

THE INHERITANCE AND MECHANISM OF
RESISTANCE OF BARLEY TO CEREAL
LEAF BEETLE, OULEMA MELANOPUS L.

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John E. Shaffner

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ABSTRACT

THE INHERITANCE AND MECHANISM OF RESISTANCE OF BARLEY TO CEREAL LEAF BEETLE, OULEMA MELANOPUS L.

By

Chung Lee

The mechanism of host plant resistance to the cereal leaf beetle in wheat is related to pubescence and a high degree of resistance has been obtained. Only a moderate degree of resistance has been observed in barley. The mechanism of resistance is not yet known although resistance has been found to be controlled by recessive genes.

The present study aims at understanding the mechanism and the inheritance of host plant resistance in barley and finding a higher degree of resistance. Resistance can be regarded as a complex trait and partitioned into three components -- ovipositional preference by the adult female, antibiosis and recovery of the plant.

A diallel cross series and the progenies of the cross between CI 6671 and CI 6469, the two varieties with the highest degree of resistance now available in barley, were used for the tests. A discriminant function was employed to combine the three components into a single trait and the

Chung Lee

function was converted into a nomographic chart for easy and efficient use.

Ovipositional preference shows a low heritability with a pattern of ambidominance. Plants at the heading stage were much less preferred than at the seedling stage.

Resistance to larval feeding at the seedling stage behaves as a recessive trait although at an older stage, this trait is controlled by another genetic system which appears to be ambidominant. The age of tissue is not responsible for the differential pattern of resistance.

Larval weight gain is a reliable measure of antibiosis.

To obtain a higher degree of resistance, more emphasis should be placed on the larval feeding response at the mature plant stage than the ovipositional preference or recovery of the plant.

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
LITERATURE REVIEW	3
MATERIALS AND METHODS	9
Plant materials	9
Experiments	9
F ₁ Test	9
Field generation test	13
Feeding damage test	14
Plant tissue age test	15
Component test.	16
Diallel cross	18
Statistical Procedures	19
Analysis of genetic variance component. . .	19
Diallel analysis.	21
Discriminant function	22
Nomography.	24

	Page
RESULTS	27
F ₁ Test	27
Field generation test	32
Feeding damage test	37
Tissue age test	45
Component test	49
Diallel cross	57
DISCUSSION.	65
SUMMARY	71
LIST OF REFERENCES.	73
APPENDIX	77

LIST OF TABLES

Table		Page
1	Plant materials used in this investigation. .	10
2	Description of the six parents used in a diallel cross observed	10
3	Stage of growth, description of plant development and age of plants used in the larval feeding experiment	11
4	Analysis of variance of cereal leaf beetle larval weight gain on three growth stages of four barley genotypes	27
5	Comparison of average weight gains of cereal leaf beetle larvae fed on three growth stages of CI 6671, CI 6469, the F ₁ generation of the cross CI6671 x CI 6469 ¹ and Larker a susceptible check	28
6	Standardized values of larval weight gain fed on three growth stages of CI 6671, CI 6469, the F ₁ generation of the cross CI 6671 x CI 6469 and Larker, a susceptible.	29
7	Average cereal leaf beetle feeding damage score on three growth stages of barley plants of four genotypes	32
8	Means and variances of damage score and number of larvae per plant observed in the field with five generations of the cross CI 6671(P ₁) x CI 6469(P ₂).	33



LIST OF TABLES (Cont.)

Table		Page
9	Analysis of variance and over-all mean of cereal leaf beetle larval mobility, feeding damage and weight gain on CI 6671, CI 6469, F ₁ , F ₂ , BC ₁ and BC ₂ generations of CI 6671 x CI 6469 and susceptible varieties Larker and Dickson.	39
10	Average values of cereal leaf beetle larval mobility, damage score and weight gain for 4 stages of plant growth over all entries and replications.	39
11	Average values of cereal leaf beetle larval mobility, damage score and weight gain on eight genotypes of plant over all plant growth stages and replications	40
12	Correlation coefficients between six measurements of the interaction between host plant and cereal leaf beetle larvae . .	41
13	Total and between treatment combination sums of squares (ss) and sums of cross products (cp) of two different mobility measurements, m ₁ and m ₂ of cereal leaf beetle larvae on barley.	42
14	Total and between treatment combination sums of squares (ss) and sums of cross products (cp) between three measurements of cereal leaf beetle larval feeding. . . .	44
15	Average weight gain in mg of larvae grown on the leaves of upper and lower parts of plants at two stages of growth	45

LIST OF TABLES (Cont.)

Table		Page
16	Mean of the number of cereal leaf beetle eggs per leaf, hatchability of eggs, number of larvae per leaf, larval weight gain, total larval weight gain and tiller survival ratio on various genotypes in two stages of plant growth	50
17	Correlation coefficients between observations on the components of resistance -- 1 = number of eggs per leaf; 2 = hatchability; 3 = number of larvae per leaf; 4 = larval weight gain; 5 = tiller survival ratio	56
18	Combined analysis of variance tables for number of larvae per plant and larval feeding damage scores at two growth stages on the F_2 generation of a 6 parent diallel cross	60
19	Total, W_r and V_r values of the number of larvae per plant for the F_2 generation of the 6 parent diallel set	61
20	Total, V_r and W_r values of the damage score at the late stage of the F_2 plants of the 6 parent diallel set	61

LIST OF FIGURES

Figure		Page
1	Standardized larval weight gain of cereal leaf beetle fed on four genotypes at three growth stages.	30
2	Damage score and larvae per plant of the cross CI 6671 x CI 6469 and the F ₁ , F ₂ , BC ₁ and BC ₂ generations.	34
3	Larval weight gain on the leaves of upper and lower parts of young plants of five genotypes.	46
4	Standardized values of larval weight gain on the leaves of upper and lower parts of five week old plants of five genotypes . .	47
5	Larval feeding damage score observed for four successive days on the barley plants at the preheading stage.	48
6	Ovipositional preference as measured by the number of eggs per leaf, hatchability and the number of larvae per leaf on eight genotypes of an early stage of plant growth	51
7	Antibiosis as measured by larval weight gain on young plants of eight genotypes. .	52
8	Antibiosis measured by the total larval weight gain (number of larvae per leaf x average larval gain) on eight genotypes of young barley plants	53

Figure		Page
9	Recovery as measured by tiller survival after larval feeding damage on eight genotypes of younger plants. . . .	54
10	Nomographic conversion of discriminant function	59
11	A diallel graph for the number of larvae per plant of the F_2 generation of the 6 parent diallel set	62
12	A diallel graph for the damage score at the late stage of F_2 plants of the 6 parent diallel set.	63

INTRODUCTION

The cereal leaf beetle, Oulema melanopus L, has shown a rapid increase accompanied by a constant broadening infestation area since its first identification from collections obtained near Galien, Michigan, in 1962. As of 1969, it has been found in several hundred counties in nine states and in the southern part of Ontario, Canada. This blankets approximately 10 percent of the small grain acreage of the U.S.A. (32).

This insect, an Eurasian graminivorous representative of Chrysomelidae, Order Coleoptera, has long been known in Europe as a pest of small grains. The cereal leaf beetle attacks small grains, especially oats, barley and wheat as a leaf feeder. Several European records indicate that rye, corn and some forage crops also may be hosts (4).

An active investigation of this insect was initiated immediately after its identification in Michigan through a joint program of the United States Department of Agriculture, Michigan State University and Purdue University to study control measures and to produce resistant varieties. In a series of screening tests, a high degree of resistance was

observed in wheat lines while only a moderate degree of resistance was recorded in barley and oats (10).

There is good evidence that the high degree of resistance in wheat is mainly ascribable to leaf pubescence.

Hahn (14), showed resistance in barley to be a genetically recessive trait and also suggested the possibility of obtaining a higher degree of resistance through transgressive segregation. However, the physical mechanism of resistance in barley is not known.

The present work is aimed at obtaining a better understanding of the mechanism and the genetics of resistance.

LITERATURE REVIEW

The first European records of the cereal leaf beetle as a pest appear as early as 1737 (4), and studies have been carried out in France, Russia, England, Hungary and Germany (32). Presently, this Eurasian pest shows extremely wide distribution over the humid and subhumid areas of the Western paleoarctic zone ranging from Sweden to Africa and England to India (7). This leaf feeder was obviously "imported" to North America from the Old World around 1960 (4), and since its first collection and identification in 1962 at Berrien county, in Southwestern Michigan, the fast expansion of infestation has been plotted through annual damage and collection surveys. The region of infestation has expanded enormously and in 1969 an area ranging from eastern Illinois to western New York and from southern Ontario, Canada to central Kentucky has become infested.

The hosts of this insect are mainly barley, wheat and oats but also listed are rye, corn, sorghum, a number of grass forage crops, melons, sunflower and hemp (4). Wilson (35, 36) reported more than 20 species of the gramineae as host plants. Gallun et al (12) and Everson

et al (7) reported that the most severe feeding damage in the field is done by larvae though the adult also feeds on the leaf. The damage to Monon wheat (CI 13278), according to Gallun et al (13), resulted in 23 percent loss in yield. Thorough studies on the systematics, morphology, life cycle, and physiology of the cereal leaf beetle have been made by Ruppel (22), Castro et al (4), Wilson (33, 34) and Sengupta et al (30).

Immediately after the identification of the insect, a series of field screening tests was initiated at Galien, Michigan to search for resistance in lines of the principal small grains. The first test was made on the adult and larval feeding damage by Gallun and Ruppel (10) during the 1962-1963 season followed in 1963-1964 for host plant resistance (11). Continuous field tests were made by Schillinger et al (25) for the 1964-1965 period. Field tests have been continued to the present. Throughout the series of screening tests, certain wheat varieties have proved to be less preferred than oats and barley for oviposition and feeding by adults and larvae. Everson et al (7) noted a large number of wheat lines with a high degree of resistance and most were of Russian or Chinese origin while the few remaining resistant lines were mainly from Asia minor and Southeastern Europe. Thus, they

suggested Asia minor as the main gene pool for resistance and indicated Spain, Portugal and Ethiopia as another possible germplasm center of resistance. Only a moderate degree of resistance has been observed in barley throughout the screening tests. Among the barley lines which show some resistance, CI 6671 and CI 6469 (15 to 40 percent of foliar damage) have been selected as the lines with the highest resistance at present (26).

Host plant resistance is the result of the complex interaction between phytophagous insects and their hosts. This relationship should be divided into two parts; (a) host selection by the insect and (b) resistance to the insect by the plant (2, 20). Painter (19) classified this complicated nature of resistance into three classes as (1) preference or non-preference: the group of plant characters and insect responses that led to or away from the use of a particular plant or variety. This preference may be for oviposition, for food, or for shelter, or for combinations of the three, (2) Antibiosis: the tendency of the plant to prevent, injure or destroy insect life by an adverse effect, and (3) tolerance: the ability of a plant to grow and reproduce itself or repair tissues even after injury. Painter also suggested the possibility of obtaining cumulative resistance by recombining genetic

factors for different types of resistance.

Most of the field and laboratory tests on the cereal leaf beetle have considered two aspects of resistance -- ovipositional preference and feeding damage by larvae. Such partition is essential to understand the mechanism of resistance to the insect. Gallun and Ruppel (10) and Schillinger (27) pointed out that the resistance of wheat to cereal leaf beetle is primarily associated with ovipositional non-preference due to the hairiness of leaves -- higher resistance being associated with denser leaf pubescence. Ringlund (21), through his genetic studies with the crosses between glabrous and pubescent wheat varieties, confirmed this association by showing a highly significant negative correlation between larval weight gain and pubescence, high pubescence density being associated with resistance.

There is also some evidence that yellow color will attract more adults than green (Wilson 37).

Gallun et al (10) and Schillinger (29) observed differential larval growth and oviposition preference among lines of barley, wheat and oats. The most resistant wheat line CI 8519 was the least preferred for oviposition and larval feeding, but the barley lines, CI 6671 and CI 6469, having the highest degree of

resistance, were not preferred for oviposition and were not different from the remaining lines in larval feeding.

The pattern of resistance was affected by various environmental factors, such as the growth stage of the host plant (Wilson 34), planting time of host (Schillinger et al 26, Schillinger 28), stage of physiological development, type of vegetative growth and disease susceptibility of the plant (Schillinger et al 25). Also Gallun (12) pointed out that preference will influence the amount of larval feeding damage per plant because the older larger larvae tend to migrate from leaf to leaf to find a preferred feeding site and presumably spend less time eating, resulting in less damage.

The first genetic study on resistance in barley was carried out by Hahn (14), using diallel cross sets. In a laboratory test, he observed feeding damage at the seedling stage, while feeding damage at the heading stage was analyzed from field plots in the F_2 generation. He showed that resistance was controlled by recessive gene action. Moreover, some evidence of transgressive inheritance was found in the field in the progenies of the cross between two sources of resistance, CI 6671 x CI 6469. He hypothesized that the mechanism

of resistance in barley was due to the negative preference by feeding larvae for the plant and to the unfavorable conditions for egg laying. He found a high correlation between the degree of resistance and the number of larvae per plant.

MATERIALS AND METHODS

Plant materials

Two lines, CI 6671 and CI 6469, the most resistant found to date (11, 26) were chosen as parents for the present genetic studies. Reciprocal crosses between these two lines were made during the Fall of 1967 and a total of about 200 seeds were obtained. Some of these F_1 seeds were planted immediately after harvest to obtain the two backcrosses and F_2 population. Subsequently, F_3 seeds were harvested from the F_2 plants. The remaining F_1 seeds were used for a series of preliminary tests in the greenhouse (Table 1). Six parents were chosen for a diallel cross. They are illustrated in Table 2.

Experiments

1. F_1 -test

The resistance to cereal leaf beetle in the F_1 generation of the cross CI 6671 x CI 6469 was examined during the winter of 1968 in the greenhouse under controlled light and temperature conditions. Four genotypes, i.e. CI 6671, CI 6469, their F_1 and Larker, known to be a susceptible variety (26), were investigated. To avoid possible errors due to irregular germination and consequently different seedling vigor,

Table 1. Plant materials used in this investigation

Genotypes	Description	Reaction to cereal leaf beetle
CI 6671 ^{a/}	Introduction from Iran	Resistant
CI 6469	Introduction from Poland	Resistant
F ₁	Cross of CI 6671 x CI 6469	-
F ₂		-
F ₃		-
BC ₁	CI 6671 ² x CI 6469	-
BC ₂	CI 6671 x CI 6469 ²	-
CI 10649	Larker	Susceptible
CI 11531	Dickson	Susceptible
^{a/} CI refers to Cereal Investigation number of Crops Research Division, Agricultural Research Service, U.S. Department of Agriculture.		

Table 2. Description of the six parents used
in a diallel cross observed

Lines	Resistance ^{a/}	Head type	Origin	Maturity	Plant vigor ^{b/}
CI 12518	Moderate	2-row	Ethiopia	Early	Low
CI 12528	Moderate	2-row	Ethiopia	Medium	Low
CI 6671	Resistant	6-row	Iran	Early	Medium
CI 6469	Resistant	6-row	Poland	Late	High
CI 12715	Moderate	2-row	Ethiopia	Late	Medium
Dickson	Susceptible	6-row	U.S.A.	Medium	High
^{a/} From the result of a screening test in 1965 (26)					
^{b/} All spring types.					

the seeds were planted in wooden flats filled with sand and only uniform seedlings were transplanted after seven days to 5 inch clay pots. Such a transplanting procedure was used for all greenhouse tests.

To reduce the variation between cultures, one individual from each of the four genotypes was planted in each culture at each planting.

Four successive plantings were made to produce plants of different stages (Table 3).

Table 3. Stage of growth, description of plant development and age of plants used in the larval feeding experiment

Stage	Stage of growth	Description	Age of plant in weeks
1st	Early seedling	2 leaf stage	3
2nd	Old seedling	3-4 leaf stage	4
3rd	Preheading	4-5 leaf stage a week before heading	5
4th	Post heading	a week after heading	7

The design used was a randomized block of 3 replications, 4 varieties, and 4 stages -- comprising 48 units, each unit of 5 cultures. When the plants reached the stages shown in Table 2, two first instar larvae reared by a standard

method in the laboratory (6) were placed on the youngest leaf of each plant. As suggested by Schillinger (27) and Chada (5), each plant was then covered with a plastic cylinder. However, high humidity within the cylinder and the difficulties of covering tall plants led to a high larval mortality and a high frequency of escape, respectively. The experiment was therefore restarted after five days from initiation of larval feeding, without such covers. After five days feeding, the larvae were removed from the plant, carefully wiped with filter paper and the body weight recorded with a 0.1 mg precision torsion balance. After all larvae were removed and weighed, the damage to the plants was scored subjectively. Throughout the whole series of experiments, the damage score was read from 0 to 4 based on the following criteria;

- 0: none to trace of feeding damage
- 1: slight feeding damage
- 2: moderate degree of feeding damage
- 3: relatively heavy feeding damage on the leaf
- 4: extremely heavy feeding damage.

Actually the scores 0 and 4 were rarely read. This method of measuring larval weight gain and scoring damage was used throughout all tests and was in contrast to that used by Hahn (14), where scores ranged from 0 to 10,

according to the proportion of damaged leaf area. Such precision was not applicable to the present material.

An analysis of variance using a two-way classification was done within each of the four individual plant growth stages.

2. Field generation test

The parents and the F_1 , F_2 , BC_1 and BC_2 generations were tested at the field nursery located near Galien, Michigan. Twenty seeds of each were space planted in each of three replications at 3-inch intervals in 6-foot rows spaced one foot apart. Approximately 70 percent of the seeds resulted in adult plants and 10 inner plants of each row were used for the observations. The feeding damage on the plants was scored and the number of larvae per plant counted at heading. Heads were harvested and the following characters were measured: average head weight, maturity ratio on a numerical basis (the proportion of perfectly filled kernels to total number of florets per spike), maturity ratio on a weight basis (the ratio between the weight of filled kernels in a spike and that of the whole spike) and 1000 kernel weight. Harvested heads from each plot were randomly subgrouped in order to calculate the genetic variance components for all characters measured in this study.

3. Feeding damage test

During June of 1968, a greenhouse test was made to determine the relative efficiency and credibility of measurements of feeding damage. The genotypes used were CI 6671, CI 6469, their F_1 , F_2 , BC_1 , BC_2 , and Larker, a susceptible check (Table 1). Plants of four different stages were tested simultaneously. The stages were identical to those illustrated in Table 3. Two seedlings were transplanted to individual pots with five replications. Each culture was considered as a replication. Three measurements, i.e., mobility, damage score and larval weight gain were observed. The mobility of larvae was observed in the following manner. One late second instar larva was placed on the youngest leaf and observed every 12 hours (at 9 a.m. and 9 p.m.) for seven days. Each movement of larva from one leaf to another was recorded by counting the number of leaves it had passed. There were a few cases in which the larva was either dead or had escaped. During the first three days of testing, the missing larvae were replaced with another larva of the same age. The data were converted to a score in two ways: Method 1. Giving one unit value for each movement across a leaf and two for escape or death. Method 2. Same as above except giving one half unit for escape or death.

The feeding damage scores were read on the third and the last day of larval feeding. After seven days, larval weight was measured excluding the ones which were replaced due to previous escape or death. All measured characters were analyzed in a factorial design and intraplot variances were calculated for each genotype at each stage. Analysis of genetic variances was examined.

4. Plant tissue age test

During the period between September of 1968 to March 1969, a series of tests was made to find the difference in larval feeding among the plant parts. Only two stages, namely the early seedling stage and preheading stage were considered. The procedures closely followed those suggested by Schillinger for determining larval weight gain (26, 27). The parents, their F_2 , F_3 , and Larker (Table 1) were tested. Four seedlings were transplanted to each pot and white quartz sand was poured on the soil surface to facilitate the spotting of stray larvae. To "protect" the larvae from food shortages, each plant was infested with one larva and the plants were covered by glass lantern globes. Plants of a later stage of development were tested without the globe. For the early stage, damage scores were read every day beginning on the second day of feeding. After five days, larval weights

were measured. Another set of tests was made with identical genotypes at two plant growth stages to observe any differences in damage between upper and lower leaves. Single first instar larvae were put on both the upper and lower leaves in 3" x 3" x 7½" plastic leaf cages, to prevent the larva from escaping or feeding on another portion of the plant. Care was taken to insure larvae adequate food by shifting the position of the leaf cages. Two leaves on the lower portion and another two leaves on the upper portion of the plant were tested. After four days of feeding, larval weights were measured.

5. Component test

Painter's classification of resistance (19) was modified for the present purpose into three components -- ovipositional preference by gravid females, resistance to larval feeding damage and recovery of the plants.

Ovipositional preference is defined as the group of plant characters and the responses of a gravid adult female that leads to the use of a particular plant or variety for oviposition.

Resistance to larval feeding damage is the expression of the interaction (reaction) between the plant and feeding young insect larvae in which the antibiotic effect of plant on insect causes a reduction in larval weight gain and the

lessening of the degree of feeding damage on plant tissue.

Recovery is a measure of resistance in which the plant grows and reproduces itself by recovering from the injury caused by larval feeding.

Tests of the components were made in the spring of 1969. The parents, CI 6671, CI 6469, and the F_2 , F_3 , BC_1 , BC_2 plus two susceptible varieties Larker and Dickson (Table 1) were transplanted to five pots for each entry, each culture containing four seedling plants; one culture was designated as a replication. At the third week after planting, all eight entries were randomized within each replication and all experimental materials were enclosed by a 1.8 x 0.9 x 0.7-m sized wooden cage (Schillinger (29)). The cage was transferred to a growth chamber in which 15 hours of light were followed by a nine-hour dark period at a temperature of 76 F. Approximately 200 laboratory grown adult beetles (6) were released inside the cage and allowed to oviposit without restriction for 36 hours. After 36 hours, the plants were removed from the cage and the number of eggs per plant counted. As there were some differences in the number of tillers and in plant vigor, the number of leaves per plant were counted and used as the denominator to calculate the number of eggs per leaf. These plants were then returned to the growth chamber to provide an environment favorable to hatching, after removing

the adult beetles. Ninety-six hours after the termination of egg laying, the numbers of hatched larvae were counted and after seven days, the average larval weight was measured. As there were differences in the stage of larval growth, as many samples as possible were taken. Finally, tiller survival ratio and average head weight were measured. For each plant, tiller survival ratio was calculated by dividing the final number of heads by the highest number of tillers observed for that plant. As the measurements were on an individual plant basis, correlation coefficients between observed characters could be calculated.

An identical set of six-week old plants was tested in exactly the same manner described above except that the period of egg laying was extended to 70 hours and the tiller survival ratio was not observed.

6. Diallel cross

During the spring and summer of 1968, a complete diallel cross series excluding reciprocals was made with the six parental lines indicated in Table 2. Among the lines, CI 6671 and CI 6469 were used as resistant parents while Dickson was chosen as a susceptible parent, based on results from the field screening tests (10, 11, 12, 25). F_2 progenies and parents were planted in a field nursery located at Galien, Michigan. Twenty seeds were space planted three inches apart

in four replications. The rows were four feet long and were spaced one foot apart. The plants in the nursery showed good infestation and data were collected on the number of larvae per plant and for damage scores at the early and late plant growth stage, roughly corresponding to stages 1 and 3 of Table 2. Each damage score was the average of 10 observations. After harvest, the average head weights per plot were measured and the data were analyzed by the Jinks-Hayman (15, 16) diallel analysis.

Statistical Procedures

a. Analysis of genetic variance component

The genetic variance components of homozygous and segregating populations of self-pollinating crops have been defined and analyses have been developed by a number of workers, especially by Fisher and Mather.

The variation in observed values within any pair of true-breeding parents and their F_1 is assumed to be exclusively due to environmental effects. On the other hand, any variation within the F_2 generation is due both to genetic difference and to environmental effects. The genetic variation within the F_2 generation of a theoretical A-a locus has been defined as $2uv(d+(v-u)h)^2 + 4u^2v^2h^2$, where u and v are the gene frequency of A and a alleles,

respectively, d is additive genetic effect (or gene effect) and h is the dominance effect exhibited by the heterozygous $A-a$ locus. However, in a population which has been artificially built up through hybridization between two homozygous parents, $u=v=\frac{1}{2}$ and thus the genetic variation of the F_2 generation is $\frac{1}{2}d^2 + \frac{1}{4}h^2$. In practice, an environmental factor, e , should be added to the above equation. If one considers a quantitative character, controlled by k genes (or effective factors) and assuming that they do not interact,

$$V_{F_2} = \frac{1}{2}D + \frac{1}{4}H + E$$

$$\text{where } D = \sum_{i=1}^k d_i^2$$

$$H = \sum_{i=1}^k h_i^2$$

E : Environmental variation.

If backcross generations are available,

$$V_{BC_1} + V_{BC_2} = \frac{1}{2}D + \frac{1}{2}H + 2E.$$

When five generations, namely two parents, F_1 , F_2 , BC_1 and BC_2 are located in one environment, E , the environmental variation, will be common to each group and can be estimated by observing the variations within populations of identical genotypes. Thus, the genetic variance components were calculated in Tests 2, 3 and 5, along the lines described above.

Environmental variances were estimated by averaging the variances of the two parents (and F_1 , where available).

Heritability is defined as the ratio of additive genetic variance in a given population to total variance of the same population. Thus heritability in the F_2 generation is,

$$h^2_{F_2} = \frac{\frac{1}{2}D}{V_{F_2}} .$$

Similarly, heritability at the F_3 generation is

$$h^2_{F_3} = \frac{\frac{1}{2}D}{V_{F_3}} .$$

The number of effective factors were also calculated as suggested by Wright and Mather (18).

b. Diallel analysis

For the diallel cross sets, the Jinks-Hayman (15, 16) W_r/V_r analysis was applied. After calculating the variances within each array (V_r) and covariance of the r array with non-recurring parents (W_r), regression equations of W_r to V_r were calculated. As $W_r^2 = V_r V_p$, points coordinated on the plane made by W_r and V_r axis will be confined by a limiting parabola $W_r = (V_r V_p)^{\frac{1}{2}}$ where V_p is the parental variance. In the presence of complete dominance, the calculated regression line will show a slope of unity with

interception at the origin and thus observing the position of interception on the W_r -axis, the degree of dominance can be determined. When the slope is significantly different from unity, the existence of non-allelic interactions is probable. Points along the slope of W_r , V_r are arranged in the dominance order of the parents. Significant difference of the regression line from either unity or zero can be tested by the t -test using the formula, $t = \frac{b - b_0}{s_b}$, where b_0 is 1 or 0, respectively.

c. Discriminant function

A discriminant function can be defined as a linear combination of available measurements (or variables) into one function. The coefficients of each variable are chosen in such a manner so that the function can minimize possible errors in using those multivariates to characterize a complex trait, and concomitantly maximize the difference between two or more classes of objects or individuals relative to the variation within the class. The actual computational method involves an application of the least squares method to a multivariate function. Descriptions of the theory and the applications of discriminant functions have been published by Fisher (8, 9), Smith (31), and Mather (17, 18). For the

present studies, three of these functions were calculated to discriminate between the two ways of measuring larval mobility, the three measurements of feeding damage and finally to find some way of combining the measurements of the three components of resistance, viz, ovipositional preference, larval feeding damage and plant recovery. If we assume three variables (measurements) L, W, T and the final outcome to be D, the proper combination of L, W and T will yield a discriminant function for D.

For this purpose, according to Mather (18) and Fisher (8), the coefficients b_L , b_W and b_T of L, W and T, respectively, should satisfy the following equations.

$$b_L(A_{LL} - \emptyset a_{LL}) + b_W(A_{LW} - \emptyset a_{LW}) + b_T(A_{LT} - \emptyset a_{LT}) = 0$$

$$b_L(A_{LW} - \emptyset a_{LW}) + b_W(A_{WW} - \emptyset a_{WW}) + b_T(A_{WT} - \emptyset a_{WT}) = 0 \text{ ---(1)}$$

$$b_L(A_{LT} - \emptyset a_{LT}) + b_W(A_{WT} - \emptyset a_{WT}) + b_T(A_{TT} - \emptyset a_{TT}) = 0$$

where A_{LL} , A_{LW} , etc. are the total sum of squares or sum of cross products between variables and a_{LL} , a_{LW} , etc. are the corresponding sum of squares or sum of the cross product between treatment combinations. $\emptyset$ was used to adjust the values of each a when they are subtracted from total sum of square or sum of cross product (A 's) and was

estimated as below. As there are three equations and four unknowns ($\emptyset$, b_L , b_W , b_T), only the relative magnitude of b 's can be estimated. By converting the above equations into the following determinant form, $\emptyset$ can be estimated.

$$\begin{vmatrix} A_{LL}-\emptyset a_{LL} & A_{LW}-\emptyset a_{LW} & A_{LT}-\emptyset a_{LT} \\ A_{LW}-\emptyset a_{LW} & A_{WW}-\emptyset a_{WW} & A_{WT}-\emptyset a_{WT} \\ A_{LT}-\emptyset a_{LT} & A_{WT}-\emptyset a_{WT} & A_{TT}-\emptyset a_{TT} \end{vmatrix} = 0 \text{ ----(2)}$$

Solution of the above determinant leads to a third power function of $\emptyset$. Among the roots, the smallest one is taken and substituted in equations of (1). From this set of equations the ratios between b_L , b_W and b_T are calculated. By setting the lowest value to 1, we can obtain the discriminant function in a form of

$$D = b_L L + b_W W + b_T T,$$

where one of the b 's has a value of 1.

d. Nomography

For more rapid and convenient uses of derived functions in evaluation of varieties for their resistance, nomographic conversion of the function was made (1).

Nomography is a special kind of graphic representation which can be used as a visual means of calculation of any

number of special cases. However, to present a three factor function in a two dimensional picture, a special treatment of coordinates is needed. A brief description of the theory is presented.

Four points $P_1(x_1, y_1, z_1)$, $P_2(x_2, y_2, z_2)$, $P_3(x_3, y_3, z_3)$ and $P_4(x_4, y_4, z_4)$ in a space are co-planar when

$$\begin{vmatrix} x_1 & y_1 & z_1 & 1 \\ x_2 & y_2 & z_2 & 1 \\ x_3 & y_3 & z_3 & 1 \\ x_4 & y_4 & z_4 & 1 \end{vmatrix} = 0$$

If we consider the four variables L, W, T, D and assume a given function, $F(L, W, T, D) = 0$, then this function F can be put in the form

$$\begin{vmatrix} L_1 & L_2 & L_3 & 1 \\ W_1 & W_2 & W_3 & 1 \\ T_1 & T_2 & T_3 & 1 \\ D_1 & D_2 & D_3 & 1 \end{vmatrix} = 0$$

where L_1, L_2, L_3 are the functions of L only and the same for W, T and D .

For a given function $L + W + T = D$, if we set

$$A = lL$$

$$B = wW$$

$$C = tT,$$

then,

$$A \cdot 1 + B \cdot 0 + C \cdot 0 + 1L = 0$$

$$A \cdot 0 + B \cdot 1 + C \cdot 0 + wW = 0$$

$$A \cdot 0 + B \cdot 0 + C \cdot 1 + tT = 0$$

$$A \cdot \frac{1}{f} + B \cdot \frac{1}{w} + C \cdot \frac{1}{t} + D = 0$$

By proper operation, the above equations will be brought to the determinant form as

$$\begin{vmatrix} 0 & 0 & 1L & 1 \\ G & 0 & sW & 1 \\ 0 & K & tT & 1 \\ \frac{1tG}{1w+wt+1t} & \frac{1wK}{1w+wt+1t} & \frac{1wtD}{1w+wt+1t} & 1 \end{vmatrix} = 0$$

Expansion of this determinant form yields the original equation $L + W + T = D$.

In this case, l , w , t are the scale multipliers or scale factors which can be used to expand or contract their respective scales. G and K are constants employed to produce a matrix in canonical form and permit varying the width of the scale. These quantities give more flexibility to the use of three dimensional functions displayed on a two dimensional picture. As the components L , W and T have their respective coefficients, b_L , b_W and b_T , l , w and t quantities were modified by the coefficients derived from the discriminant function.

RESULTS

1. F_1 test^{1/}

The aim of this test was to examine the response of F_1 plants to larval feeding as compared with the parents. The mean values of larval weight gain and feeding damage score of each genotype are shown in Tables 5 and 7, respectively. Due to the drying out associated with maturity, about 50 percent of the first instar larvae placed on the flag leaf of seven-week old plants died and hence the last growth stage was dropped from the analysis. The remaining three stages showed either significant or highly significant differences for larval weight gain among the four genotypes tested -- Tables 4 and 5.

Table 4. Analysis of variance of cereal leaf beetle larval weight gain on three growth stages of four barley genotypes

Source	Degree of freedom	Mean square	F
Replications	2	8.67	1.82
Stage of growth	2	17.86	3.76*
Genotypes	3	40.06	8.43**
Stage X Genotype	6	34.48	7.97**
Error	22	4.75	

*P = .05

**P = .01

^{1/} Materials and methods section 1.

Table 5. Comparison of average weight gains of cereal leaf beetle larvae fed on three growth stages of CI 6671, CI 6469, the F_1 generation of the cross CI 6671 x CI 6469 and Larker a susceptible check

Genotypes	Growth stage ^{a/}		
	T_1	T_2	T_3
F_1 generation	16.2 mg	18.1 mg	15.0 mg
CI 6671	12.9	14.2	16.0
CI 6469	12.4	17.6	16.9
Larker	15.1	17.8	17.8
F-value	5.48*	7.21**	25.03**

* $p = .05$

** $p = .01$

^{a/} T_1 : 3-week old plants

T_2 : 4-week old plants

T_3 : 5-week old plants

The data in Table 5 were adjusted so that the mean and standard deviation for the different plant growth stages were in the same units. The transformation was

$$Y'_{ij} = \frac{Y_{ij} - \bar{Y}_i}{s_{d_i}}$$

where Y_{ij} : standardized value of jth entry
in ith stage

Y_{ij} : original value of jth entry in
ith stage

$\bar{Y}_i$: mean value of ith stage

s_{d_i} : standard deviation of ith stage.

By this transformation, the values at each stage are rearranged around a mean of 0 and a standard deviation of

1. These new values are shown in Table 6 and Figure 1.

Table 6. Standardized values of larval weight gain fed on three growth stages of CI 6671, CI 6469, the F_1 generation of the cross CI 6671 x CI 6469 and Larker, a susceptible check.

Entry	Growth stage ^{a/}		
	T_1	T_2	T_3
F_1 generation	3.56	1.61	-1.33
CI 6671	-2.31	-3.86	- .38
CI 6469	-3.02	1.00	.47
Larker	1.78	1.28	1.23

^{a/} T_1 : 3-week old plant

T_2 : 4-week old plant

T_3 : 5-week old plant

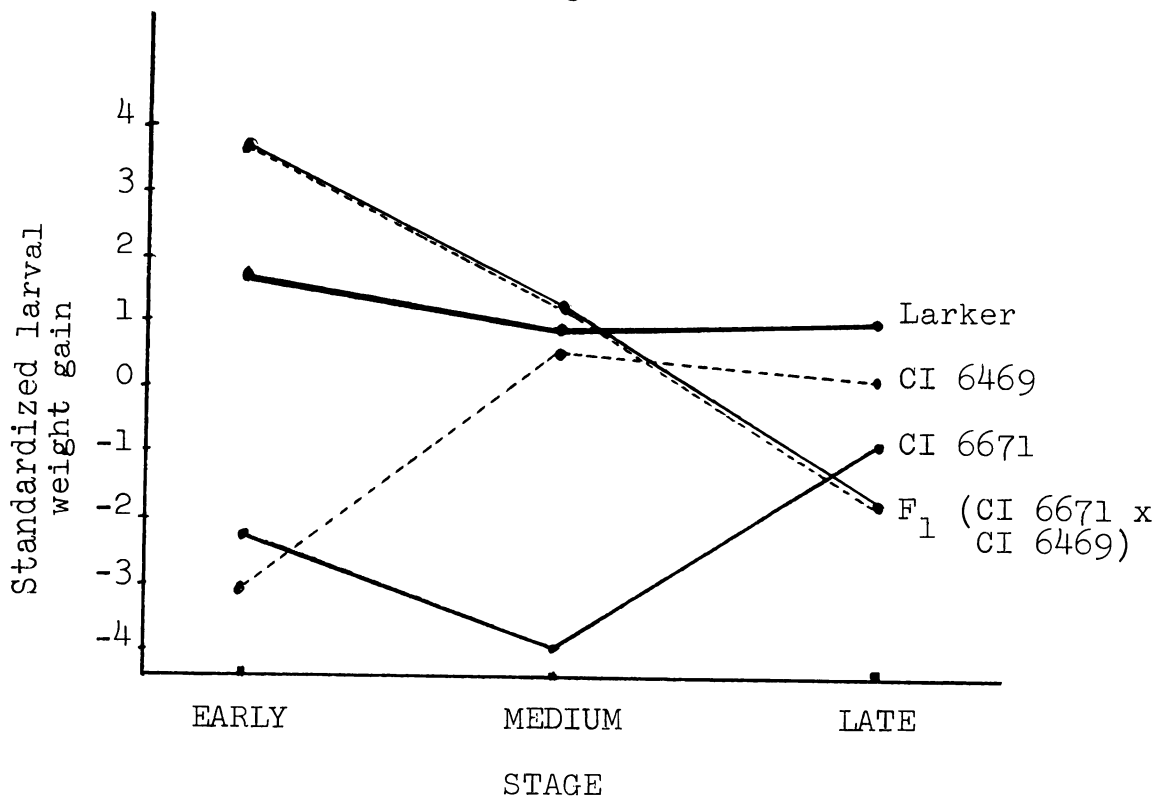


Figure 1. Standardized larval weight gain of cereal leaf beetle fed on 4 genotypes at 3 growth stages.

From Fig. 1 the following points are noted:

1. At the youngest stage of plant development, the two resistant parents CI 6671 and CI 6469 show a much higher degree of resistance than either Larker or the F₁ of the cross CI 6671 x CI 6469. At this stage, the hybrid between the two resistant lines is as susceptible as Larker. This agrees with Hahn (14).
2. At the middle stage, CI 6671 is more resistant than the remaining three lines, which do not differ greatly among themselves.

3. At the late stage, the resistance of the F_1 plants exceeds that of all other lines. Line CI 6671 shows considerable resistance while CI 6469 appears as susceptible as Larker.
4. The F_1 generation seems to increase in resistance with plant age whereas CI 6469 decreases.

The variety CI 6469 appears to be resistant to larval feeding at the early stage but its resistance is weakened at later stages. On the other hand, the F_1 plants are quite susceptible at the early stage but at later stages, their resistance is reinforced for some reason and they display an even higher degree of resistance than the parents. But, CI 6671 and Larker show relatively constant resistance and susceptibility, respectively.

The damage score reading failed to indicate any statistically significant difference between lines, as shown in Table 7. This may be due in part to the inadequacy of the measurements or to the limited number of samples. A difference in growth habit could also contribute to the failure of significance tests for damage score since CI 6469 shows a high degree of plant vigor and CI 6671 is a line with a short stem and a small number of tillers. Such differential plant vigor could cause some confusion in

judging the amount of damage, and could lead to the evaluation of CI 6469 as the line of highest resistance over all stages. In subsequent tests, the factor of differential vigor was carefully considered when a damage score was read.

Table 7. Average cereal leaf beetle feeding damage score on three growth stages of barley plants of four genotypes

Genotypes	T ₁	Stage of growth ^{a/}	
		T ₂	T ₃
F ₁	2.20	2.26	2.13
CI 6671	2.40	2.56	2.26
CI 6469	1.93	2.13	1.80
Larker	1.93	2.86	2.66
F-value ^{b/}	3.81 ^{NS}	1.21 ^{NS}	2.04 ^{NS}

^{a/} T₁ = 3-week old plant

T₂ = 4-week old plant

T₃ = 5-week old plant

^{b/} F values were calculated for each stage; NS = no significant difference

2. Field generation test^{1/}

The mean and variance values of damage scores and number of larvae per plant are entered in Table 8 and also in

^{1/} Material and Methods section 2.

Figure 2. These observations were made at the heading stage which was equivalent to the third stage in the previous test.

Table 8. Means and variance of damage score and number of larvae per plant observed in the field with five generations of the cross CI 6671 (P_1) x CI 6469 (P_2).

Population	Damage score		Number of larvae plant	
	Mean	Variance	Mean	Variance
P_1 (CI 6671)	5.1	.359	5.1	8.537
P_2 (CI 6469)	5.5	.287	12.6	43.530
F_1	3.8	.275	8.7	38.337
F_2	4.9	.536	7.5	23.040
BC_1	4.8	.496	5.3	18.388
BC_2	5.3	.371	10.0	36.174
F-value	2.610† ^{a/}		2.81†	
H (non-additive genetic variance)		.096		52.24
D (additive genetic variance)		.410		0
h^2 (Heritability)		38.24%		0
K (number of effective factors)		1 or 23		

^{a/}† : significant at 10% level



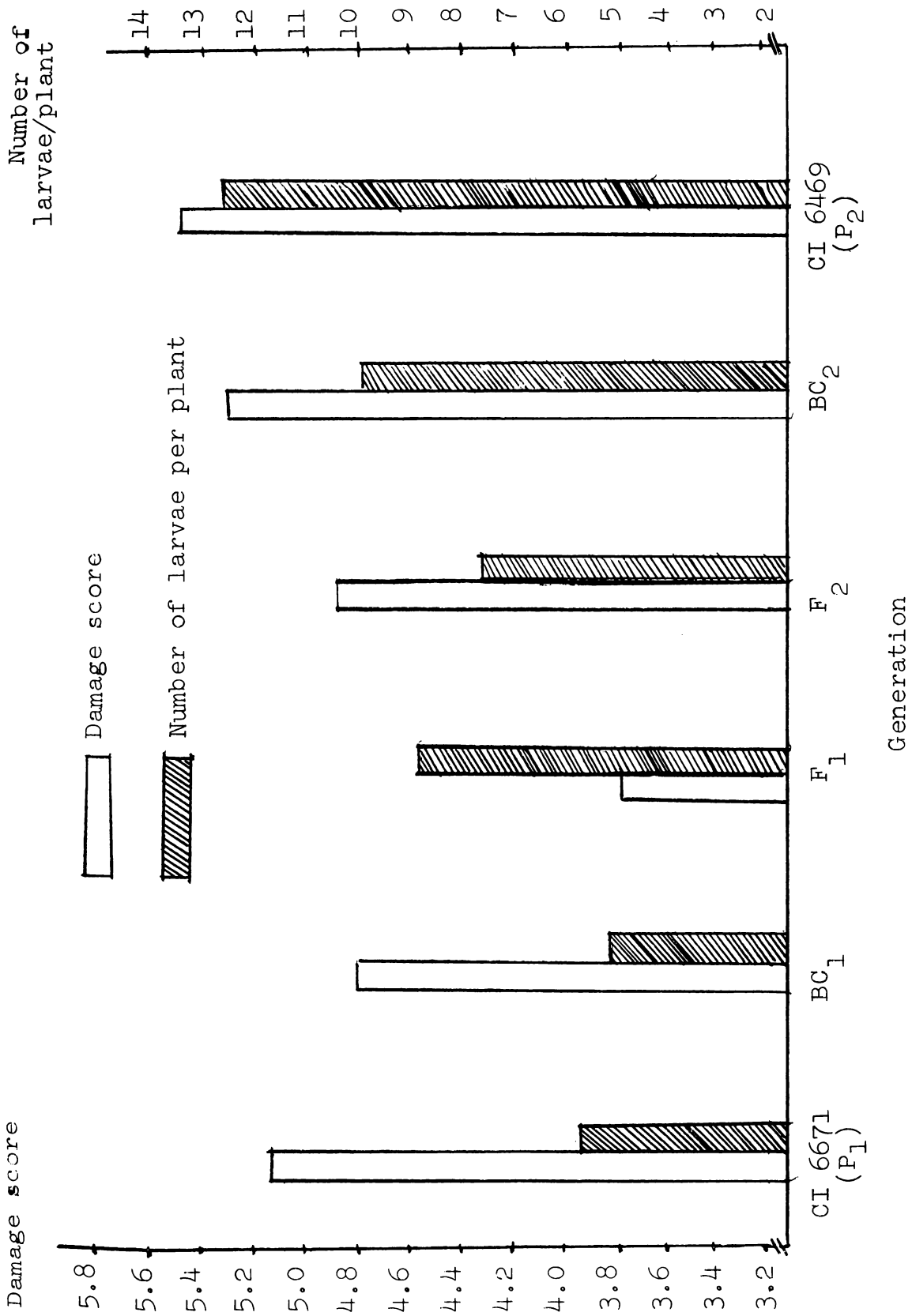


Figure 2. Damage score and larvae per plant of the cross CI 6671 x CI 6469 and the F₁, F₂, BC₁ and BC₂ generations.

The damage score shows that the progenies are more resistant than the parents and that the F_1 is the most resistant followed by the F_2 . Through the analysis of genetic variance components by the methods of Fisher and Mather (18), a heritability value of 32.24 percent was obtained for the F_2 generation for larval feeding damage score. The number of effective factors for the traits could be calculated in two ways with the present data.

If we assume k effective factors which have equal additive genetic effect, that is, $d_a = \dots = d_k = d$ where d_a is the additive genetic effect (gene effect) of a th factor and d is the average of all d 's and again assuming that all positive genes are concentrated in one parent and all negative genes to the other, we can see $\bar{P}_1 - \bar{P}_2 = \sum_{a=1}^k (d_a) = kd$. By

definition D is the sum of squares of d 's and with the first assumption, $D = \sum_{i=1}^k d_i^2 = kd^2$. Thus, if both assumptions are

holding, $\frac{(\bar{P}_1 - \bar{P}_2)^2}{D} = \frac{k^2 d^2}{kd^2} = k$. The calculated k value will

be underestimated when (1) linkage exists; (2) increments of positive genes produce an unequal effect; (3) when genes are isodirectionally distributed between parents. The use of the above method resulted in a k value of 0.4 for feeding

damage. This is a very low value but considering that both parents are resistant, it may be that the genes are of an isodirectional distribution between parents which could very well cause a downward estimation. Another way of estimating k values uses the dominance effect, h . Under the identical assumptions made above, $\bar{F}_1 - (\text{mid parent}) = \sum_{a=1}^k h_a = kh$,

where the absolute values are from the mean of the observed populations and d_a is the dominance effect caused by the heterozygosity of the a th factor (locus). As H is defined as $\sum_{i=1}^k h_i^2$ with equal dominance effects among k factors,

$$H = kh^2 \text{ and therefore, } \frac{\left(\bar{F}_1 - \frac{\bar{P}_1 + \bar{P}_2}{2} \right)^2}{H} = \frac{k^2 h^2}{kh^2} = k.$$

This method led to a calculated k value of 23. Such a high value is in striking contrast to that calculated by the previous method, and the inconsistency suggests a complex pattern of inheritance. Calculation of the heritability of the number of larvae per plant factor was not done since the value of additive genetic variance was negative. The plant materials were harvested and measured for yield characters as shown in Appendix 1. The observed values are a function of both genotypic yield characters and of the response to larval feeding. Due to the absence of damage-free check

plots, it is impossible to isolate the damage response by insect feeding. The results do not indicate any definite trends except that the F_1 shows a degree of plant vigor as high as CI 6469, the vigorous parent. As for the number of larvae per plant, the present results in Table 8 indicate that CI 6671 is much less favored for oviposition than CI 6469 while the F_1 shows an intermediate level.

3. Feeding damage test^{1/}

Feeding damage is the result of the interaction between larval feeding and the host plant. This relationship can be measured and judged in various ways, but there has been no direct way of combining such multimeasurements or deciding their relative efficiencies as yardsticks. The conventional way of measuring this relationship has been either the subjective scoring of feeding damage by visual observation or the relative amount of larval weight gain after a certain period of feeding. These two measurements are two facets of the host parasite interaction; the former is a measure of the response of plant parts to insect feeding while the latter is the response of the insect by feeding the plant. Another possible measurement of larva-plant

^{1/} Materials and Methods section 3.

response is the mobility of larvae on the plant. As stated by Gallun et al (12), an insect larva, when forced to feed on a plant of undesirable "quality," tend to move from one place to another to examine the possibility of getting more agreeable food. The present test was aimed at finding a way of combining these measurements into a single character and then testing their relative efficiencies as a measurement. The above three measurements were observed with seven genotypes at four different stages, the F values of which are shown in Table 9. Over-all mean values for each stage and genotype is shown in Table 10 and Table 11, respectively. Two measurements on larval mobility were made. During the testing period there were cases in which larvae were dead or escaped and these were at first interpreted as an expression of an avoidance reaction. However, the possibility exists that it may be by chance only. Such difference in interpretation resulted in two mobility measurements as shown in Tables 9, 10 and 11.

Damage scores were read twice, one soon after the larvae started feeding and one about the end of the feeding period. The average of the two observations was calculated. The means and the variances within treatment combinations of each entry on each stage are shown in

Table 9. Analysis of variance and over-all mean of cereal leaf beetle larval mobility, feeding damage and weight gain on CI 6671, CI 6469, F₁, F₂ BC₁ and BC₂ generations of CI 6671 x CI 6469 and susceptible varieties Larker and Dickson.

Traits Observed		Mobi- lity ^a / (I)	Mobi- lity ^a / (II)	Damage score ^a / (I)	Damage score ^a / (II)	Damage score ^a / (Ave.)	Larval weight gain in mg.
Source	Degree of Freedom	F-values					
Reps	4	3.05	1.18	4.88**	4.29*	3.01	.92
Stage	3	8.34** ^b	7.28**	1.97**	9.26**	1.96 ^b / _†	2.45*
Entry	7	1.32	1.74	1.48	1.85* ^b / _†	1.75 [†]	7.81**
SXE	21	.94	1.12	1.71	1.86*	1.74*	6.73**
Over-all	mean	4.55	3.25	1.75	1.98	1.86	1.69

^a/ For the differences in measurements, see text.

** = significant at 1% level. * = significant at 5% level.

^b/ † = significant at 10% level.

Table 10. Average values of cereal leaf beetle larval mobility, damage score and weight gain for 4 stages of plant growth over all entries and replications.

Stage	Age of Plant (week)	Mobi- lity (I)	Mobi- lity (II)	Damage Score (I)	Damage Score (II)	Damage Score (Ave.)	Larval Weight gain in mg.
1	3	5.51	3.65	2.02	1.61	1.82	1.70
2	4	4.30	3.28	1.62	1.97	1.80	1.62
3	5	4.54	3.47	1.77	2.20	1.98	1.79
4	7	3.84	2.61	1.58	2.14	1.86	1.66

Appendix 2. The correlation coefficients between the six measurements are presented in Table 12. A series of t-tests

with the formula, $t = \frac{r}{\sqrt{(1-r^2)/(N-2)}}$ indicates that the mobility of larvae is independent of damage score or larval weight gain. Highly significant correlation coefficients were obtained between larval weight gain and damage score observed at later stage of feeding and average damage score.

Table 11. Average values of cereal leaf beetle larval mobility, damage score and weight gain on eight genotypes of plant over all plant growth stages and replications.

Entry	Mobi- lity (I)	Mobi- lity (II)	Damage score (I)	Damage score (II)	Damage score (Ave.)	Larval weight gain in mg.
CI 6671(P ₁)	4.72	3.20	1.72	2.20	1.96	1.60
CI 6469(P ₂)	4.80	3.35	1.85	2.02	1.93	1.67
F ₁ (P ₁ x P ₂)	4.85	3.60	1.65	1.90	1.77	1.60
F ₂	4.35	2.75	1.85	1.72	1.78	1.14
BC ₁	3.82	3.02	1.67	1.92	1.80	1.60
BC ₂	4.47	3.52	1.60	1.97	1.78	1.97
Larker	4.82	3.35	1.92	2.12	2.02	1.75

Table 12. Correlation coefficients between six measurements of the interaction between host plant and cereal leaf beetle larvae.

Measurement	Mobility (I) ^{a/}	Mobility (II) ^{a/}	Damage score (I) ^{a/}	Damage score (II) ^{a/}	Damage score (Ave.) ^{a/}	Larval weight gain
Mobility (I)	1.000					
Mobility (II)	.760	1.000				
Damage score (I)	.248	.189	1.000			
Damage score (II)	-.123	.003	-.001	1.000		
Damage score (Ave)	.070	.127	.657	.752	1.000	
Larval wt. gain	.054	.110	.004	.428	.392	1.000

^{a/} - For the difference between measurements, see the text.

From Table 10, larvae move more on the plants at an early stage, though there is no differential movement between genotypes. This indicates that there is no larval feeding preference. Another computation of variances within each stage also failed to show any significant difference in larval movement between genotypes of the host plant at any stage of growth. Thus, larval movement is affected by the age of the plant but genotypes do not influence mobility. To compare the two different ways of interpreting and evaluating mobility, a discriminant function was calculated. Total and between

treatment combinational sum of squares and sum of cross products between the two measurements were calculated from original data, as illustrated in Table 13.

Table 13. Total and between treatment combination sums of squares (ss) and sums of cross products (cp) of two different mobility measurements, m_1 and m_2 of cereal leaf beetle larvae on barley.

	m_1m_1 (ss)	m_2m_2 (ss)	m_1m_2 (cp)
Total	1328	608	683
Between	209	107	115

$\emptyset$ had a value of 6 and the final function was

$$M = 1.46m_1 + m_2$$

where M is the combined mobility index from the two different measurements of mobility m_1 and m_2 . From this function, it can be suggested that an evaluation of mobility by the former method (m_1) is more reliable and accurate. Larval death or escape may be an expression of extreme negative preference or antibiosis.

Of the three measurements obtained for feeding damage, that taken near the end of feeding exhibited a significant difference among entries and among stages together with the existence of interactions between the two factors. Despite

some indication of statistical significance, damage scores taken early during the feeding period do not show any noticeable trends. Perhaps more time for feeding should be allowed in order to observe the true nature of resistance, and then more credence may be given to the results obtained near the end of the feeding period. From the feeding damage score observed, the F_1 plants of CI 6671 and CI 6469 were again rather susceptible in the early seedling stage but became quite resistant by the preheading stage. A similar trend was observed for larval weight gain. This is in good agreement with the results obtained from the two previous tests. However, the stagewise pattern of resistance observed in two previous tests was not found to hold for the parents in this test.

The main objective of the present test was to compare and combine the three different measurements into one single trait. Again a discriminant function was built on mobility, damage score and larval weight. The first measurement of larval mobility was used because it proved more effective than the second by the previously calculated function. Sums of squares and sums of cross products for total and between treatment combinations are shown in Table 14.

Table 14. Total and between treatment combination sums of squares (ss) and sums of cross products (cp) between three measurements of cereal leaf beetle larval feeding.

ss or cp ^{1/}	11(ss)	44(ss)	66(ss)	14(cp)	16(cp)	46(cp)
Total	1328	173	44	-59	18	13
Between	209	32	24	-33	8	4

^{1/} 1 = mobility (1) 4 = damage score (2)
6 = larval weight gain

Calculated $\emptyset$ values were 3, a double root, and 11.

Taking the value 3, the following equation was calculated

$$LD = M + 3.6S + 8.4W$$

where LD: combined estimate of damage due to larval feeding

M: mobility,

S: damage score

W: larval weight gain.

Using this function, coefficients of each measurement were obtained by which different measurements were weighted in such a way as to minimize the subjective error in judging a true response of a plant to larval feeding. Since the conventional measurements do not include mobility, another function was worked out which eliminates the mobility variable:

$$LD = S + 2.3W$$

This function indicates that larval weight gain is the more reliable and accurate measurement of feeding damage.

4. Tissue age test ^{1/}

A different pattern of response to larval feeding between the two growth stages of the host plants is evident. It could well be that tissue age rather than growth stage causes such a difference. In pursuit of this point of tissue age, three-week old and five-week old plants were tested for differential feeding on the upper and lower leaves. The results are shown in Table 15.

Table 15. Average weight gain in mg of larvae grown on the leaves of upper and lower parts of plants at two stages of growth.

Stage of Plant	Early (3 weeks old)		Late (5 weeks old)	
	Upper leaf	Lower leaf	Upper leaf	Lower leaf
CI 6671	6.19 mg	1.46 mg	8.10 mg	6.26 mg
CI 6469	7.43	2.16	9.42	6.30
F ₂	6.33	1.54	6.30	2.94
F ₃	8.45	2.21	5.64	3.13
Larker	11.29	4.44	8.66	6.70
F-value ^{2/}	11.127**	20.66**	10.54**	8.84*

^{2/} F ratio calculated for each leaf position

^{1/} Material and Methods section 4.

Figure 3 shows a striking difference between the larval weight gain on upper versus lower leaves. The pattern of gain, however, remains relatively constant over varieties.

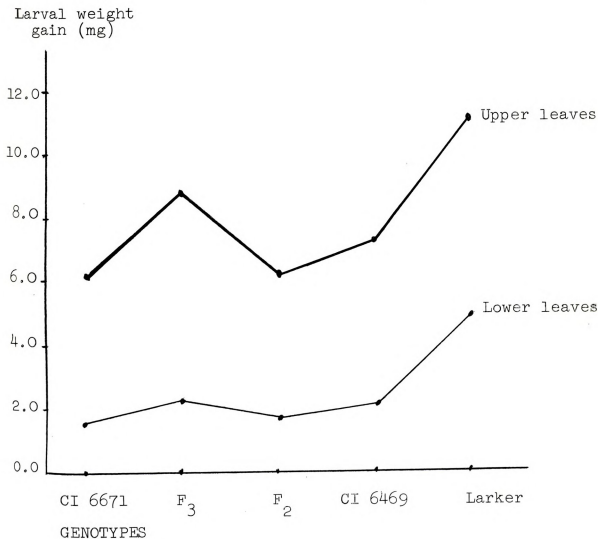


Figure 3. Larval weight gain on the leaves of upper and lower parts of young plants of five genotypes.

Larval weight
gain (mg)

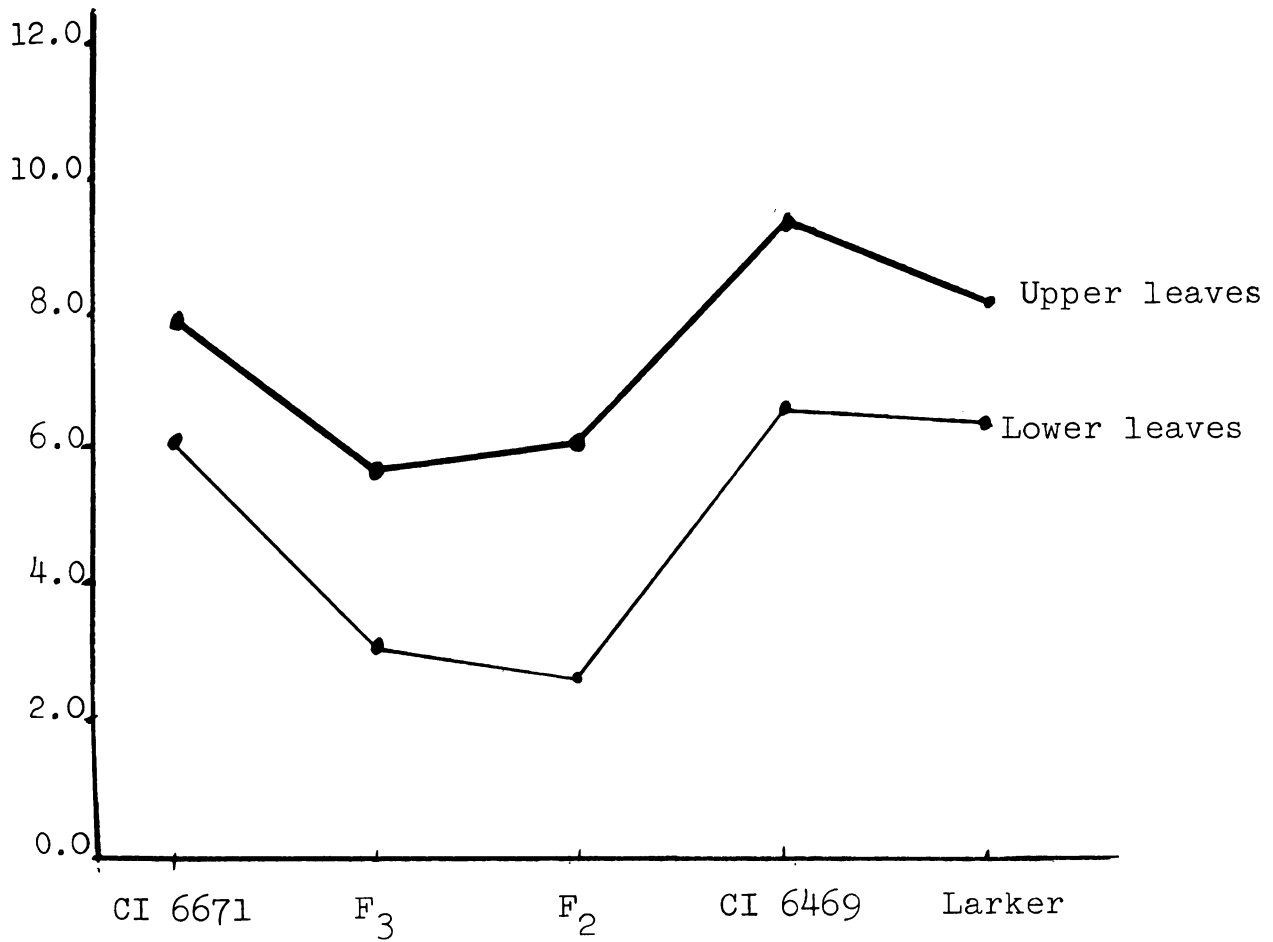


Figure 4. Standardized values of larval weight gain on the leaves of upper and lower parts of five week old plants of five genotypes.

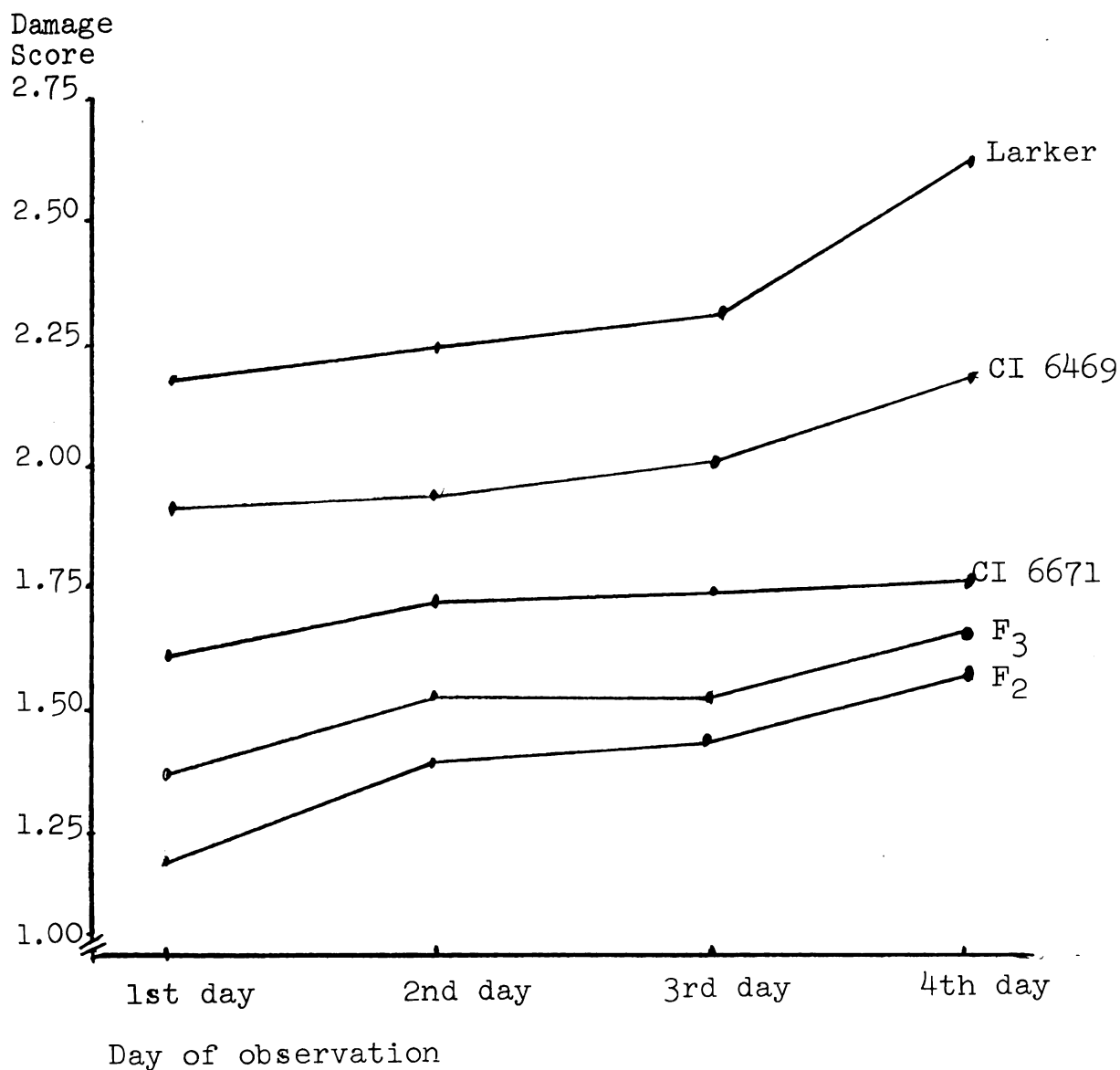


Figure 5. Larval feeding damage score observed for four successive days on the barley plants at the preheading stage.

5. Component test

Resistance or susceptibility of a plant to an insect is the end result of many factors. In the present study, the resistance character was partitioned into three components. They are ovipositional preference, antibiosis and recovery. This classification is a slight modification from that made by Painter, and the modification will be discussed. The relationships and patterns of these components were examined in a series of tests. Sequential observations were made on the characters as shown in Table 16. Under conditions of equal ovipositional preference between barley lines, the number of eggs laid should be proportional to the leaf area. To eliminate errors due to differential plant vigor, the number of eggs per plant was divided by the number of leaves of that plant. Table 16 shows those characters observed at seedling and preheaded stages of growth. The means and variances within each genotype are shown in Appendix 3.

A great difference in ovipositional preference as measured by the number of eggs per plant exists among the genotypes tested. More specifically (see Figure 6) CI 6671 is least preferred followed by plants of the F_2 generation and next by the backcross generation of CI 6671 x F_1 . CI 6469 is favored for oviposition over CI 6671, though much less

Table 16. Mean of the number of cereal leaf beetle eggs per leaf, hatchability of eggs, number of larvae per leaf, larval weight gain, total larval weight gain and tiller survival ratio on various genotypes in two stages of plant growth.

Entry	Number of eggs/leaf		Hatchability		Number of larvae/leaf		Larval Weight Gain		Total Larval Weight Gain		Tiller Survival Ratio	
	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late
CI 6671	1.77	.261	.572	.493	1.018	.122	14.16	10.6	14.41	1.29	.902	-
CI 6469	2.48	.606	.614	.208	1.748	.192	10.86	12.4	18.98	2.38	.632	-
F ₂	2.11	.345	.594	.566	1.234	.186	15.48	9.8	19.10	1.82	.886	-
F ₃	2.65	.436	.546	.420	1.372	.172	14.16	5.1	19.43	.88	.854	-
F ₄	-	.580	-	.341	-	.197	-	6.6	-	1.30	-	-
BC ₁	2.44	.380	.530	.398	1.374	.134	14.58	8.7	20.03	1.16	.954	-
BC ₂	3.03	.536	.714	.421	2.256	.391	13.44	8.2	30.32	3.21	.792	-
Larker	3.18	.614	.486	.630	1.516	.356	12.30	12.8	18.64	4.55	.568	-
Dickson	2.91	.919	.620	.428	1.648	.413	13.04	9.0	21.49	3.72	.536	-
Over-all												
Mean	2.57	.519	.584	.434	1.521	.240	13.50	9.8	20.53	2.35	.765	-
F-value	3.15*	3.43*	1.34-	1.12	4.638**	6.27**	1.427-	2.10			1.68-	-
a/ Total larval weight gain = number of larvae/plant x larval weight gain.												
b/ Total larval weight gain = number of larvae/leaf x larval weight gain.												

than the two susceptible checks. Analysis of genetic variance shows a low heritability of about 6 percent. The trends for larvae number is quite similar to that of the number of eggs, but CI 6469 and the backcross to this parent had large numbers of hatched eggs. This is probably due to the relatively high degree of ovipositional preference and favorable "hatchability."

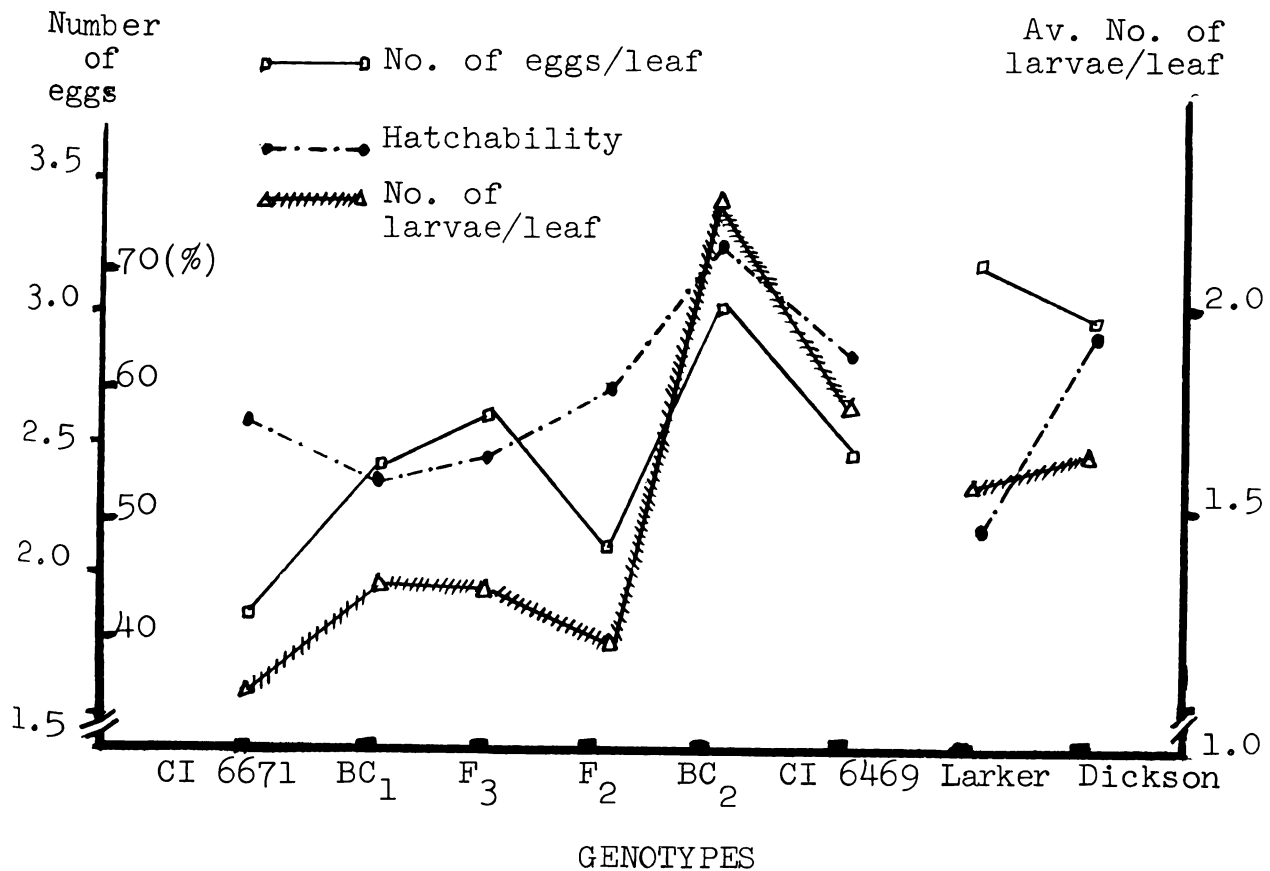


Figure 6. Ovipositional preference as measured by the number of eggs per leaf, hatchability and the number of larvae per leaf on eight genotypes of early stage of plant growth.

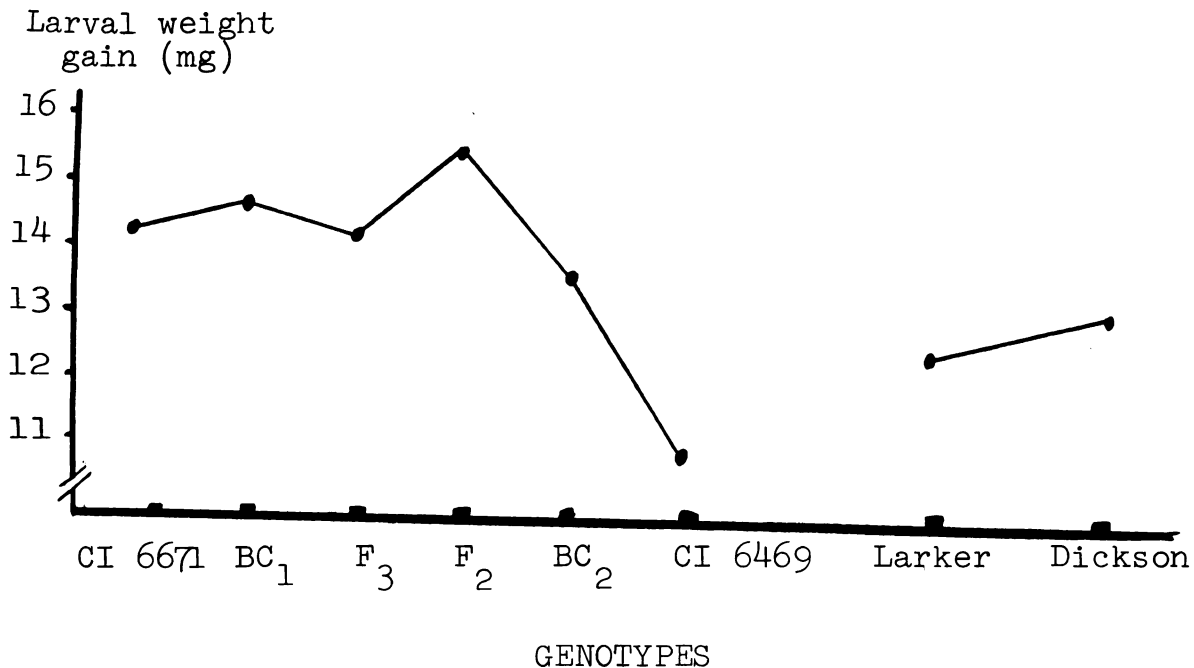


Figure 7. Antibiosis as measured by larval weight gain on young plants of eight genotypes.

Results of the larval weight gain show a pattern which differs from that observed in Test 2. This might be the result of the large larval population per plant, thus individual larvae are placed under a more competitive situation. To remove this competition factor, total larval weight gain per leaf was calculated by multiplying the number of larvae by average larval weight, as shown in Table 16. This value shows the total amount of feeding on each leaf under the condition of free host selection by the adult female beetles.

These new values are plotted in Figure 8. This new figure shows a similar pattern to those in Figures 1 and 3, from test 1 and test 2, respectively.

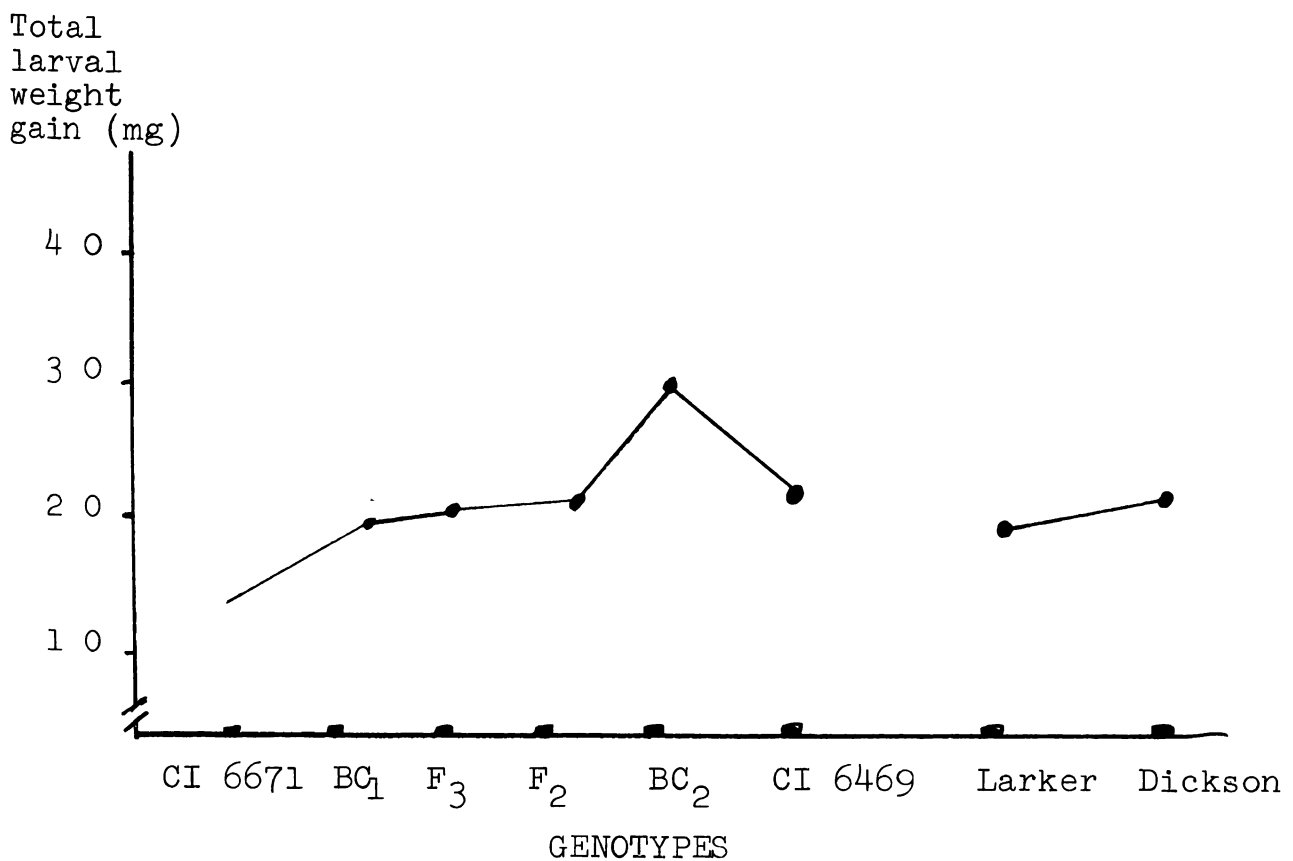


Figure 8. Antibiosis measured by the total larval weight gain (number of larvae per leaf x average larval gain) on eight genotypes of young barley plants.

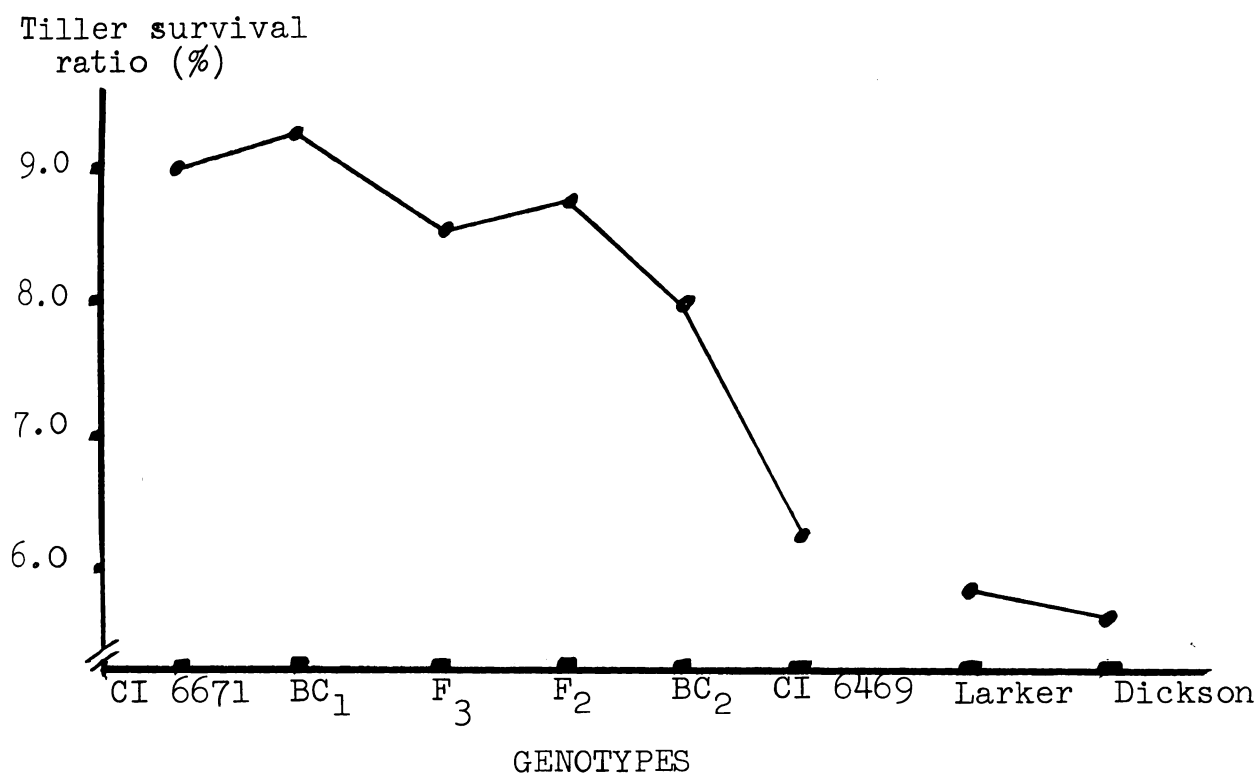


Figure 9. Recovery as measured by tiller survival after larval feeding damage on eight genotypes of younger plants.

Despite an increased time for ovipositing, the total number of eggs was much lower than at the early stage. This indicates that the adult beetle does not prefer to oviposit on plants at the mature stage and thus, the ovipositional preference at the later stage is not so important. However, the results of Table 16 show that there are differential ovipositional preferences between genotypes at the late

stage and that the pattern of differential preference is quite similar to that of the early stage. It is interesting that at the late stage, the hatchability curve is almost a mirror image of the curves of the egg or larval population. This fact may suggest that the hatching ratio is environmentally rather than genetically controlled.

Due to the sparse larval population on mature plants, there was little competition between larvae. The patterns of larval weight gain coincides with patterns observed on the plants in their late stage shown in previous tests. As the ovipositing started at the heading stage in this test, the larval feeding did not affect the tiller survival ratio.

Estimation of the heritability for each trait was not successful except for the two traits, number of eggs per leaf and larval weight gain with calculated values of about 6 percent and 28 percent, respectively. Heritability of approximately 28 percent for larval weight gain agrees well with about 32 percent heritability obtained in the field test (Test 2).

Correlation coefficients between the observed values are presented in Table 17. This table indicates that the three components of resistance are relatively independent of each other. There is some indication of a correlated

response between larvae per leaf and egg number and hatchability.

Table 17. Correlation coefficients between observations on the components of resistance --
1= number of eggs per leaf; 2= hatchability;
3= number of larvae per leaf; 4= larval
weight gain; 5= tiller survival ratio.

1	1				
2	-.155	1			
3	.524	.585	1		
4	.293	.128	-.140	1	
5	.237	.156	-.112	.327	1
	1	2	3	4	5

A third discriminant function was calculated to combine the three components into one character. The resulting function is

$$D = L + 2.91W + 1.22 T$$

where D: a combined character measuring degree of damage

L: number of larvae per leaf (measure of ovipositional preference)

W: larval weight gain (measure of
antibiosis)

T: tiller survival ratio (measure of
recovery).

This function was converted to a nomogram as shown in Figure 11, by the process described in Material and Methods. For the present function, coefficients were calculated as

$$l = 1.5, \quad w = 0.5, \quad t = 1 \quad G = 8 \quad \text{and} \quad k = 8.$$

The use of the nomogram is demonstrated on the page facing Figure 11. The principle is to find the intersection point of the D axis with the plane determined by the three specific points on the L, W and T axis, respectively.

6. Diallel cross

To obtain further genetic information of the resistance mechanism a six parent diallel cross series was planted in the field nursery and the following observations were made -- the number of larvae per plant and damage score at the early and late stage. An analysis of variance on these observations is presented in Table 18. Among the three measurements, damage score read at the early stage of plant development showed a significant difference between entries only at the 10 percent level, due to a high intraplot variation. The remaining two measurements show highly significant differences between genotypes.



Figure 10. Nomographic conversion of discriminant function

A discriminant function derived from the present test was

$$D = L + 2.91W + 1.22T$$

where

- L: Ovipositional preference as measured by the number of larvae per leaf
- W: Antibiosis as measured by larval weight gain
- T: Recovery as measured by tiller survival ratio
- D: Over all damage index combined from above three components.

L, W and T values are obtained from actual observation by scoring from 0 to 10 and D values are obtained from the nomogram as next.

1. Locate L, W and T values on their respective axis at the points P₁, P₂ and P₃, respectively.
2. Introduce a plane which contains D-axis (transparent sheet), and meets XZ plane and YZ plane on lines l₁ and l₂, respectively.
3. Connect P₁, P₃ and P₂, P₃. These lines should meet the new plane at points q₁ and q₂ on lines l₁ and l₂, respectively.
4. The line passing q₁ and q₂ is on the new plane and should intercept D-axis at a point q₃. This is the solution point.

$$D = L + 2.91W + 1.22T$$

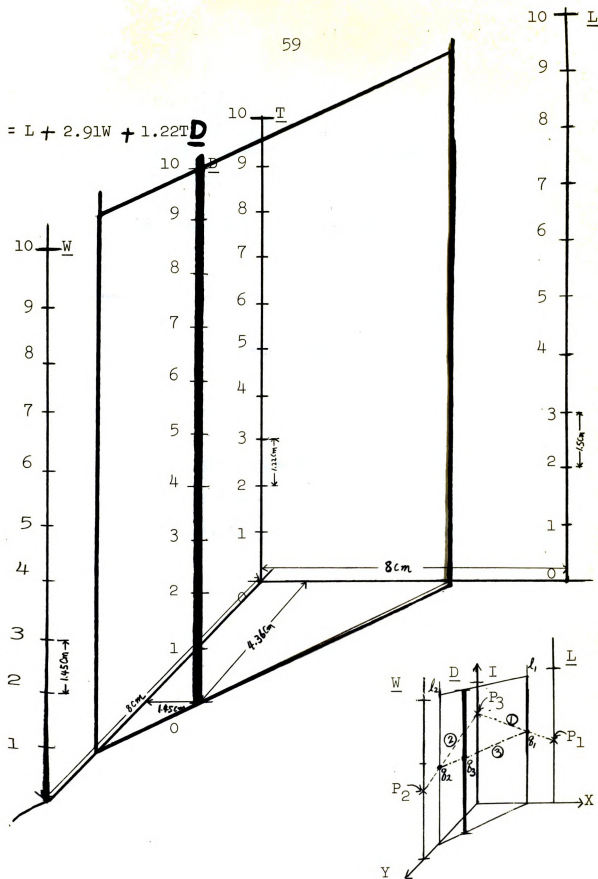


Figure 10. Nomographic conversion of discriminant function.



$$D = L + 2.91W + 1.22T$$

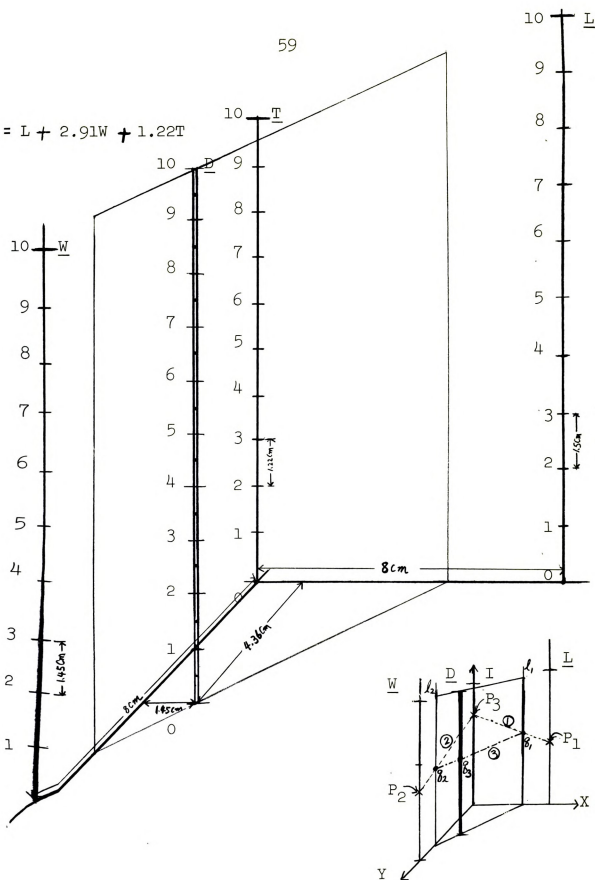


Figure 10. Nomographic conversion of discriminant function.

Table 18. Combined analysis of variance tables for number of larvae per plant and larval feeding damage scores at two growth stages on F_2 generation of 6 parent diallel cross.

Source traits	Number of larvae/plant			Damage score			
				Late seedling Stage		Heading stage	
	df	MS	F	MS	F	MS	F
Block	3	2.087	1.49	.109	1	.8357	6.65**
Entry	20	12.920	9.25**	.362	1.43	.4448	3.54**
Error	60	1.397		.251		.1256	

The genetic relationship between parents and their progenies were analyzed by the Jinks-Hayman W_r/V_r graphic analysis. For this analysis, the values from four replications are pooled as shown in Tables 19 and 20, for the number of larvae per plant and the damage score at the late stage, respectively. Pooled values for the damage scores at the early stage are shown in Appendix table 4. Diallel graphs were constructed as Figure 11 and Figure 12. The regression line on the graph of the number of larvae was significantly different from 0 but also significantly different from 1. General inspection of this graph indicates this character is of an ambidominant nature. The term, ambidominance, was first

Table 19. Total, Wr and Vr values of the number of larvae per plant for the F₂ generation of the 6 parent diallel set.

Parental number	Parents	1	2	3	4	5	6	Vr	Wr
1	CI 12518	15.9	13.2	12.8	14.5	15.0	22.1	.1150	.0930
2	CI 12528	13.2	12.1	15.1	12.7	14.9	14.7	.0163	-.0087
3	CI 6671	12.8	15.1	9.9	15.9	11.7	12.4	.0490	.0290
4	CI 6469	14.5	12.7	15.9	15.7	14.4	14.1	.0136	-.0035
5	CI 12715	15.0	14.9	11.7	14.4	10.9	14.1	.0307	.0398
6	CI 11531	22.1	14.7	12.4	14.1	14.1	18.6	.1317	.2365
Sum		93.5	82.7	77.8	81.0	81.0	96.0	2.248	1.328

Table 20. Total, Vr and Wr values of the damage score at late stage of the F₂ plants of the 6 parent diallel set

Parental number	Parents	1	2	3	4	5	6	Vr	Wr
1	CI 12518	6.7	7.3	8.6	7.2	6.6	7.7	.540	.344
2	CI 12528	7.3	7.6	7.1	7.3	7.1	7.3	.034	.080
3	CI 6671	8.6	7.1	7.3	7.6	6.3	6.9	.596	.152
4	CI 6469	7.2	7.3	7.6	7.1	6.5	8.5	.440	.344
5	CI 12715	6.6	7.1	6.3	6.5	5.6	7.1	.316	.356
6	CI 11531	7.7	7.3	6.9	8.5	7.1	7.4	.322	.052
		44.1	43.7	43.8	44.2	39.2	44.9	2.248	1.328

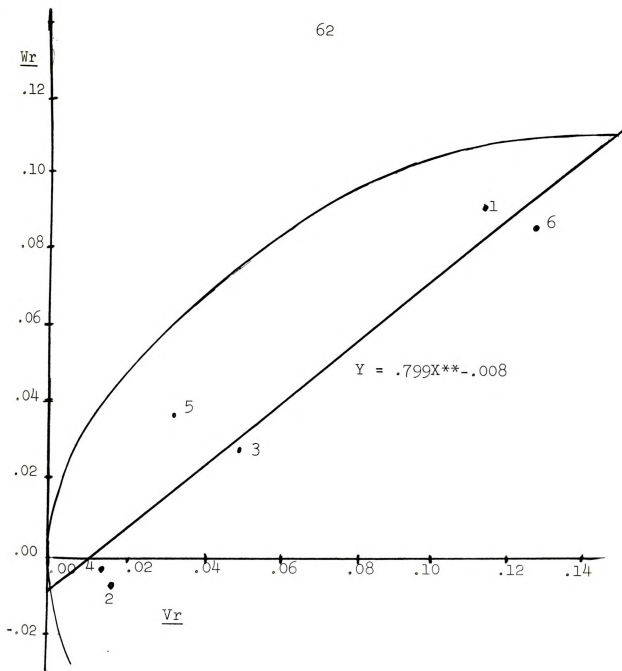


Figure 11. A diallel graph for the number of larvae per plant of the F_2 generation of the 6 parent diallel set.

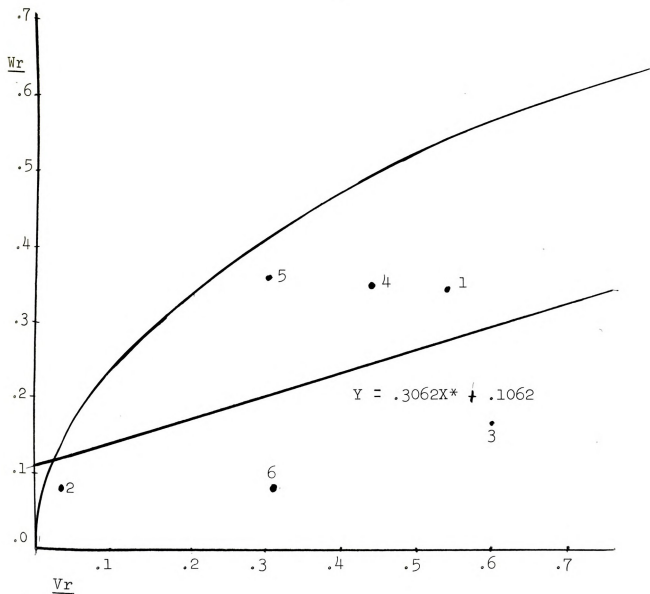


Figure 12. A diallel graph for the damage score at late stage of F_2 plants of 6 parent diallel set.

used by Breese (3), to indicate the pattern of a trait which shows both dominance and recessive inheritance for a high expression of a character. Together with the evidences of the existence of non-allelic interaction ($b \neq 1$), this ambidominance indicates the complex nature of the inheritance of ovipositional preference. The regression coefficient of the damage score at the late stage was also significantly different from the zero and unity slope. The arrangement of parental lines on the W_r/V_r plane also indicates the pattern of ambidominance as was shown in the number of larvae per plant.

DISCUSSION

Resistance of a plant to a parasitizing insect is a character highly complex and very difficult to measure. Not only is resistance the result of interactions between plant and insects, but also both the plant and insect have factors which make the pattern of resistance complicated. Frequently the environment also plays an important role in the expression of resistance (a good example of the latter is pseudo-resistance as illustrated by Painter (19)). Yield is often partitioned into several components which are easier to handle and to predict. So far, however, resistance to insects or to pathogens has been regarded as a simple character, partly due to lack of careful attention or to the impracticability of paying too much attention to "secondary characters." However, the more crop yields increase, the more important an understanding of resistance becomes for higher yield.

Painter (19, 20) classified resistance into three categories, as preference, antibiosis and tolerance, though Beck (2) dropped the last category. However, Painter's classifications are difficult to use as components of

resistance because:

1. The three categories are not sequential;
2. Some of the categories are overlapping;
3. These measurements of resistance are difficult to assess on a field basis.

In this respect, the present study suggests three components which are slight modifications of Painter's categories, namely (1) ovipositional preference; (2) antibiosis; and (3) the recovery of plants. The first component is the relationship between the ovipositing adult beetle and the host plant. The second component is the interaction between the feeding larvae and the plant while the third component measures the potential recovery of the plant. The present study shows that these three components are somewhat independent of each other. The category of tolerance which corresponds to recovery in the classification used in this work is important because toleration and recovery from a given degree of damage is probably heritable and may help to increase yield and/or quality.

Even though all three components may be measured and used for comparing plant material upon an individual component base, we need a reasonable way of combining the three into one index accompanied by proper weighting according

to their relative importance and reliability. In the present study, a discriminant function is suggested which would be suitable for the purpose of giving a single value from the three measurements. By converting the function to a nomographic chart, breeders or other field workers can save time and reduce the chance of erroneous decisions using the nomogram while rating the field selections.

The main purpose of the present study is to understand the genetics of resistance and to examine the possibility of obtaining a higher degree of resistance than is now available. Hahn (14) also worked on genetics of resistance but posed some puzzling problems since he found the resistance to be recessive and yet transgressive inheritance was found in the F_2 generation. The present study allows some explanation of this point. The resistance of barley to the cereal leaf beetle has different genetic resistance patterns depending on stage of growth. Thus, each genotype has a two-fold resistance pattern. At the early stage, the resistance is genetically recessive and therefore the F_1 between the two resistant parents appeared susceptible, but at the late stage of plant development, the resistance shows an ambidominance and the genetic pattern of resistance is changed. Field observation indicated inferiority of CI 6469 to CI 6671

in resistance. The present study suggests that both genotypes are almost equally resistant in the early stage but at the late stages CI 6469 is not as resistant as CI 6671 when measured on a similar age of leaf. This fact suggests that a genotype should be evaluated for its response to insect feeding at two different stages. Through a series of experiments shown in test 4, the age of tissue was not responsible for the two-pronged nature of resistance. One possible hypothesis is that resistance at the late stage is due to a build-up of certain defense mechanisms as the plant matures. Another possibility is the differential rate of accumulating some toxic or indigestible material, which would have an anti-biotic effect especially on young larvae and perhaps on the eggs. And if we assume that both CI 6671 and CI 6469 are not provided with a high degree of resistance at the late stage, then we can expect transgressive inheritance in further generation. This is what happened in the present tests where the F_1 was susceptible at the early stage but showed reinforcement in resistance at the late stage. Through component study, the difference in ovipositional preference was more indicative of resistance than the response to larval feeding. Especially CI 6671 showed a high degree of ovipositional nonpreference. A significant

difference among lines in ovipositional preference but little difference in feeding damage score observed in the present tests agrees with the result obtained by Schillinger (29). The lack of a high degree of resistance to larval feeding especially at the later stage could be the reason that barley lines do not show the degree of resistance known in wheat lines. This suggests that breeding schemes for resistance of barley to the cereal leaf beetle need to put more emphasis on feeding response at the later stage than on ovipositional preference. At the same time, care should be taken not to neglect plant recovery because this will be very helpful in ameliorating the damage even though this trait is ancillary to antibiosis. These points are emphasized in the discriminant function presented herein, for combining the measurements of three components.

More emphasis should be placed on feeding damage with a heritability value of 38 percent in comparison with that of ovipositional preference of only five percent which indicates better genetic control of feeding damage. However, as the heritability values are subject to change with different generations, parents and environments, such information must be used with appropriate reference points.

The scheme to estimate the number of loci involved in each component was not successful probably due to isodirectional distribution of genes. Larval feeding damage is estimated from the larval damage score on the plant and/or the larval weight gain. The mobility of larvae is not affected by different genotypes, and cannot be a way of judging resistance.

The present study shows that larval weight gain is a more reliable measure of resistance than damage score. But as the larval weight gain is hard to observe or even estimate under field conditions or even in laboratory tests dealing with a large number of lines, damage score is probably a more effective estimate even though the discriminant function indicates that it is about half as reliable as larval weight measurement.

SUMMARY

The thesis describes a series of tests on the mode of inheritance and mechanisms of resistance to cereal leaf beetle in barley and examines the possibility of obtaining a higher degree of resistance.

Resistance was defined as a complex with three components -- ovipositional preference, antibiosis, and plant recovery. These three components are found to be relatively independent of each other.

The genetic situation of ovipositional preference appears to indicate ambidominance and the heritability is quite low. The age of plant tissue influences the ovipositing by adult beetles, older plants being much less preferred and there are apparent differences in genotype in this respect.

There are two different patterns of inheritance in feeding preference -- at the early stage of plant development, resistance to larval feeding is controlled by recessive genes but ambidominance appears at the late stage. Over several sets of tests, a heritability of approximately 30 percent was observed at both stages. Tissue age was shown not to be responsible for this differential pattern

of resistance. Two ways of measuring this aspect of resistance were employed -- a subjective feeding damage score and larval weight gain where the latter was shown to be more reliable, but more difficult to measure.

Varietal difference in plant recovery after insect damage was observed, but the patterns of inheritance appear to be complicated and no heritability estimates could be made for this character.

A discriminant function combines these three components observed into a single formula. Furthermore, a nomograph was constructed to facilitate rapid estimation of combined resistance from this function.

LIST OF REFERENCES

1. Adams, D. P. 1964. Nomography, theory and application. Archon Books. Chapters 1, 2, 5.
2. Beck, S. D. 1965. Resistance of a plant to insects. Annual Review of Entomology 10: 207-232.
3. Breese, E. L. 1960. The assessment of breeding material. Proceedings of the 8th International Grassland Congress 45-49.
4. Castro, T. R., R. F. Ruppel, and M. S. Gomulinski. 1965. Natural history of the cereal leaf beetle in Michigan. Mich. Agr. Exp. Sta. Quart. Bull. 47:623-653.
5. Chada, H. L. 1950. Insectary technique for testing the resistance of small grains to the green-bug. Journ. of Econ. Entomol. 52: 276-279.
6. Connin, R. V., D. L. Cobb, J. C. Arnsman, and G. Lawson. 1968. Mass rearing the cereal leaf beetle in the laboratory ARS 33-125, U. S. D. A.
7. Everson, E. H., R. L. Gallun, J. A. Schillinger, D. H. Smith, and J. C. Craddock. 1966. Geographical distribution of resistance in Triticum to the cereal leaf beetle. Michigan State Univ., Agr. Exp. Sta. Quart. Bull. 48: 565-569.
8. Fisher, R. A. 1936. The use of multiple measurements in taxonomic problems. Ann. Eugen. 7: 179-189.
9. Fisher, R. A. 1937. The statistical utilization of multiple measurements. Ann. Eugen. 8: 376-386
10. Gallun, R. L. and R. R. Ruppel. 1963. Cereal leaf beetle resistance studies. Special Report W-178, Entomology Research Division U. S. D. A. ARS.
11. Gallun, R. L., E. H. Everson, R. Ruppel and J. C. Craddock. 1964. Cereal leaf beetle resistance studies. Spec. Rep. W-200. Ent. Research Div., U. S. D. A., ARS

12. Gallun, R. L., R. Ruppel and E. H. Everson. 1966. Resistance of small grains to the cereal leaf beetle. Journ. Econ. Ent. 59: 827-829.
13. Gallun, R. L., R. T. Everly and W. T. Yamazaki. 1967. Yield and milling quality of Monon wheat damaged by feeding of cereal leaf beetle. Journ. of Econ. Ent. 60: 356-359.
14. Hahn, S. K. 1968. Resistance of barley to the cereal leaf beetle. Crop Sci. 8: 461-464.
15. Hayman, B. I. 1954. The theory and analysis of the diallel cross. Genetics 39: 789-809.
16. Jinks, J. L. 1954. The analysis of quantitative inheritance in a diallel cross of Nicotiana rustica varieties. Genetics 39: 767-788.
17. Mather, K. 1943. Statistical analysis in biology. Interscience Publishers, Inc. p. 152-159.
18. Mather, K. 1949. Biometrical genetics. Dover Publication, Inc. p. 31-37, p. 102-114.
19. Painter, R. H. 1951. Insect resistance in crop plants. The Univ. Press of Kansas. Chapters I, II, III, IX.
20. Painter, R. H. 1958. Resistance of plants to insects. Ann. Rev. of Ent. 3: 267-290.
21. Ringlund, K. 1967. Leaf pubescence in common wheat and resistance to the cereal leaf beetle. Crop Sci. 8: 705-710.
22. Ruppel, R. F. 1964. Biology of the cereal leaf beetle. Proc. North Central Branch E.S.A. 19: 122-124.
23. Ruppel, R. F. 1964. Control of the cereal leaf beetle. Proceedings North Central Branch E.S.A. 19: 127-128.
24. Ruppel, R. F. 1966. Current status of the cereal leaf beetle. Ent. Soc. Amer. N. Cent. Br. Proc. 20: 98-99.
25. Schillinger, J. A., R. L. Gallun, E. H. Everson, D.H. Smith, and J. C. Craddock. 1964. Cereal leaf beetle resistance studies (1964-1965). Spec. Rep. W-207, Ent. Res. Div. U.S.D.A. ARS.

26. Schillinger, J. A. 1966. Laboratory screening of wheat for resistance to the cereal leaf beetle. Special report W-217, Entom. Res. Div. U.S.D.A. ARS.
27. Schillinger, J. A. 1966. Larval growth as a method of screening *Triticum* spp. for resistance to the cereal leaf beetle. *J. Econ. Ent.* 5: 1163-1166.
28. Schillinger, J. A. 1967. Relationship of pubescence to resistance in wheat to the cereal leaf beetle. *Pro. N. Cent. Ent. Soc. Amer.* 22: 98.
29. Schillinger, J. A. 1969. Three laboratory techniques for screening small grains for resistance to cereal leaf beetle. *Journ. of Econ. Ent.* 62: 360-363.
30. Sengupta, G. C., and B. K. Behura. 1957. On the biology of *Lema praeusta* Fab. *Journ. Econ. Entomo.* 50: 471-474.
31. Smith, H. F. 1936. A discriminant function for plant selection. *Ann. Eugen.* 7: 240-250.
32. Wellso, S. G., J. A. Webster, and R. F. Ruppel. 1969. A bibliography of the cereal leaf beetle. *Bull. Entom. Soc. Amer.* (In press).
33. Wilson, M. C. 1964. History, distribution, dispersion and economic significance of the cereal leaf beetle. *Proc. North Central Bran. Ent. Soc. Amer.* 19: 120-122.
34. Wilson, M. C. 1964. Host-plant cereal leaf beetle relationship. *North Central Branch Ento. Soc. Amer.* 19: 124-127.
35. Wilson, M. C. and R. E. Shade. 1964. The influence of various gramineae on weight gains of postdiapause adults of the cereal leaf beetle. *Ent. Soc. Amer.* 57: 659-661.
36. Wilson, M. C. and R. E. Shade. 1964. Adult feeding, egg deposition and survival of larvae of the cereal leaf beetle on seedling grains. *Purdue Univ. Agric. Exp. Sta. Progress Report* 97.

37. Wilson, M. C. and R. E. Shade. 1967. Relative attractiveness of various luminescent colors to the cereal leaf beetle and meadow spittlebug. Jour. of Econ. Entomol. 60: 578-580.
38. Yun, Y. M. 1966. Some effects of environment on the cereal leaf beetle. Ent. Soc. Amer. N. Cent. Br. Proc. 20: 65.

APPENDICES

APPENDIX 1. Means and variances of yield characters observed in the field on the barley plants of five generations of the cross CI 6671 x CI 6469

Traits observed	Head weight (gr.)	Maturity ratio (weight base) (%)	Maturity ratio (number base) (%)	Av. grain weight (gr/1000)				
Genotypes	Mean	Var.	Mean	Var.				
CI 6671 (P_1)	1.15	.0651	70.19	19.538	47.73	98.104	26.25	5.185
CI 6469 (P_2)	1.18	.0434	75.39	17.187	53.28	46.118	23.25	4.624
F_1	1.35	.0291	73.70	14.148	57.20	51.258	27.13	4.522
F_2	.75	.1511	63.80	128.250	48.50	76.024	21.99	17.189
BC_1	.79	.0420	69.51	43.366	43.53	81.706	21.09	2.812
BC_2	.99	.0401	73.19	60.233	50.84	121.154	23.33	5.735
F-value	3.20*	1	1.37				4.84*	

APPENDIX 2. Means and variances of mobility, damage score and larval weight gain for CI 6671, CI 6469, F₁, F₂, BC₁ and BC₂ generation of the cross CI 6671 x CI 6469 and susceptible varieties Larker and Dickson at four stages of plant growth.

traits							
Genotypes	Mobility (I)		Damage score (I)		Larval weight gain (Gr.)		
STAGE 1. (Two weeks old)							
	mean	var.	mean	var.	mean	var.	
CI 6671	5.9	2.3	1.6	.60	1.644	.0228	
CI 6469	5.6	4.6	2.5	.50	1.568	.0063	
F ₁	5.5	.1	2.0	.40	1.850	.0050	
F ₂	5.7	8.3	2.3	.50	1.051	.0891	
BC ₁	5.0	3.7	2.0	.40	1.284	.0693	
BC ₂	4.8	1.8	1.5	.30	1.052	.0236	
Larker	6.1	1.7	2.3	.30	1.750	.0207	

STAGE 2. (Three weeks old)							
	mean	var.	mean	var.	mean	var.	
CI 6671	4.7	2.1	1.6	.20	1.278	.006	
CI 6469	4.3	3.1	1.5	.30	1.742	.261	
F ₁	5.0	2.2	1.3	.10	1.881	.013	
F ₂	3.8	1.8	1.8	.40	1.331	.155	
BC ₁	3.0	2.2	1.9	.30	1.786	.124	
BC ₂	4.8	1.6	1.5	.30	1.738	.021	
Larker	4.5	3.5	1.8	.40	1.599	.144	

APPENDIX 2 (Cont.)

Genotypes	traits		Damage score		Larval weight	
	Mobility (I)		(I)		gain (Gr.)	
STAGE 3 (Four weeks old)						
	mean	var.	mean	var.	mean	var.
CI 6671	5.1	5.5	1.7	.70	1.518	.064
CI 6469	4.2	1.6	1.9	.20	1.643	.042
F ₁	4.0	3.6	1.9	.10	1.553	.054
F ₂	4.4	1.2	1.7	.70	1.923	.113
BC ₁	4.1	1.1	1.6	.90	1.766	.049
BC ₂	5.4	5.8	1.8	.50	2.302	.051
Larker	4.6	2.2	1.8	.50	1.833	.045
STAGE 4 (Six weeks old)						
	mean	var.	mean	var.	mean	var.
CI 6671	3.2	3.0	2.0	.40	1.638	.047
CI 6469	5.1	1.9	1.5	.30	1.764	.072
F ₁	4.9	.3	1.4	.20	1.141	.002
F ₂	3.5	11.7	1.6	.20	1.452	.109
BC ₁	3.2	7.2	1.2	.20	1.570	.062
BC ₂	2.9	1.9	1.6	.20	1.791	.013
Larker	4.1	4.1	1.8	.20	1.819	.034

APPENDIX 3. Means and variances of three components of resistance-ovipositional preference, larval feeding damage and plant recovery on the eight different genotype of early stage of plant growth.

Traits observed	Number of eggs per leaf		Hatchability		Number of larvae per leaf	
Genotypes	mean	var.	mean	var.	mean	var.
CI 6671	1.715	.622	.571	.053	1.907	.303
CI 6469	2.489	.497	.615	.034	1.681	.474
F ₂	2.277	.755	.548	.045	1.154	.554
F ₃	2.668	.767	.497	.071	1.251	.498
BC ₁	2.309	.704	.586	.058	1.321	.420
BC ₂	3.027	.769	.674	.036	2.218	.412
Larker	3.176	.562	.463	.034	1.430	.425
Dickson	2.906	.406	.564	.054	1.598	.494
h ²	6.357%					

Traits observed	Tiller survival ratio		Larval weight Gain (Gr.)		Av. head weight (Gr.)	
Genotypes	mean	var.	mean	var.	mean	var.
CI 6671	.0885	.000330	1.439	.0147	.0627	.000417
CI 6469	.0637	.000641	1.110	.0312	.0891	.000310
F ₂	.0867	.000415	1.455	.0808	.0725	.000333
F ₃	.0823	.000411	1.450	.0535	.0790	.001394
BC ₁	.0946	.000154	1.520	.0910	.0478	.000151
BC ₂	.0794	.000359	1.361	.0680	.1109	.000575
Larker	.0604	.000602	1.172	.0431	.1226	.000537
Dickson	.0824	.000414	1.291	.0793	.1450	.000837
h ²	28.09%					

APPENDIX 4. Total Vr and Wr values of the damage score at late seedling stage of F_2 plants of 6 parent diallel.

Parental number	Parents	1	2	3	4	5	6	Vr	Wr
1	CI 12518	7.6	7.0	8.0	7.5	7.8	9.8	.94	.806
2	CI 12528	7.0	7.8	8.4	6.2	10.4	7.9	2.04	.002
3	CI 6671	8.0	8.4	9.2	8.6	6.4	8.0	.89	.308
4	CI 6469	7.5	6.2	8.6	8.2	6.8	7.2	.79	.296
5	CI 12715	7.8	10.4	6.4	6.8	7.8	6.2	2.39	-.998
6	CI 11531 (Dickson)	9.8	7.9	8.0	7.2	6.2	10.0	2.18	.606
Sum		47.7	47.7	48.6	44.5	45.4	49.1	9.23	1.02





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