damage ratings were made, where damage caused by larval feeding was easily distinguishable from the damage caused by adult feeding. Damage from adult feeding was very little compared to that of larval feeding.

The number of larvae on $F_2$ progenies in the field was determined by actual count on 10 $F_2$ plants which were randomly chosen. This was repeated twice.

All the data from the laboratory larval feeding for the $F_1$ and field larval feeding test for $F_2$ progenies of the 8 x 8 diallel cross were analyzed according to the technique evolved by Jinks (8) and Hayman (7). This method of genetic analysis was applied in this study because the resistance of barley to cereal leaf beetle measured by larval feeding damage appeared to be rather continuous and not clearly discrete. This method provided information on the dominance order of parents, genetic relationship among the parents and presence of a certain type of genetic interaction.

In the analysis, the second degree statistics such as variance ($V_r$) and covariance ($W_r$) were calculated and the regression of the latter to the former was obtained. Where $W_r$ is the covariance of the offspring of $r^{th}$ array with non-recurring parents, $V_r$, the variance of the offspring of $r^{th}$ parental array. The fact that $W_r{}^2 \leq V_r\ V_p$, where $V_p$ is the variance of parents, implies that all the $V_r$ and $W_r$ points of the graph lie inside the limiting parabola, $W_r{}^2 = V_rV_p$.

In the absence of dominance, the variances and covariances of arrays estimate the points $\overline{W}_r = \frac{1}{2}D$, $\overline{V}_r = \frac{1}{4}D$; where $\overline{W}_r$ is the mean of the covariances, $\overline{V}_r$ is the mean of the variances and D is the additive dominance. In the presence of dominance the regression line has a unit slope and passes through the origin ($H_1 = D$). If the dominance is partial the regression line intersects the $W_r$ axis on the positive side ($H_1 < D$), whereas in the case of overdominance ($H_1 > D$) it intersects on the negative side. In the absence of non-allelic interaction the array variance ($V_r$) and array covariances ($W_r$) are:

$$V_r = \Sigma \; u_i \; v_i \; (d_i \pm h_i)^2$$

$$W_r = \Sigma \; 2u_i \; v_i \; d_i \; (d_i \pm h_i)$$

Where negative the signs correspond to positive alleles in the $r^{th}$ parent and vice versa. The points on the ($W_r$, $V_r$) graph lie in order of dominance along the straight line from the complete dominant with minimum $V_r = \Sigma \; u_i \; v_i \; (d_i - h_i)^2$ and $W_r = \Sigma \; 2u_i \; v_i \; d_i \; (d_i - h_i)$ to complete recessive with maximum $V_r = \Sigma \; u_i \; v_i \; (d_i + h_i)^2$ and $W_r = \Sigma \; 2u_i \; v_i \; d_i \; (d_i + h_i)$, where $u_i$ and $v_i$ are the frequency of dominant genes and recessive genes, respectively. And $d_i$ is the additive genetic effect and $h_i$ is the dominant effect.

On the ($W_r$, $V_r$) graph, array points of the regression line depict the dominance order of the parents, and the distance between points provides a measure of the effectiveness of the dominant and recessive alleles of the extreme genotypes. The above conclusions are reliable, provided the following restrictions hold for the material under study: (i) homozygous parents, (ii) no multiple allelism, (iii) genes independently distributed in the parents, and (iv) no genic interaction.

Failure of the hypotheses is indicated by a non-significant regression or when the regression is significantly different from a slope of unity. Non-significance of regression may also arise if all $h_i = 0$. Test of significance of regression of $W_r$ on $V_r$ was done by the t test using the formulae:

$$(a)\ t = \frac{b - 0}{s_b}, \quad (b)\ t = \frac{1 - b}{s_b}$$

Where, $s^2{}_b = \frac{s^2_{y \cdot x}}{\Sigma x^2}$, and the appropriate degree of freedom is $(r - 2)$, r being the number of arrays. When regression coefficient is significantly different from zero, dominance is present and when b is significantly different from 1, it indicates that gene interaction plays a part in determining the control of the characters examined.

# RESULTS

The intent of this study was to obtain genetic information on the resistance to the cereal leaf beetle among selected barley lines. These lines are discussed first on the basis of the results obtained from the laboratory and field larval feeding tests for the $F_1$ and $F_2$ diallel cross and secondly on the basis of the field feeding test for the $F_2$ backcross progenies.

The first step in the diallel analysis was to test the variability of parents and hybrids for larval feeding damage scores. The results of analysis of variance for larval feeding scores from the laboratory test on $F_1$ of six parental diallel cross is given in Table 2. There

TABLE 2.--Analysis of variance for larval feeding damage from the laboratory test; six parental diallel cross, $F_1$.

| Source | Degree of Freedom | Mean Square | F |
|---|---|---|---|
| Total | 62 | -- | --- |
| Reps. | 2 | 5.32 | 16.63** |
| Lins | 20 | 9.72 | 30.38** |
| Error | 40 | 0.32 | |

**Significant at the 1 percent level.

are highly significant differences among hybrids. The means of larval feeding damage in the $F_1$ larval test range from 2.5 to 5.3. This indicates that among barley strains there may be some difference in resistance to cereal leaf beetle which might be due to differences in genetic background.

Having found significant differences among parents and hybrids in resistance to larval feeding, the genetic relationship among parents and their diallel cross was investigated using the Jinks-Hayman's diallel analysis and graphical analysis based on array variances and covariances. In the analysis of the $F_1$, laboratory data of three replications were pooled and subjected to the diallel analysis. The pooled $F_1$ data of laboratory larval feeding scores from the 6 x 6 diallel cross set are given in Table 3, where each figure is a total of $F_1$ values of three replicates for each combination. The variances and covariances of arrays are presented in the right hand column of the table. Using the statistics $V_r$, $W_r$, and $V_p$, the ($W_r$, $V_r$) graph was drawn and the limiting parabola was constructed using the formula $W_r^2 = V_r V_p$. The graphical analysis provides the degree of dominance, dominance order of parents, and additional information about the genetic relationship among the parents. The graphical analysis is shown in Figure 1. Inspection of Figure 1 shows that analysis of the data for all arrays gives an

TABLE 3.--Larval feeding damage score from the laboratory test, total of three replications; six parental diallel cross, $F_1$.

| Parental Number | Parent | 3 | 4 | 5 | 6 | 7 | 8 | $V_r$ | $W_r$ |
|---|---|---|---|---|---|---|---|---|---|
| 3 | CI 1031 | 14.0 | | | | | | 0.1222 | -0.1000 |
| 4 | CI 5057 | 15.0 | 12.0 | | | | | 0.1882 | 0.2204 |
| 5 | CI 6469 | 16.0 | 15.0 | 14.0 | | | | 0.1519 | 0.1185 |
| 6 | CI 6671 | 15.0 | 12.5 | 13.0 | 7.5 | | | 0.7556 | 0.7389 |
| 7 | CI 10001 | 13.0 | 14.0 | 14.0 | 13.0 | 14.0 | | 0.0630 | 0.1259 |
| 8 | CI 10968 | 14.0 | 13.0 | 13.0 | 14.0 | 15.0 | 14.5 | 0.0713 | 0.0352 |

TABLE 3.--Larval feeding damage score from the laboratory test, total of three replications; six parental diallel cross, $F_1$.

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| 6 | CI 6671 | 15.0 | 12.5 | 13.0 | 7.5 | | | 0.7556 | 0.7389 |
| 7 | CI 10001 | 13.0 | 14.0 | 14.0 | 13.0 | 14.0 | | 0.0630 | 0.1259 |
| 8 | CI 10968 | 14.0 | 13.0 | 13.0 | 14.0 | 15.0 | 14.5 | 0.0713 | 0.0352 |

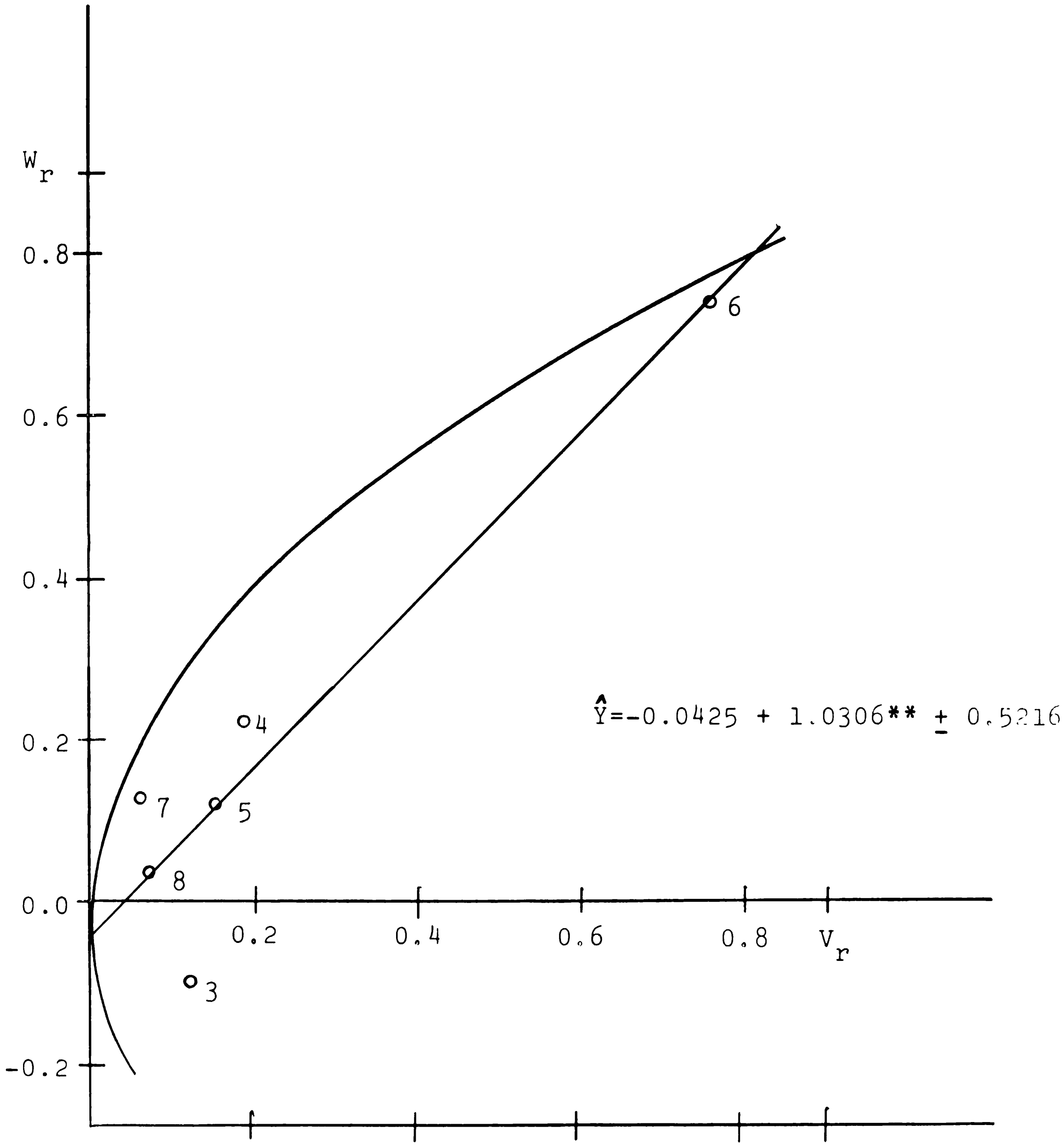

Figure 1.--A diallel graph for larval feeding damage in the laboratory test; 6 parental diallel cross, $F_1$.

excellent linearity. The regression of $W_r$ on $V_r$ is significantly greater than zero and not significantly different from a unit slope, indicating a very good fit to the assumptions underlying the diallel cross analysis. From the graph it will be noted that the regression line passes very near the origin and that array 6 is at the recessive position and the others are near the origin. This indicates that array 6 (CI 6671) possesses recessive genes for resistance to larval feeding. It is worth noting that variety 6 (CI 6671) has been the most resistant barley variety from the successive field and laboratory tests since 1962. This result indicates that resistance to larval feeding is recessive.

The analysis of variance for the $F_2$ field test data taken prior to heading is given in Table 4.

TABLE 4.--Analysis of variance for larval feeding damage prior to heading from the field test; eight parental diallel cross, $F_2$.

| Source | Degree of Freedom | Mean Square | F |
|---|---|---|---|
| Total | 71 | -- | --- |
| Blocks | 1 | 0.170 | 0.327 |
| Lines | 35 | 2.968 | 5.708** |
| Error | 35 | 0.520 | |

**Significant at 1 percent level.

Table 4 shows highly significant differences in larval feeding scores among the progenies of an 8 x 8 diallel cross. The means of larval feeding damage range from 3.5 to 8.0. As there are significant differences among parents and their progenies in resistance, the genetic relationship among parents and their progenies were investigated also. The pooled data of the field test on larval damage prior to heading are given in Table 5. Each figure in the table is a total of non-reciprocal $F_2$ progenies of two replications for each combination.

These data in Table 5 were used for analysis. The array variances and covariances are presented in the right hand column in Table 5. The diallel graph is shown in Figure 2, where the analysis gives a somewhat random scatter of points. The regression line of $W_r$ on $V_r$ for the $F_2$ data prior to heading is significantly different from slope $b = 0$ and from $b = 1$. Accordingly, it is difficult to draw any conclusion about gene action for resistance to beetle by observing this diallel graph. The indeterminant results are thought to be partly due to the suppressed leaf beetle activity because of the abnormal weather in the spring of 1966.

The result of analysis of variance for the data taken after heading for the same progenies from 8 x 8 diallel cross are given in Table 6.

TABLE 5.--Larval feeding damage score prior to heading from the field test, total of two replications; eight parental diallel cross, $F_2$.

| Parental Number | Parent | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | $V_r$ | $W_r$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 411-1 | 15.0 | | | | | | | | 0.5134 | 0.8169 |
| 2 | CI 938 | 14.5 | 14.0 | | | | | | | 0.4542 | 0.5022 |
| 3 | CI 1031 | 16.0 | 14.5 | 15.0 | | | | | | 1.3203 | 1.3638 |
| 4 | CI 5057 | 14.5 | 15.0 | 12.0 | 10.0 | | | | | 1.1328 | 0.7879 |
| 5 | CI 6469 | 12.0 | 11.0 | 9.0 | 9.0 | 10.0 | | | | 0.8393 | 0.9375 |
| 6 | CI 6671 | 12.0 | 13.0 | 11.0 | 13.0 | 7.0 | 7.0 | | | 1.4419 | 1.0938 |
| 7 | CI 10001 | 14.0 | 15.0 | 13.0 | 14.0 | 12.0 | 10.5 | 14.0 | | 0.7277 | 0.7723 |
| 8 | CI 10968 | 15.0 | 14.5 | 12.0 | 12.0 | 8.0 | 9.5 | 10.5 | 12.0 | 1.3917 | 1.1362 |

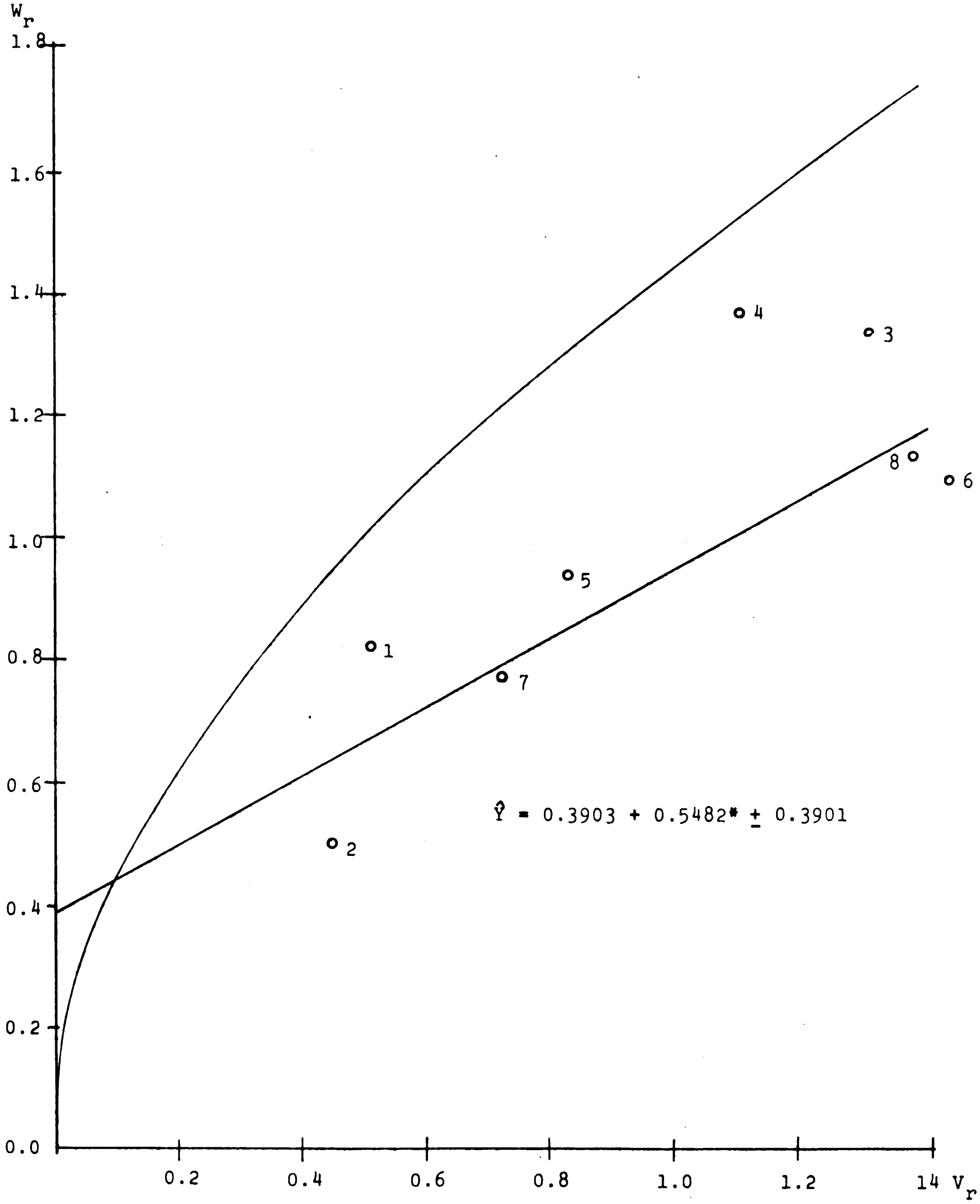

Figure 2.--A diallel graph for larval feeding damage prior to heading in the field test; 8 parental diallel cross, $F_2$.

TABLE 6.--Analysis of variance for larval feeding damage after heading from the field test; eight parental diallel cross, $F_2$.

| Source | Degree of Freedom | Mean Square | F |
|---|---|---|---|
| Total | 71 | | |
| Blocks | 1 | 0.030 | 0.066 |
| Lines | 35 | 2.931 | 6.470** |
| Error | 35 | 0.453 | |

**Significant at 1 percent level.

The pooled data with their array variances and covariances are given in Table 7. When these data were analyzed, the regression of $W_r$ on $V_r$ showed very good linearity and its coefficient is significantly greater than zero but significantly different from a unit slope. The graphical analysis is shown in Figure 3. Array 6 is near the recessive end and is differentiated from the susceptible arrays.

These results show good agreement with that of the laboratory test even though two more arrays were included for analysis. The fact that the regression line is significantly different from unity suggests that there is some type of genic interaction involved.

Tables 5 and 7 show that the most resistant combination of the eight parental diallel cross set is the

TABLE 7.--Larval feeding damage score after heading from the field test, total of two replications; eight parental diallel cross, $F_2$.

| Parental Number | Parent | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | $V_r$ | $W_r$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 411-1 | 18.0 | | | | | | | | 0.2098 | 0.3884 |
| 2 | CI 938 | 18.0 | 18.0 | | | | | | | 0.5000 | 0.3750 |
| 3 | CI 1031 | 18.0 | 18.0 | 17.0 | | | | | | 0.9821 | 1.0625 |
| 4 | CI 5057 | 18.0 | 18.0 | 16.0 | 15.0 | | | | | 0.4955 | 0.3973 |
| 5 | CI 6469 | 16.0 | 14.0 | 12.0 | 14.0 | 13.0 | | | | 1.2991 | 1.1205 |
| 6 | CI 6671 | 17.0 | 18.0 | 15.0 | 17.0 | 9.0 | 10.0 | | | 2.7455 | 1.7991 |
| 7 | CI 10001 | 17.0 | 18.0 | 17.0 | 17.0 | 15.5 | 13.0 | 17.0 | | 0.6417 | 0.9308 |
| 8 | CI 10968 | 19.0 | 18.0 | 17.0 | 16.0 | 11.5 | 14.0 | 15.0 | 17.0 | 1.4364 | 1.2969 |

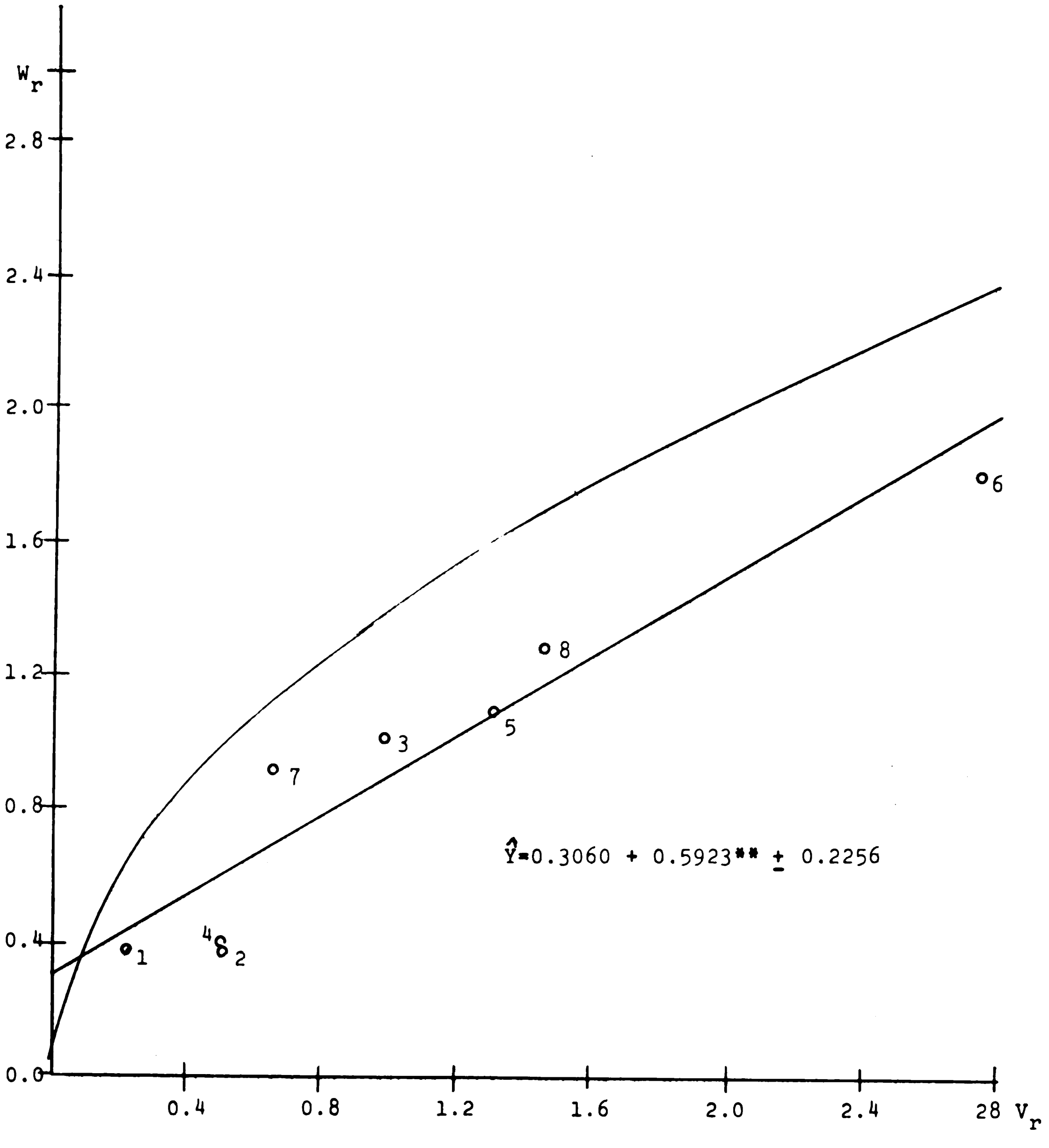

Figure 3.--A diallel graph for larval feeding damage after heading in the field test; 8 parental diallel cross, $F_2$.

cross CI 6671 x CI 6469. This combination resulted in the most highly resistant strain among all the barley entries tested in the field nursery in 1966. The picture is presented in Figure 4.

The 60 $F_2$ progenies from the backcross $\text{Larker}^2$ X CI 6671 were tested in the field nursery with two replications. Strain CI 6671 was used as the resistant parent. In the field test, two entries for each parent and one entry for each progeny were included. Notes concerning feeding damage were taken at two different times, before heading and after heading.

The analysis for the data of larval feeding scores from the $F_2$ backcross progenies are given in Table 8.

TABLE 8. Analysis of variance for larval feeding damage prior to and after heading from the field test; backcross $\text{Larker}^2$ X CI 6671, $F_2$.

| Source | Degree of Freedom | Mean Square | | F | |
|---|---|---|---|---|---|
| | | Prior to Heading | After Heading | Prior to Heading | After Heading |
| Total | 127 | | | | |
| Blocks | 1 | 46.32 | 36.120 | 54.49** | 70.34** |
| Lines | 63 | 1.506 | 1.194 | 1.77* | 2.34* |
| Error | 63 | 0.850 | 0.510 | | |

*Significant at 5 percent level.

**Significant at 1 percent level.

Figure 4.--The most resistant $F_2$ progeny resulting from the cross, CI 6671 X CI 6469.

There were significant differences among the progenies in resistance to larval feeding under field conditions.

Comparing the feeding damage of progenies with that of their parents, there was remarkable segregation in resistance to the cereal leaf beetle. Even the parental difference was not as distinctive. In the observations made prior to heading, the progenies showed variation in resistance ranging from the least damage 4.5 to the most 8.5, when compared to their parents: 5.8 for Larker and 4.5 for CI 6671. For the observation made after heading, the variation was from 6.8 to 9.5, compared to 8.4 and 6.4 for their parents, Larker and CI 6671. The histogram of the distribution of the feeding damage scores is shown in Figure 5. When the backcross is made, there is a tendency to move to the side of the recurrent parent Larker which is susceptible to the beetle. The tendency is much more noticeable after heading when a great number of older larvae have migrated into the nursery. This again indicates that the resistance to cereal leaf beetle is recessive. Resistant strain CI 6671 has a glossy leaf character. The problem is, whether or not the glossy character is related to cereal leaf beetle resistance.

The comparisons of means of larval feeding between the progenies segregating with glossy character and the homozygous normal ones are given in Table 9.

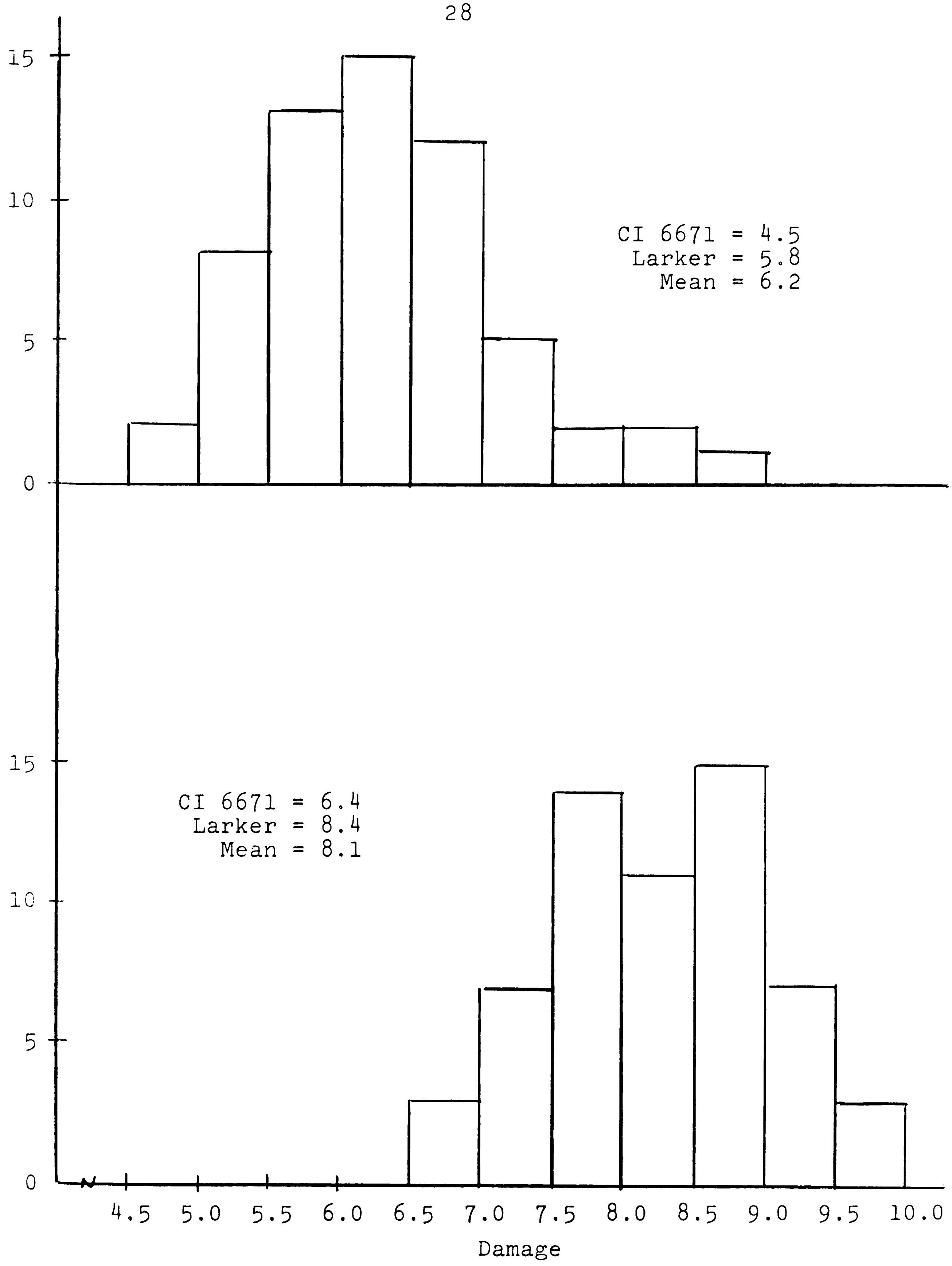

Figure 5.--A histogram of distribution of feeding damage scores for the $F_2$ backcross progenies from Larker$^2$ x CI 6671. Upper: before heading. Lower: after heading.

TABLE 9.--Mean larval feeding damage between glossy and normal progenies.

| Character | Number of Lines | Mean Damage | |
|---|---|---|---|
| | | Before Heading | After Heading |
| Glossy | 25 | 12.42 | 16.04 |
| Normal | 35 | 12.24 | 16.14 |

Before and after heading, there were no differences in feeding damage between the progenies segregating with the glossy character and the homozygous normal ones. Hence, it could be concluded that the glossy character is not associated with resistance to cereal leaf beetle in the cross. The segregation ratio of normal to glossy was checked as 3 to 1, suggesting that a single recessive gene is governing the glossy character. The test result is given in Table 10.

TABLE 10.--$X^2$-test for normal to glossy, 3:1.

| Character | Number of Seedlings From Segregating Lines | $X^{2*}$ |
|---|---|---|
| Glossy | 113 | $1.08^{n.s.}$ |
| Normal | 380 | |

$*X^2_{.05,1} = 3.84$.

n.s.: nonsignificant

From this backcross progeny test, it was observed that the lines 201-2-11 and 201-2-18 were most resistant to feeding damage from the cereal leaf beetle.

Correlations between damage scores from the laboratory test and those from the field test failed to show significance prior to or after heading. The correlation coefficient for before heading was r = 0.32 and that for after heading was r = 0.36. These correlations were calculated using the progeny values of the larval feeding scores from six parental diallel cross.

In order to examine whether there was any relation between the number of larvae and larval feeding damage, correlation coefficients were calculated for both observations. The observed data of number of larvae per plant and larval feeding damage for each combination are compared in Table 11. The correlation coefficient for before heading was r = 0.64 and that for after heading was r = 0.71. Both correlation coefficients are highly significant. These correlation coefficients were calculated from the field nursery data before and after heading of eight parental diallel cross. This indicates that damage in the barley line is proportional to the number of larvae--providing there are no significant differences among the cause and further suggests that there are differences in preference of larval feeding in barley. Hence, this could be an indication that the resistance mechanism associated with cereal leaf beetle in barley might be due to

TABLE 11.--Number of larvae per plant and larval feeding damage score; eight parental diallel cross, $F_2$.

| Parental Number | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | | 7 | | 8 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L* | S* | L | S | L | S | L | S | L | S | L | S | L | S | L | S |
| 1 | 6.35 | 9.0 | | | | | | | | | | | | | | |
| 2 | 5.90 | 9.0 | 4.30 | 9.0 | | | | | | | | | | | | |
| 3 | 5.40 | 9.0 | 5.05 | 9.0 | 3.95 | 8.5 | | | | | | | | | | |
| 4 | 4.60 | 9.0 | 4.50 | 9.0 | 4.55 | 8.0 | 3.30 | 7.5 | | | | | | | | |
| 5 | 5.50 | 8.0 | 4.25 | 7.0 | 3.10 | 6.0 | 4.65 | 7.0 | 4.40 | 6.5 | | | | | | |
| 6 | 4.35 | 8.5 | 5.10 | 9.0 | 5.45 | 7.5 | 3.40 | 8.5 | 2.30 | 4.8 | 1.55 | 5.0 | | | | |
| 7 | 5.85 | 8.5 | 6.55 | 9.0 | 5.85 | 8.5 | 4.10 | 8.5 | 5.75 | 7.8 | 2.80 | 6.5 | 6.15 | 8.5 | | |
| 8 | 5.70 | 9.5 | 5.60 | 9.0 | 6.25 | 8.5 | 5.70 | 8.0 | 3.90 | 5.8 | 4.20 | 7.0 | 5.20 | 7.5 | 6.05 | 8.5 |

*L = Number of Larvae; S = Damage score after heading.

non-preference for the barley plant. The correlation coefficient for after heading was stronger than that for before heading. This would mean that the genetic difference could be more readily detected after heading than prior to heading when the size of the insect and its population are big enough and when enough time has been given the insect to seek preferred plants. The result of the analysis of variance for number of larvae on ten plants prior to heading from eight parental diallel cross is given in Table 12.

TABLE 12..--Analysis of variance for number of larvae on ten plants prior to heading from the field test; eight parental diallel cross, $F_2$.

| Source | Degree of Freedom | Mean Square | F |
|---|---|---|---|
| Total | 71 | | |
| Blocks | 1 | 64.22 | 0.70 |
| Lines | 35 | 288.57 | 3.14** |
| Error | 35 | 91.82 | |

**Significant at 1 percent level.

There are highly significant differences in number of larvae on ten plants among lines. This shows that on resistant lines there are significantly smaller numbers of larvae.

# DISCUSSION

In barley, resistance to the cereal leaf beetle is not as complete as in wheat but it appears to be on a high enough plane to be useful.

Resistance seems to be greatly influenced by the stage of physiological development and type of vegetative growth of the plant. It is also influenced very much by environmental variation and by the activity of the adult beetle and larvae. Resistance appears to be complex, is not clearly understood and the genetics of resistance to cereal leaf beetle would not be simple.

Accordingly the diallel technique evolved by Jinks-Hayman was used for genetic analysis of resistance. From graphical diallel analysis of the larval feeding damage scores from the 6 x 6 $F_1$ diallel cross, array 6 (CI 6671) is at the recessive position and others are at near dominant positions (Figure 1). Since variety 6 (CI 6671) is most resistant to cereal leaf beetle, it can be said resistance to cereal leaf beetle appears to be recessive. When the larval feeding data made prior to heading in the field nursery were analyzed, the eight parental diallel graph showed a random scatter of points (Figure 2). It is difficult to draw any conclusion about gene action of resistance by observing the diallel graph. This indeterminant result is thought to be due to the differential expression of resistance as the growth stage of the plant advances. Suppressed leaf beetle activity because of the abnormal spring weather in 1966 might also be a reason. However, the graphical diallel analysis (Figure 3) for the field data which were taken after heading shows that array 6 is near the recessive end as is true for the laboratory data. The result of this analysis shows good agreement with that of the laboratory test except that the regression line is significantly different from unity, suggesting that gene interaction plays a part in determining the control of the resistance to cereal leaf beetle.

From the diallel analyses for both laboratory and field test data, it appears that the most resistant variety 6 (CI 6671) possesses recessive genes for governing the resistance to cereal leaf beetle. This indicates that the resistance to cereal leaf beetle is recessive. The genetic constitution of variety 5 (CI 6469) which has shown resistance in the field nursery is not clear from the diallel graph. The most resistant combination from the 8 x 8 diallel cross was CI 6671 X CI 6469. This combination was more resistant than its parents and also most resistant among the barley entries tested in the field nursery in 1966. The parental varieties CI 6671 and CI 6469 are from the countries where the cereal leaf beetle has been a pest of small grains for many years. The variety CI 6671 is originally from Iran and the variety CI 6469 is from Poland. It could be assumed that these varieties might have been screened for a long period of time in these areas. It is proposed that the areas around these countries might be a primary center of germ plasm resistance.

Testing the $F_2$ progenies from the backcross, Larker$^2$ X CI 6671, it was observed that there were significant differences among the progenies in resistance to larval feeding damage in the field nursery. This supports the existence of genetic control of resistance to cereal leaf beetle. When the backcross was made to the susceptible recurrent parent, Larker, the progenies moved to the side of the susceptible parent. This again supports the observation that resistance to cereal leaf beetle is recessive.

The resistant strain CI 6671 has a glossy character. It is shown that there is no difference in feeding damage between the progenies segregating for the glossy character and homozygous normal ones. It can be concluded that the glossy character is not associated with resistance to cereal leaf beetle.

The larval feeding damage scores from the laboratory test were not consistent with those from the field test.

Examining the relationship between the number of larvae and the larval damage for eight parental diallel field data, high correlation coefficients were obtained; $r = 0.64$ before heading and $r = 0.71$ after heading when the insect was highly active. This indicates that the

feeding damage in barley is proportional to the number of larvae and further suggests that there is a difference in preference for larval feeding in barley. This could be an indication that the resistance mechanism associated with cereal leaf beetle in barley might be due to nonpreference for the barley plant.

## SUMMARY

This study attempts to obtain genetic information for the control through plant breeding of resistance of barley to larval feeding damage caused by the cereal leaf beetle.

The resistance to cereal leaf beetle in barley appears to be recessive. Variety CI 6671 seems to possess the genes governing resistance to cereal leaf beetle. Genetic expression of resistance seems to be different as plant growth stage advances and it is greatly influenced by environment and by larval activity.

The larval feeding damage scores from the laboratory test appears to be significantly inconsistent with those from the field test in certain lines.

The most resistant combination from the eight parental diallel cross was CI 6671 X CI 6469. The parental varieties of the combination are from the countries where cereal leaf beetle has been a pest for many years, CI 6671 being from Iran and CI 6469 from Poland. It was proposed that the primary center of germ plasm resistance might be the areas around these countries.

The glossy character of the variety CI 6671 is not associated with resistance to cereal leaf beetle. A

highly significant correlation between the number of larvae and feeding damage was obtained. This indicates that the feeding damage in barley is proportional to the number of larvae in the field nursery and further suggests that resistant barley lines are less preferred by larvae. The resistance mechanism associated with cereal leaf beetle in barley seems to be due to nonpreference of the barley plant by feeding larvae. Transgressive inheritance was found in the cross of two lines which indicates the possibility of obtaining higher resistance.

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