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RESISTANCE TO CEREAL LEAF BEETLE, *OULEMA MELANOPUS*, (L.), OF PUBESCENT *AVENA STERILIS*, *AVENA SATIVA* HYBRIDS

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ABSTRACT

RESISTANCE TO CEREAL LEAF BEETLE, OULEMA MELANOPUS, (L.), OF PUBESCENT AVENA STERILIS, AVENA SATIVA HYBRIDS

By

Carrie Young

Cereal leaf beetle resistance in wheat is highly correlated with length and density of leaf pubescence. This relationship also exists in wild Hordeum sp. However, additional criteria for selection for resistance in oats must be used because the level of trichome length and density in oats is much lower than in wheat.

The USDA World Collection of Small Grains was screened for field larval feeding damage by USDA-CLB project workers. A pubescent Avena sterilis line, PI 311677, was selected because of field resistance. Entries C.I. 521, C.I. 1625, C.I. 4867, and C.I. 4893 also exhibited some resistance. These five lines, with varieties Froker and Korwood, formed the base populations from which initial testing and resistance studies in oats began.

A. sativa entries were not significantly different in oviposition preference tests. Line P.I. 311677 was significantly different from C.I. 4867 in number of eggs per plant and exhibited antibiosis in larval weight gain tests.

A diallele analysis was made on a series of crosses to observe complementation of genes for resistance. If different genes

for resistance located at different loci were present in two lines crosses, transgressive segregation could be expected and increase in host plant resistance to the cereal leaf beetle might result. Susceptible lines were included as checks.

Dr. Fred Collins of the University of Arkansas contributed pubescent lines. The pubescence was from A. sterilis entries P.I. 295919 and P.I. 320793.

The Arkansas lines and the four most pubescent lines from progeny of the diallele crosses were carried forward for further testing. Segregates within each line were selected on the basis of field larval feeding damage tests, oviposition preference tests and trichome density evaluation. Several of these segregates were more pubescent than the original parents and progeny of the initial cross. Crosses among the superior segregates from these progenies formed the basis for the next cycle of recurrent selection. Within line crosses brought together again genes for resistance from the same parent. The trichome counts of parents, F_1, and F_2 of each line were analyzed to determine the number of loci and dominance or recessiveness of trichome expression. These progeny were tested for host plant-beetle interaction.

The F_1 exhibited increased pubscence density and decreased egg counts compared to the midparent. In the F_2, due to the difficulties with single plant observations, these gains were not confirmed.

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INTRODUCTION

The cereal leaf beetle, Oulema melanopus (L.), is a chrysomelidae which was first identified in Michigan in 1962. The insect spread rapidly through Michigan, Indiana and Ohio aided by prevailing westerly winds. The beetle has been identified in Illinois and Wisconsin to the west and far into Canada and several states to the east.

This Eurasian insect has long been a pest of small grains in Europe. Wheat, oats and barley are damaged excessively. Many native grasses, rye and maize serve as alternate hosts (55).

The United States Department of Agriculture, Michigan State University and Purdue University plant geneticists and entomologists screened the World Collection of Small Grains. Field screening followed by laboratory testing found resistant wheat lines. The more resistant wheat lines were highly pubescent. Moderate resistance was discovered in oats and barley.

Further work by Hahn (17, 18) and Lee (22) concluded that oviposition preference, larval feeding damage and plant recovery in barley are independently inherited and that resistance is not due solely to leaf pubescence.

Several Avena sativa cereal investigation entries were found to be slightly resistant. An A. sterilis entry, P.I. 311677, was pubescent and exhibited an antibiosis effect on larvae (42).

Cereal investigation entries and P.I. 311677 were used to test the host plant-insect interaction under field and laboratory conditions. The inheritance of oat pubescence and its role in resistance were also studied.

LITERATURE REVIEW

The cereal leaf beetle, Oulema melanopus (L.), is believed to have been introduced into the United States in the late 1950's. The beetle was first noticed in Berrien county in Southwestern Michigan (4).

"Black slugs" were found on plants in small grain fields, and unidentified beetles were also seen. The appearance of these insects prompted spraying of insecticides in 1959 (44).

In 1962, the slugs (larvae) and beetles were identified as different life cycle stages of cereal leaf beetle. "Watch for the Cereal Leaf Beetle" (56) was published by the United States Department of Agriculture in 1963 to alert growers of the presence and life cycle stages of this phytophagous insect. Fearing insect spread to the grain growing areas in the plains, screening of germplasm, insecticide tests and formation of quarantine laws began (29).

When infested wheat plants were compared to non-injured plants, a 12% reduction in kernel number and a 22.6% reduction in yield was observed (15). Wilson and Shade (54) found larval infestation and larval feeding damage highly correlated with yield reduction in oats.

Screening of the U.S.D.A. Wheat, Oat and Barley World Collections began in 1962. In the 1963-64 growing season, 34,000

entries were tested. All of the oat and barley lines experienced larval feeding damage. Only four percent of the oat lines, Avena sp., and two percent of the barley lines, Hordeum sp., had trace damage. Overall, twelve percent of the wheat lines, Triticum sp., had trace or no damage. The plants in the pubescent nursery of the Wheat World Collection had 18% of the entries with trace or no larval feeding damage (11). Those wheat lines with no larval feeding damage were highly pubescent (16). Gallun et al. (14) observed that not only was wheat less preferred for oviposition than oats and barley, wheat lines had less adult and larval feeding damage. Oat lines showed twice as many eggs as wheat lines.

Scanning the origin of resistant lines, no single center of resistant germplasm was discovered. Many of the resistant lines are native to China and Russia. Asia, Asia Minor, Eurasia and Eastern Africa are possible germplasm centers (10). The cereal leaf beetle occurs widely throughout Europe and Asia. The most common and serious outbreaks are in Siberia and the Balkans (44). Resistance in varieties where the beetle is not indigenous is due to inadvertent use of resistant parents in the breeding program (10).

Resistance may be due to the plants' physiological state of development, type of vegetative growth or disease susceptibility (36). When many lines are planted together, individual lines may miss infestation and appear resistant by chance alone. Vernalization of winter types causes morphological and physiological changes which may affect host selection of the insect (35). When winter types are spring planted, the decumbent growth habit may enhance the chance of escape from beetle attack (48).

Adult beetles confined to two leaves of the same plant laid significantly more eggs on the younger leaf. Adults did not distinguish between leaf ages when feeding on 'Clintland 64' oats. Less feeding occurred on the younger leaf of vernalized 'Genessee' wheat and in conjunction with this late planted fall grains and early planted spring grains appear to have more cereal leaf beetle damage (29).

Variation in the phenotypes of host plants makes defining resistance difficult. Seedling laboratory tests are used to minimize these differences (35).

Twice as many eggs were oviposted on oat seedlings 4.3 inches high as on seedlings at 7.2 inches (55). The angle of illumination and leaf width affect positioning of the eggs on the leaf blade. When the plants were inverted, the number of misplaced and fallen eggs increased (52).

Field collected females exhibited greater egg production efficiency after feeding on oats as compared to wheat (49). Oviposition preference, reduction in egg production, larval weight gain and survival were observed for the insect when fed on wheat, oat and barley lines (31). Larval weight gain and survival were measured for lines susceptible and resistant to larval feeding damage in field trials. Larval tests substantiated field test results (34). Seedling mortality, after exposure to pre-diapause adult feeding, was highly correlated with larval feeding in the field (47).

Adults exhibited differences in oviposition preference when four wheat lines, with different pubescence densities, were compared.

Differences in percent egg hatch and larval weight gain were seen. Ten percent of the first instar larvae survived after confinement to densely pubescent wheat for three days (33). Six lines differing in pubescence density and length were studied to observe insect reaction. Lines with many long trichomes (30 per mm^2, 0.25 mm long) had the fewest eggs per plant and the lowest percent larval survival (19). Oat leaf hairs tend to be longer and less rigid than those of resistant wheat (46).

Eggs laid on densely pubescent leaves are more susceptible to desiccation and have low hatch percent. Slow larval weight gain was the result of ingestion of trichomes as the larvae tried to reach the leaf surface (32). First instar larvae bit each trichome as many as three times before reaching the nutritious leaf epidermis. Fourth instar larvae ingest the trichomes whole. Undigested trichomes may penetrate the mid-gut epithelium. Larvae fed on resistant C.I. 8519 grew slowly (51), as did larvae fed P.I. 311677, an A. sterilis line (39).

Johnson (20) has examined the environmental effects and ecological importance of plant pubescence. A general overview of pubescence of many species was made. Uniform leaf expansion was important when determining trichome density of small grains (45). The first leaf of seedlings grown in closed petri dishes was more pubescent than those grown in peat pellets (41). Plants grown at high light intensity exhibited fewer trichomes than those grown under low light conditions when temperature and relative humidity were held constant (12). Profuse increases and decreases in trichome density

were observed in several Triticum and Hordeum species after chronic gamma irradiation. The optimum dose for maximum hair production varied with species and variety. Extra visible incandescent light affected hair length and density in H. spontaneum. Increased hairiness was not transmitted to the offspring, but rather appears to be an immediate physiological response of the leaf epidermis (21).

The inheritance of small grain leaf pubescence has been studied. In 1968, Ringlund and Everson (28) found that pubescence in wheat is quantitatively inherited and is due to partial dominance and additive effects. Wallace et al. (43) found 3:1 pubescent to glabrous segregation in F_2 wheat populations. Leisle, in 1974, working with durum wheat, described trichome expression as the result of two or three dominant genes for density which are additive for length. All glabrous F_2 plants had no pubescent segregates in the F_3 (23). Segregates of wild Hordeum sp. indicate that pubescence is dominant but complex in inheritance (13). Resistance to larval feeding damage of barley appeared to be recessive and due to genetic interaction (17). Pubescence in oats appeared dominant or partially dominant, as segregates were predominantly pubescent (25). Sarkarung (30) found two genes for pubescence expression in oats. Modifying genes increased trichome counts of progeny of his crosses over density of the A. sterilis parental lines.

Since oat and barley lines have few trichomes, alternative methods for securing resistance may be needed. Oviposition preference was significantly different between substitution lines of Hope wheat (40). Identification of a resistant genome may be useful in oats.

Larvae feed between the veins. Feeding scars are parallel to the veins (50). Antibiosis occurs in lines which have veins too close together for larvae to feed (37, 38).

Narrow leaves or curly leaf blades may be less preferred for oviposition; leaf cuticle structure and leaf color may also be of importance (46).

PLANT MATERIAL

The plant materials used in the following tests were advanced generation progeny of a diallele constructed by Dr. Robert Steidl. Dr. Fred Collins of the University of Arkansas contributed eleven pubescent segregates, three of which were used for various crosses.

The parents for Steidl's diallele were selected on the basis of field screening tests for resistance to the cereal leaf beetle (Smith and Webster,unpublished data). An Avena sterilis L. line, P.I. 311677, was selected for its resistance and leaf pubescence. Of the progeny of the 7 × 7 diallele only those crosses with P.I. 311677 as a parent exhibited any pubescence. These crosses, 5, 11, 12, 13, 14 and 15, were screened in later tests. Lines 5 and 15 were eliminated, Table 1.

Nine segregates of Nora X TAM O-301 from the University of Arkansas were screened for pubescence density. Segregate 105-2, labeled line A-6, was retained for further testing. Two segregates of Nora X NCCR-3 were available and both were retained for further testing.

Two crosses in addition to the diallele were made: (Nora X NCCR-3)X P.I. 311677 and (Nora X TAM O-301)X P.I. 311677. Because the pubescence was from two different A. sterilis sources, genetic complementation could result.

TABLE 1. Line Identification Numbers and Pedigree

Line	Pedigree	Pubescence Source
5	'Korwood' C.I. 9167, X P.I. 311677	P.I. 311677
11	'Froker' X P.I. 311677	P.I. 311677
12	C.I. 521 X P.I. 311677	P.I. 311677
13	C.I. 1625 X P.I. 311677	P.I. 311677
14	C.I. 4867 X P.I. 311677	P.I. 311677
15	C.I. 4893 X P.I. 311677	P.I. 311677
A-6	Nora X TAM 0-301 (105-2)	P.I. 295919
A-10	Nora X NCRR-3 (114-1)	P.I. 320793
A-11	Nora X NCCR-3 (114-5)	P.I. 320793
29	A-6 X P.I. 311677	P.I. 295919, P.I. 311677
Q	A-10 X P.I. 311677	P.I. 320793, P.I. 311677
E	P.I. 311677	P.I. 311677
MAR	'Mariner' C.I. 9195	NONE

Crosses for Recurrent Selection

Line	Frequency
11	6
12	14
13	10
14	2
A-6	1
A-10	2
A-11	0
29	2
Q	1

TESTS

Painter (27) described insect resistance in plants as the heritable qualities that influence the host plant-insect interaction. Plants could be morphologically alike but physiologically different. The tests used to observe cereal leaf beetle resistance in oats were based on three aspects of resistance; preference, antibiosis and tolerance.

Beck (1) described host plant-insect interaction as having two aspects, host selection by the insect and plant resistance to the insect. Resistance components were defined as preference and antibiosis. Beck stated that tolerance was solely a plant characteristic not related directly to plant-insect interaction.

Lee (22) examined cereal leaf beetle preference in barley lines by oviposition preference tests, antibiosis by larval weight gain and feeding damage, and tolerance by plant recovery. He concluded that these aspects of resistance operate independently of each other and inheritance of each is complex.

Preference or non-preference is due to plant characteristics which cause insect movement away from the plant for food, oviposition or shelter. Leaf pubescence decreased feeding and oviposition on wheat lines. Without the "right kind" of contact stimulus, oviposition would not occur. The effect of trichomes on adults may be visual or tactile.

Preference was evaluated by oviposition preference tests under both field and greenhouse conditions. The test plants were infested with adult cereal leaf beetles. After three days of feeding and oviposition, the number of eggs on each plant were counted. Plants with fewer eggs were less preferred as oviposition sites. The number of eggs and larvae were counted for five stems of each test row in the field. Outdoor tests permitted evaluation of plant material under more natural conditions.

Antibiosis occurs when resistant plant material is fed to insects and a decline in viability results. Individual plants vary in suitability for insect food. The nutritional quality of the food is important. Ingestion of high fiber, low nutrient, leaf trichomes resulted in prolonged larval development and slow weight gain. Larvae appear restless when confined to highly pubescent wheat plants.

Antibiosis was estimated through larval feeding damage scores. Plants more severely damaged were more suitable food sources. Resistant plants were less acceptable food sources, less damage resulted.

Tolerance measures the plants' ability to recover after insect attack. Replacement and regrowth of tillers is necessary with an infestation of chewing insects like the cereal leaf beetle because damaged plant tissue is beyond repair. Cereal leaf beetle tolerance was not evaluated due to difficulty of determining recovery.

1. Trichome Counts

High trichome density is correlated with CLB resistance in wheat. Trichomes of .20 - .30 mm in length and 30 mm^2 reduce adult and larval feeding damage. This association also occurs in certain wild Hordeum species. Evaluation of trichome density in oats is a method of screening for CLB resistance in the laboratory.

Materials and Methods

Several techniques for evaluating relative trichome density have been developed. The leaf blade rolled over the forefinger and held to the light gives an estimate of density. A section of the blade examined with a dissecting microscope permits a more accurate estimation. Light microscope evaluation is more satisfactory in oats because pubescence density is too scarce to evaluate accurately solely with a dissecting scope.

After full expansion of the third leaf had occurred, a section was cut from the mid portion of the blade. A straight cut, perpendicular to the margin, was made near the center of the leaf. Holding the leaf with the adaxial side up, a second cut was made at a 45° angle from lower right to upper left. Cutting in this manner assured identification of the adaxial surface for proper mounting. The leaf section was placed in a vial containing 50 v : 50 v phenol-chloral hydrate. The vial was labeled and corked.

Phenol and chloral hydrate crystals were mixed together in equal proportions by weight. A squeeze bottle with a spout was used to dispense appropriate portions into vials. Vials were corked and placed in a cool dark cabinet to prevent deterioration of the

solution. Storage life is limited to approximately two weeks. Solution reuse depends on the amount of discoloration that has taken place.

Phenol-chloral hydrate removes chlorophyll from the leaf leaving a skeleton of cell walls. Trichomes, which are an extended cell wall, also remain. Clearing takes two days at 90°F, longer at room temperature.

The cleared leaf section was rinsed in 85% lactic acid. The sections were mounted on a labeled slide, adaxial side up, in lactic acid.

The slide was observed through a light microscope at 100X power. A field of view was selected adjacent to the midrib. The area of surface in a field of view was 2.717 mm^2. Because the leaf tissue was skeletonized, care was used to assure focus on the upper epidermis rather than the lower. Trichomes on the lower surface are located between the two rows of stomata. Trichomes appear between the stomata and veins on the upper leaf surface. Many trichomes are on the veins on both adaxial and abaxial surfaces.

Trichomes in each field were measured with a calibrated ocular micrometer, and classified into three groups by length. Long trichomes were longer than .4 mm, intermediate .15 - .4 mm, and short less than .15 mm. This classification system is very natural since trichomes rarely exceed the limits of these classes. With experience, the observer is able to classify each trichome without measurement.

The number of trichomes on the vein and between veins for each length classification was recorded. Five fields were observed on each leaf section. Totals were tabulated and transferred to separate data sheets.

Trichome Observations - Fall 1977

During the first week of September in 1977 segregates of lines A-6, A-10, 29 and E were planted to observe trichome expression of greenhouse grown plants, Table 1. Ten segregates of lines A-6 and E were selected. Individual plants of line 29 were harvested from a caged field test and packaged separately. Seed in fourteen of these packages was selected at random for further observation. Line A-10 was not evaluated in the field prior to the laboratory test as there was not enough seed. Twelve seeds were planted for each segregate in 4 inch pots.

Germinated seedlings were transplanted into individual pots and labeled. Six plants of each segregate were selected. Plants were labeled number one through six and leaf samples were collected. Collection vials were labeled with segregate and plant number. Numbered plants of each segregate were individually harvested. Leaves of the remaining plants were not sampled. Seed of these plants was bulked for each segregate at harvest.

An analysis of variance was calculated for trichome observations, Table 2. Differences between lines were significant at $P \leq 0.05$. Differences between segregates within lines were highly significant at $P \leq 0.01$. Because there were unequal number of observations in each line, normal multiple range tests were not

TABLE 2. Analysis of Variance of Trichome Counts Per Microscope Field of Greenhouse Seed Increased (Fall of 1977)

Lines Tested: A-6, A-10, 29 and E

Source	df	Mean Square	F Test
Total	229		
Lines	3	269.670	4.195*
Segregates (Lines)	36	64.286	3.025**
Error	190	21.255	

Mean Trichome Number ***

E	14.76^{a}
A-10	12.47^{ab}
29	12.02^{b}
A-6	9.45^{c}

*$P \leq 0.05$

**$P \leq 0.01$

***$P \leq 0.05$ Duncan's Multiple Range Test

appropriate. An individual $S_{\bar{x}}$ was calculated for each pair of means compared, Table 2. The mean trichome count of lines E and A-10 were not significantly different nor were lines A-10 and 29. Line A-6 had significantly less hairs than the other lines tested.

2. Resistance as Measured by Ovipositional Preference

Oviposition tests determine cereal leaf beetle resistance as measured by adult preference. In these tests the adults are free to feed at random and the females lay eggs where they feed. A more favored food source will have more feeding damage and thus more eggs. This test evaluated relative preference within the cages in the greenhouse or plant growth chamber.

Plant size; i.e., height, number of leaves, and total leaf area affect adult contact with plants and relative amount of leaf area available for feeding.

The number of eggs oviposited per row sharply influences potential larval feeding damage (LFD) which is dependent upon the number of eggs hatched and the suitability of the host for larval feeding.

Materials and Methods

Planting took place after the number of lines to be tested were determined. Two holes were punched in the bottom of 5 ounce paper Dixie cups. The cups were filled with steamed soil and the soil tamped. One seed was planted per cup after the cups were labeled with three inch plastic stakes. Three cups planted for each of two lines to be tested is usually adequate. More cups are needed

for paired comparisons as in parent/progeny tests to assure an adequate supply of plants. Plants with Avena sterilis germplasm require more pots to accommodate dormancy factors which delay germination.

The cups were placed on cafeteria trays (35 per tray). Trays were placed in a warm greenhouse set at 80°F with a 16h photophase to optimize germination. As the seedlings emerged, individual Dixie cups were removed to a cool greenhouse or growth chamber set at 60°F with a 16h day and 55°F with an 8h night. The cool temperature slows seedling growth in an attempt to keep rapid and slow germinators near the same size.

Ten days after planting a daily tabulation of the number of seeds germinated was made. Seedlings available to test were randomized with the aid of random number tables.

Beetle-plant interaction varies greatly. "Hot spots" occur where much feeding and oviposition take place. For this reason, a randomized block design is preferred over completely randomized design. A segregate of each line was randomly assigned to each replication.

Two trays end to end fit across the width of the cage with six trays along the length. Four hundred twenty plants can be tested at once in each cage. A susceptible check border to spread beetles was used around the perimeter, limiting the number of test plants to 336 for each test. The twenty replications used were adequate to distinguish differences between lines.

The cage dimensions were 7' by 3' by 1'. The long sides each had three doors for moving plant material into the cage. The ends and top were made of lumite screen, and the base was plywood. The screen mesh (32 × 32) was small enough to contain adults but permit water and light entry. Plants were watered with a mist nozzle through the side doors.

After plants were arranged in randomized groups and watered, adult cereal leaf beetles were counted and introduced. One beetle for every two plants produces consistent test results. It was assumed, from test to test, that the male:female ratio was about one to one. This assumption eliminated the need for sex determination which is tedious and time consuming.

Laboratory reared beetles require fourteen days of preparation prior to use in oviposition preference tests. Post aestivation adults are removed from cold storage and placed in a small cage with 'Larker' barley seedlings, where they feed and oviposit. Initiation of oviposition occurs after ten days. Maximum egg output is desired for oviposition preference tests.

Adults collected from the field were used when available, usually for tests in May. Field collected adults were held in cages in a cold dark growth chamber until test material was ready. Warming the adults and having food available resulted in less feeding damage to test material after introduction into the oviposition cage.

Tests during winter months were conducted in the greenhouse at 80°F with a 16h photophase. Cold outdoor ambient temperature permitted cooling of the greenhouse if sunny weather prevailed while

testing. Spring tests were conducted in a growth chamber at 80°F, 16h light; 70°F, 8h dark. Adequate cooling in the greenhouse was not available to maintain 80°F through spring and summer months.

Adult feeding damage and egg production were observed closely. Temperature reduction slows feeding and prolongs oviposition. Beetle source, field collected or laboratory reared, and previous food available affect oviposition and feeding rate. When feeding damage and eggs were observed on most of the plants the adults were removed and the total number of eggs per plant and the number of leaves per plant were recorded. Plants should be moved to a cool greenhouse or growth chamber 60°F, 16h light, 55°F, 8h dark to recover. Cool temperature slows the internal development of the eggs and eventually the eggs turn brown and die. When cool recuperation space was not available, plants were fumigated when larvae emerged.

Each pot was labeled with an additional stake denoting oviposition test number and indicating the replication and position in the cage.

After the test was completed the plants were transplanted into 4 inch clay pots by peeling the Dixie cup from the root ball and filling in the pot with additional steamed soil.

When plants reached the five leaf stage, the third leaf was cut and cleared in 50v:50v phenol-chloral hydrate as indicated in the trichome section.

Statistical analysis followed with calculation of separate analysis of variance for trichome number and egg counts. A correlation coefficient was obtained between trichome density and egg count.

Special techniques were used when testing parents and progeny of crosses.

Oviposition Test - Spring 1978

On 7 March 1978, twelve Dixie cups of each segregate of lines A-6, A-10, 29 and E were planted for an oviposition preference test. 'Mariner' was included as a susceptible check. All seed was dehulled by hand prior to planting. Poor germination of line E was due to dormancy factors typical of A. sterilis. Line E was eliminated from further participation in this test. Because of erratic and late germination of many of the segregates, only part of the plants were tested for oviposition preference. All plants were sampled for trichome evaluation.

One hundred eighty-two plants were arranged in a completely randomized design. The plants were placed in the cage in a warm greenhouse. Line 29 was represented by 51 plants, A-6 by 68 plants, and A-10 by 18 plants. Forty-five Mariner plants were included. The position of each segregate was recorded.

On 21 March 1978, one hundred post-aestival adult cereal leaf beetles were introduced into the cage. Feeding, mating and oviposition continued for three days at which time the plants were removed and adults collected. The number of eggs on each seedling was recorded with segregate number and cage position.

Seedlings were transplanted into 4 inch clay pots and placed in a cool growth chamber to recover.

After full expansion, the third leaf was cut and cleared in phenol-chloral hydrate. Leaf samples were evaluated for trichome length and density.

An analysis of variance was calculated for trichome counts of plants included in the oviposition test. An additional analysis, including late germinating plants not included in the test, was calculated. Differences in trichome counts between lines included in the oviposition test were significant at $P \leq 0.01$. Segregates were significant at $P \leq 0.01$, Table 3.

An analysis of variance was calculated for egg counts. Variation between lines and between segregates were statistically highly significant at $P \leq 0.01$, Table 3.

A modified Duncan's Multiple Range was used to test differences in mean egg count of each line. Mariner had 6.556 eggs per plant. Lines 29, A-6, and A-10 were not significantly different at $P \leq 0.05$. Line means were 2.647, 3.013, and 3.0 respectively.

The egg count was regressed on trichome count for each line, Table 4. Mariner was not included in regression or correlation calculations. A consistent zero for trichome density would upset the relationship between egg count and trichome density for those lines exhibiting variation.

The correlation coefficients in Table 4 are an estimate of zero, which indicates a lack of relationship between trichome number and egg laying. This may indicate no cause and effect or it may be due to sampling. In view of this strong relationship in wheat and some information on oats which will be introduced later, I believe that sampling numbers are at fault, or it may be that trichomes may be too few to be biologically significant.

TABLE 3. Analysis of Variance of Oviposition Test Egg and Trichome Counts (Spring of 1978)

Lines Tested: A-6, A-10, 29 and Mariner

Egg Counts per Plant

Source	df	Mean Square	F Test
Total	181		
Lines	3	154.290	6.707**
Segregates (Lines)	27	23.006	4.046**
Error	151	5.686	

Trichome Counts, Included in Oviposition Test

Source	df	Mean Square	F Test
Total	168		
Lines	3	3848.267	35.873**
Segregates (Lines)	26	107.256	1.825**
Error	139	58.787	

Trichome Counts, Five Microscope Fields Per Leaf

Source	df	Mean Square	F Test
Total	280		
Lines	3	3771.093	59.688**
Segregates (Lines)	27	175.330	2.775**
Error	250	63.180	

**$P \leq 0.01$.

TABLE 4. Correlation and Regression of Egg Counts on Trichome Number of Oviposition Test (Spring 1978)

Line	df	Regression	Correlation	Mean Trichomes Per Field*	Mean Egg Count Per Plant*
29	45	-0.049	-0.1998	3.287^{b}	2.647^{b}
A-6	58	-0.028	-0.0760	2.293^{b}	3.015^{b}
A-10	16	0.017	0.1138	4.033^{a}	3.000^{b}
Mariner		---	---	0.0^{c}	6.556^{a}

*Duncan's Multiple Range Test $P \leq 0.05$.

The mean trichome density per field was calculated. Differences between lines were tested with a modified Duncan's Multiple Range test as the number of observations per mean were not equal. Mariner had no trichomes. A-10 had 4.033 per field. Lines 29 and A-6 were not significantly different, with 3.287 and 2.923 respectively. Segregates within lines were found significant at $P \leq 0.01$, as were lines in analysis over all of the plants, Table 4.

Oviposition Line Test - Winter 1979

During the third week of January in 1979 seed was planted for two oviposition preference tests. One test was an overall comparison between lines that had been used in crosses. The other was a direct comparison between parents and their F_1. When supplies of seedlings for crosses tests were inadequate, excess plants from the line test were used. Further discussion of the crosses test follows in the crosses section.

On January 16 and 17, 1979 lines 11, 12, 13, 14, A-6, A-10, A-11, 29, Q and E were planted for the line test. The number of seedlings from each line was tabulated. Plants were arranged in a randomized block design with a representative plant of each line in each of twenty replications. Mariner was included in each replication as a susceptible check. A single border row of cups of Mariner encircled the entire test. A segregate from each line was assigned to each replication at random.

On 30 January 1979, plants were placed in position on cafeteria trays and set inside the oviposition cage. The test was conducted in the greenhouse with two hundred twenty test plants and

sixty-six border row plants in the cage. One hundred fifty laboratory reared post aestival adult beetles were introduced.

Two days later, on 1 February 1979, after the adults were collected, the plants were removed from the cage. The total number of eggs and plant height in cm was recorded along with line and position for each entry. Individual stakes were made for each Dixie cup indicating replication number and position within the replications.

After transplanting, the third leaf was sampled. Trichome length and density were evaluated.

An estimation of variance was calculated partitioning the total variance into replication, between line, segregate within lines, and plant variability for both egg count and trichome density data, Table 5.

Differences between egg counts of segregates within each line were found significant at $P \leq 0.01$. Differences between replications were not significant.

The total trichome counts of five microscopic fields per leaf were tested for significance. Differences between replications were not significant. Differences between lines and between segregates within each line were highly significant, $P \leq 0.01$, Table 5.

The correlation coefficient between trichome number and egg count for each line was calculated. Correlation Coefficients ranged from -.63 for line 11 to .39 for line E. Mariner was not included in the correlations as it has no trichomes and would skew the results. Lack of variation in one variable brings the correlation to zero, Table 6.

TABLE 5. Analysis of Variance of Oviposition Line Test (Winter of 1979)

Lines Tested: 11, 12, 13, 14, A-6, A-10, A-11, 29, Q, E and Mariner

Egg Counts per Plant

Source	df	Mean Square	F Test
Total	219		
Replications	19	15.363	0.811^{ns}
Lines	10	87.383	4.612**
Segregates (Lines)	32	18.946	1.488*
Error	158	12.729	

Trichome Counts, Five Microscope Fields per Leaf

Source	df	Mean Square	F Test
Total	219		
Replications	19	1353.946	1.042^{ns}
Lines	10	9106.721	7.006**
Segregates (Lines)	32	1299.836	19.047**

*$P \leq 0.05$.

**$P \leq 0.01$.

TABLE 6. Correlation and Regression of Egg Count on Trichome Number from Oviposition Preference Test (Winter of 1979)

Line	Regression*	Correlation	Mean Egg Count**	Mean Trichome Number per Field**
11	-0.161	-0.631	4.45^{cd}	4.74^{de}
12	0.041	0.155	5.45^{bcd}	2.69^{e}
13	0.011	0.029	8.70^{a}	5.54^{d}
14	-0.011	-0.056	6.25^{abcd}	2.24^{ef}
A-6	0.082	0.326	6.55^{abc}	6.41^{cd}
A-10	0.002	0.030	3.95^{d}	11.48^{a}
A-11	-0.086	-0.546	7.05^{ab}	2.69^{e}
29	-0.015	-0.083	7.25^{ab}	9.05^{b}
Q	-0.089	-0.273	7.65^{ab}	8.17^{bc}
E	0.044	0.390	1.65^{e}	12.25^{a}
Mariner	0.0	0.0	4.10^{cd}	0.00^{f}

*18 df.

**Duncan's Multiple Range Test $P \leq 0.05$.

Egg counts were regressed on trichome density. Regression Coefficients ranged from .028 to .358. Regression Coefficients are presented in Table 6.

A Duncan's Multiple Range test was used to test significance of line differences of mean egg count and mean trichome count per field. Line E had the fewest eggs and the most trichomes. Line 13 had the highest egg count mean of 8.7. Line 14 had the fewest trichomes with 2.24 per field, Table 6.

3. Larval Feeding Damage

Larval feeding damage observations show the reaction of the cereal leaf beetles to plant material in the field under natural conditions. The intensity of larval feeding damage (LFD) is a function of the interaction between the host and the insect. Three cages were used to establish three levels of infestation.

Materials and Methods

Large LFD cages (10' × 9' × 5') were constructed in the field each year. Each cage was designed to accommodate 600 rows. Six rows ran across the width, planted end to end, and were each 1.5' long. One hundred rows, 9 inches apart, were planted the length of the cage. The cage size may be increased if needed (Smith and Webster, unpublished).

After soil preparation, a rolling barrel marker was used to mark the rows (6). Coin envelopes of seed were hand planted. The cage was constructed after the seedlings emerged.

Nine 10' two-by-six inch boards were laid on edge in shallow trenches and staked. Soil was filled in along the boards to prevent beetle escape. The boards forming the length of each side were held together end to end with metal brackets. Another 10' board was nailed across the cage at each end.

Two curved pieces of aluminum conduit were fitted together to form an arch. An arch was anchored to each bracket where two boards joined. Three pieces of wire were threaded through hose clamps and placed on the arches to string them together. The wire was stretched and the hose clamps tightened together to form a secure framework. The wire was secured to the boards at each end.

Two 9' × 100' tobacco plant bed covers (Grade 3A) were sewn together to form an 18' × 100' sheet. The cover was stretched across the cage framework and stapled to the boards along the sides and across the southwest end. Excess material at the north end was rolled up on a two-by-four to close the cage but still permitted reopening for entrance into the cage.

Post-aestival adult cereal leaf beetles collected in the field (7) were counted in the laboratory, prior to release in several locations inside the cages.

The adults were free to fly around and select plants at random for feeding. Upon landing on non-preferred plant material, the beetles resumed flying in search of a more favorable food source. Feeding occurred intermittently with oviposition. The female oviposits where she feeds. Susceptible plants received more eggs.

The attachment of eggs was poor. Eggs haphazardly perched on the tips of trichomes frequently desiccate or are blown or washed off by rain prior to hatching.

The cages were removed when larval and egg counts reached the maximum. The plant bed cover shaded the plants and was removed at the earliest possible date. Egg and larval counts were made at this time.

Five tillers were selected at random within a row. The number of eggs and number of larvae were recorded. Analysis of variance was calculated to test significance of differences between lines.

Five days after oviposition the larvae emerged. Emergence was delayed or inhibited by cool temperature. The larvae began feeding on the leaf where the eggs were laid. Movement from leaf to leaf in search of food occurred. The larvae can move from plant to plant. Increased movement of larvae and less feeding resulted on resistant plant material.

After an extended period of feeding, larval feeding damage was evaluated and recorded. A scale of one to nine was used. One indicates little feeding damage, less than 10% of the leaf consumed. Two indicates 20% of the leaf consumed, etc. A distinction must be made between adult and larval feeding and damage. Adult feeding penetrates the leaf causing shredding. Larvae strip the upper surface, usually leaving translucent skeletal tissue intact.

Additional data such as height, maturity and growth habit may be evaluated to determine any effect on larval feeding damage.

An analysis of variance was calculated for each trait. Multiple regression may be used to determine the relative importance of each trait measured and influence on larval feeding damage.

Larval Feeding Damage Field Test - Summer 1977

In May 1977 Dr. Robert Steidl, a post-doctorate with the project, planned and planted a larval feeding damage test at the MSU Crops Farm. The data and resulting analysis are from my own observations of this material.

Thirty lines were planted in twenty replications. Replications were arranged to minimize variation due to soil and light gradient differences.

The lines planted were segregates and parents of Dr. Steidl's diallele. Lines A-6 and 29 were also included for field evaluation. Lines A-6 and 29 were not included in diallele crosses.

The cage was constructed when the plants had approximately three leaves per tiller. On 23 May, 3,500 field collected adults were introduced into the cage. Five hundred additional beetles were added on 27 May, to replace those which had escaped or died. The cage was removed on 4 June. Thus, the beetles were confined to the test plants for twelve days.

Five plants from each row were selected at random. The third leaf was cut and cleared in 50v:50v phenol-chloral hydrate. Only one sample per plant was made for rows with less than five plants. Vials were labeled for replication and row number rather than line number to prevent bias when trichome evaluations were made.

The trichomes were measured and classified by length. An analysis of variance was calculated. Replications and lines exhibit significance at $P \leq 0.01$, Table 7. An analysis of variance was calculated using only pubescent lines. The F Tests exhibit significance at $P \leq 0.01$ for both replications and lines. Because of this significance, replications and replication data will be used for segregates of each line in future tests.

Trichome number per field was averaged over twenty replications. Means of pubescent lines were compared using Duncan's Multiple Range. The analysis of variance and results of the range test appear in Table 7. Lines with the same letter are not significantly different at $P \leq 0.05$.

Larval feeding damage was evaluated on July 1. The scale of 1 through 9 described previously was used. An analysis of variance over all of the lines was calculated. Replications and lines exhibited significance at $P \leq 0.05$, Table 7. An analysis of variance for trichomes using only pubescent lines also found highly significant differences between lines and between replications, Table 8.

A Duncan's Multiple Range test of line mean larval feeding damage scores over twenty replications found lines not significantly different from each other at $P \leq 0.01$. Avena sterilis line E, stood alone as the most resistant entry in this test, Table 9.

Plant growth habit was also evaluated on July 1. Decumbent plants may miss beetle attack. A scale of one to five was used to classify decumbency with one as decumbent and five as upright. All of the A. sterilis plants were scored as one. The remaining parents

TABLE 7. Analysis of Variance Using All Thirty Lines From Field Data (Summer of 1977)

Trichome Frequency per Microscope Field

Source	df	Mean Square	F Test
Total	599		
Replications	19	0.7197	1.966**
Lines	29	15.4697	42.267**
Error	551	0.3660	

Larval Feeding Damage

Source	df	Mean Square	F Test
Total	599		
Replications	19	5.4718	6.116**
Lines	29	3.8982	4.357**
Error	551	0.8947	

Decumbency

Source	df	Mean Square	F Test
Total	599		
Replications	19	0.3137	1.407^{ns}
Lines	29	13.1942	62.533**
Error	551	0.2229	

**$P \leq 0.01$.

TABLE 8. Analysis of Variance of Pubescent Lines From Field Test (Summer of 1977)

Trichome Counts, Five Microscope Fields per Leaf

Source	df	Mean Square	F Test
Total	179		
Replicates	19	2.333	2.076**
Lines	8	13.154	11.706**
Error	152	1.240	

Larval Feeding Damage

Source	df	Mean Square	F Test
Total	179		
Replicates	19	4.576	4.659**
Lines	8	4.476	4.557**
Error	152	0.982	

Decumbency

Source	df	Mean Square	F Test
Total	179		
Replicates	19	0.3096	0.427^{ns}
Lines	8	30.800	42.457**
Error	152	0.725	

**$P \leq 0.01$.

TABLE 9. Duncan's Multiple Range Test of Pubescent Line Means From Field Test (Summer of 1977)

Line	Mean Trichome Number/Field*	Larval Feeding Damage*	Decumbency*
5	$.323^{f}$	4.6^{b}	4.5^{b}
11	$1.489^{c,d,e}$	4.15^{b}	$4.45^{a,b}$
12	$1.38^{d,e}$	4.6^{b}	4.85^{a}
13	$1.377^{d,e}$	4.1^{b}	4.85^{a}
14	$2.168^{b,d}$	4.0^{b}	3.45^{c}
15	$.971^{e,f}$	4.2^{b}	$4.3^{a,b}$
E	$1.755^{b,c,d}$	3.0^{a}	1.0^{d}
29	3.142^{a}	4.15^{b}	3.0^{c}
A-6	2.253^{b}	4.35^{b}	4.2^{b}

*$P \leq 0.05$, Duncan's Multiple Range.

and many of the progeny exhibited upright growth habit. A. sterilis hybrid progeny exhibited segregation for growth habit.

An analysis of variance of all thirty lines was calculated. An F test found variation between lines highly significant at $P \leq 0.01$, Table 7. When growth habit of the pubescent lines was analyzed separately, replication mean squares were positive but not significant at $P \leq 0.01$. A highly significant difference between pubescent lines was observed, $P \leq 0.01$, Table 8. The results of a Duncan's Multiple Range test are also shown in Table 9. Larval feeding damage was regressed on trichome count and growth habit. Growth habit was correlated with trichome count, Table 10. Individual replication observations were used for the basic unit. Each correlation coefficient was based on twenty paired observations. Each line was harvested by rows, except for line 29, which was harvested by individual plants.

Three Levels of Infestation - Summer 1978

During the second week of May, seed was planted in the field for three cages which would be used to simulate three levels of beetle infestation. Ten segregates of six lines (11, 12, 13, 14, A-6, and E) plus Mariner, a susceptible check, were included in each of ten replications. In addition, line A-11 was included in only six of the ten replications due to limited seed.

Lines were randomized within replications independently. Segregates are confounded with replication because the segregates occur in the same replication in each cage.

TABLE 10. Correlation and Regression Between Traits Measured During the Field Test (Summer of 1977)

Line	Regression of LFD on Trichome Count*	Regression of LFD on Growth Habit*	Correlation of Trichome Count and Growth Habit*
11	-0.106	0.028	0.028
12	-0.041	-0.264	0.036
13	0.412	-0.374	0.388
14	0.169	0.183	0.523
E	-0.045	0.0	0.0
29	-0.141	-0.022	-0.039
A-6	0.628	-0.269	0.041

*18 df.

Trichome Count = Mean of Five Microscope Fields per Leaf.

On 31 May, the three separate cages were constructed. One thousand, 2,000, and 4,000 field collected adult cereal leaf beetles were introduced to simulate a density of 1, 2, and 4 beetles per square foot of cage floor area respectively.

On 22 June, when eggs and larvae were visible on the plants, the low level of infestation cage was removed. The intermediate and high level cages were removed the following week.

Larval feeding damage was evaluated on 4 July. A scale of 1 through 9 was used. An analysis of variance partitioned total variation into variation between levels of infestation, replication by infestation interaction, differences between lines, and line by infestation interaction. The residual variation was used as the error term. Levels of infestation were found to be statistically significant at $P \leq 0.01$. Variation between lines and the line by infestation level interaction term are highly significant at $P \leq 0.01$, Table 11. A Duncan's Multiple Range test was made to test significance of differences between lines. Line E experienced the least larval feeding damage; Mariner the most. The results are presented in Table 11.

Three Levels of Infestation - Summer 1979

On 7 May, seed was planted for simulation of three levels of infestation. Ten replications of eleven lines were planted in each cage. The lines included were 11, 12, 13, 14, A-6, A-10, 29, Q, and E. Mariner was also included as a susceptible check.

On 23 May, the three cages were constructed over the test plants and on 25 May field collected adult cereal leaf beetles were

TABLE 11. Analysis of Variance and Comparison of Larval Feeding Damage Scores (Summer of 1978)

Source	df	Mean Square	F Test
Total	207		
Infestation	2	41.94	6.32**
Rep (Infest)	27	6.34	
Line	6	14.46	5.96**
Line (Infest)	12	9.12	4.00**
Error	162	2.43	

Line	Mean*
E	5.86^{a}
A-11	6.19^{ab}
13	6.56^{abc}
A-6	6.98^{bcd}
11	7.06^{bcd}
14	7.17^{cd}
12	7.55^{cd}
Mariner	8.03^{d}

*$P \leq 0.05$, Duncan's Multiple Range Test.

**$P \leq 0.01$.

introduced into the three cages. The cage covers were removed on 20 June.

The number of eggs and larvae were recorded for 5 tillers/row on 20 and 21 June. Larval feeding damage was evaluated on 28 June using a 1-9 scale. Plant height and growth habit were also measured on 28 June. Height measurement of plants in cage 2 was delayed until 2 July.

Maturity observations were made on 6 July. A scale of 1-5 was used. One represented plants in the seedling stage, 2; tillering, 3; heads in the boot, 4; heads extruding, and 5 when heads had fully emerged.

A correlation matrix was calculated for all of the traits observed. When larval feeding damage was correlated with plant growth habit, height, egg count, larval count, egg plus larval count, and maturity, the correlation coefficient was near .5 in each case. Plant height, growth habit and maturity are highly correlated with each other as are egg count, larval count and egg plus larval counts. Decumbency was associated with plant height as plant height was associated with maturity. Egg count plus larval count or "Count"* was a direct function of egg counts and larval counts. "Count" is more highly correlated with larval feeding damage, height and growth habit than either larval count or egg count alone.

An analysis of variance was calculated to determine the level of significance of variation between lines tested and between levels

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*"Count" equals egg count plus larval count.

of beetle infestation. Differences in egg counts, larval counts and "Count" were highly significant, $P \leq 0.01$, between both lines and cages.

Differences between lines were significant for both maturity and growth habit although variation between cages was not significant. Uniformity between cages and variation between lines was as expected.

Variation in height was significant between lines and levels of infestation. Differences between lines were expected. The plants in cage 2, the intermediate level of infestation, were significantly taller. Height measurements in cage 2 were made four days after cages 1 and 3 due to adverse weather conditions.

The mean "Count" of cages 2 and 3 was not significantly different. The plants in cage 3 had more eggs and larvae but not significantly more; subsequently, more larval feeding damage resulted. Larval feeding damage to the plants was significantly different between the three cages.

Several multiple regression equations were calculated to explain the relative importance of each trait observed for estimation of larval feeding damage. Larval feeding damage was regressed on lines and growth habit. Growth habit explained more variation in larval feeding damage than did lines. Variation between lines was not significant at $P \leq 0.05$ by F Test. Growth habit was highly significant, $P < 0.01$.

Larval feeding damage scores were regressed on levels of infestation, "Count" and line. Cage and "Count" were highly

significant $P < 0.01$. Lines were not significant at $P \leq 0.05$ by F Test.

Larval feeding damage scores were then regressed on all of the variables. Level of infestation, egg count, larval count, and plant height were highly significant in estimating larval feeding damage. Growth habit was significant at $P \leq 0.01$. Lines and maturity were not significant. Lines were significantly different for larval feeding damage.

The analysis of variance for larval feeding damage scores and "Count" appear in Table 12. Line means were compared by Duncan's Multiple Range Test, Table 13.

4. Recurrent Selection Experiments

The purpose of within line crosses was to allow re-assessment of genes for trichome expression. Entries were selected from the World Oat Collection and crossed. Progeny of these original crosses were selected, those retained were then tested for various aspects of cereal leaf beetle resistance. Pubescent segregates of each original cross were intercrossed within each line to bring together again genes from the original parents. When segregates possessing different alleles for trichome expression are intercrossed, an increase in trichome length and density should occur.

Materials and Methods

Trichome density and field larval feeding damage scores were determined during the summer of 1977. Advanced generation segregates of progeny of Steidl's diallele set of crosses

TABLE 12. Analysis of Variance of Larval Feeding Damage and "Count" (Summer of 1979)

Larval Feeding Damage

Source	df	Mean Square	F Test
Total	329		
Level Infestation	2	135.545	20.09**
Replicate (Level)	27	6.747	
Lines	10	28.275	87.03**
Lines (Level)	30	10.917	33.60**
Error	259	0.325	

"Count"

Source	df	Mean Square	F Test
Total	329		
Level Infestation	2	3026.722	26.60**
Replicate (Level)	27	113.782	
Lines	10	184.193	39.09**
Line (Level)	30	225.225	47.79**
Error	259	4.713	

**$P \leq 0.01$.

TABLE 13. Comparison of Means for Larval Feeding Damage and "Count" (Summer of 1979)

Line	Larval Feeding Damage*	"Count"*
11	3.77^{bc}	14.67^{de}
12	4.97^{c}	16.03^{fg}
13	3.57^{b}	14.07^{cde}
14	3.97^{bc}	15.90^{fg}
A-6	3.73^{bc}	14.47^{de}
A-10	4.03^{c}	15.07^{ef}
A-11	3.80^{bc}	13.40^{cd}
29	3.67^{bc}	11.93^{b}
Q	3.72^{bc}	13.15^{c}
E	1.63^{a}	7.73^{a}
Mariner	5.60^{e}	16.70^{g}

*$P \leq 0.05$ Duncan's Multiple Range Test.

Mean over Three Levels of Infestation.

possessing more trichomes and lower larval feeding damage scores were intercrossed. Within line crosses for several lines were made.

Trichome counts and larval feeding damage scores were compared. Segregates within each line were ranked according to decreasing trichome counts and separately for low larval feeding damage. Of the twenty segregates in each line, the three or four with the most trichomes and lowest larval feeding damage scores were selected for intercrossing. When seed quantity was insufficient, the next best segregate in the ranking was selected. Selection of segregates of lines 29 and A-10 was based on trichome data from seed increased during the fall of 1977. Data used for selection is presented in Table 8. Segregates of line A-11 were used without previous test data.

Selected parental lines were planted in 4" clay pots during consecutive weeks to increase opportunity for "nicking".

Many of the lines were decumbent and tillered profusely. Initially four seeds were planted per pot. As the first crosses were made, it became apparent that fewer plants per pot would be easier to work with. Three seeds were planted in the remaining pots. Occasionally poor germination occurred. This was due to poor seed quality or dormancy from the A. sterilis parent in the cross.

After coleoptile emergence, pots were moved to a growth chamber set at 16h light at 60°F with 8h dark at 55°F.

When the fifth leaf had emerged from all of the seedlings in the pot, a portion of the third leaf was cut and cleared in phenol-chloral hydrate. The pot was then moved to the greenhouse.

Plants of the same line were placed together for identification for crosses.

Leaf hairs were measured for length, counted, and tabulated for five microscopic fields per leaf. Significance of trichome counts for line X planting date interaction was tested. Because this interaction term usually serves as the error term an estimate of error was needed. A weighted mean was calculated for treatments. Within treatment sum of squares, the error term was found by subtraction. This preliminary error sum of squares, S_p^2, divided by the simple harmonic mean n_o was needed for an estimate of error and retained error degrees of freedom. The estimate of error mean square was calculated.

The unweighted means were calculated for total sum of squares. Variation due to lines and planting dates was calculated. Line by planting date interaction sum of squares was found by subtraction. The estimate of error from the preliminary analysis of variance was used as the denominator of F tests.

Crosses were made by the approach method (2, 5, 8, 24, 26). A five inch wide piece of aluminum foil wrapped on the outside of the dialysis tubing slows desiccation of the emasculated female head.

Seed set was poor, as may be expected for greenhouse crosses. Two weeks after pollination, the male parent and hybrid heads were harvested. A tiller selected from the female plant was harvested for seed. Heads were packaged separately and dried.

Parents and progeny of crosses were compared by the oviposition preference test and trichome evaluation. If transgressive segregation had occurred, some of the progeny could be used to test the relationship. A test of the variance of the difference, S_d^2, of mid-parent and progeny indicated if a significant change had taken place.

Crosses - Spring 1978

Segregates of eight lines (11, 12, 13, 14, A-6, A-11, 29, and Q) were selected for spring crossses. Four pots per line with four seeds per pot were planted during five consecutive weeks beginning 20 March. The pots were moved to a cool growth chamber after germination in a warm greenhouse.

Half of the plants of each line for each planting were transplanted to the field for use as pollen parents. Eighty pots of plants were planted on two foot centers. The four plants of each pot were knocked out of the pot together and planted with the root ball intact. Each clump of plants was labeled with line, segregate number and planting date.

After full expansion, the third leaf was cut from all of the plants remaining in the growth chamber. The leaf section was cleared in 50v:50v phenol-chloral hydrate. Three hundred eighty-three plants were sampled. Plants were moved to the greenhouse after the leaf sample was taken.

Crosses were made in the greenhouse using the approach method. High temperatures caused dehiscence of pollen while the head was far down in the boot. Opening and clipping of the

florets while very young increased the drying. No seed set occurred.

During the first week in June an outdoor greenhouse was constructed of 2" × 4" lumber and lath snowfencing. Plants in the lath-house grew at ambient temperature and were exposed to variation in weather conditions. Florets were more mature at pollen dehiscence and more pollen was visible on the inside surface of the dialysis tubing than greenhouse grown plants. A modification of emasculation and clipping techniques was made. Heads with the uppermost floret already dehiscing were selected. The ten most mature florets were used. The remaining florets were cut off. Lemma and palea were clipped shorter exposing more of the stigma. A low percent seed set resulted.

Because the outdoor greenhouse was also used for entomological studies, pesticide dust was not permitted. Misinformation on formula concentration resulted in an overdose of dimethoate, a systemic insecticide. The entire parental population died.

Transplanted plants were not treated with dimethoate. Good seed set permitted replanting in the greenhouse in the fall.

A weighted mean for trichome counts was calculated for variation between the sum of 5 microscopic fields per leaf for forty treatments (eight lines by five planting dates). The preliminary error sum of squares was found by subtraction. This estimate of error retains the 343 degrees of freedom for calculation of estimate error mean square.

The forty unweighted treatment means were used for total sum of squares with 39 degrees of freedom. Trichome variation between the eight lines and five planting dates was calculated. The line by planting date interaction was found by subtraction. Using this interaction term an F test was calculated. Planting date mean squares were not statistically significant but lines were at $P \leq 0.01$.

Trichome density variation between lines, between planting dates and the interaction term exhibit significance at $P \leq 0.01$ when an F value is calculated using the estimate of error term for preliminary analysis of variance, Table 14.

Crosses - Fall 1978

Seed harvested from plants transplanted for crosses was dried and dehulled by hand. Seed from nine lines (11, 12, 13,14, A-6, A-10, A-11, 29, and Q) was planted during seven consecutive weeks beginning on 1 August. Five pots were planted with three seeds per pot for each line.

Plants were germinated in the greenhouse and moved to the growth chamber to encourage vegetative growth. The third leaf was sampled from each plant in a pot. The leaf section was cleared and trichome length and density evaluated.

When the pots were returned to the greenhouse, cool fall weather had begun. Temperature was controlled by allowing cool air from outdoors to enter the greenhouse. Pollen dehiscence was delayed until after the head had emerged from the boot.

TABLE 14. Analysis of Variance of Trichome Counts per Microscope Field for Eight Lines and Five Planting Dates

Lines Tested: 11, 12, 13, 14, A-6, A-11, 29 and Q

Preliminary Analysis of Variance

Source	df	Mean Square	F Test
Total	382		
Treatment	39	2115.348	13.083**
Error	343	161.686	

Error Estimate = S^2/n_o = 554.3843/0.1576

Unweighted Mean Analysis of Variance

Source	df	Mean Square	F Test	F Est.
Total	39			
Lines	7	384.353	3.582**	15.08**
Planting Date	4	133.284	1.24^{ns}	5.23**
Planting Date × Line	28	107.312		4.21**
Error Estimate	343	25.482		

**$P \leq 0.01$.

Plants of the same line were placed together on the greenhouse bench. Plants within each line were systematically observed. Those ready for crossing were prepared and the cross set up. Crossing began 2 October. Each line was observed and crosses made twice a week. Approximately the same number of crosses were made within each line. The final cross was completed on 17 December.

Parent and Progeny Relations for First Cycle Recurrent Selection-Winter 1979

On 17 and 18 January, parents and a portion of the F_1 seeds were planted for each successful cross. Dehulled seed was planted in Dixie cups and placed in a warm greenhouse until germination. The number of Dixie cups planted to parents was proportional to the amount of F_1 seed available.

Complete crosses, those that had both male and female parents and F_1 emerged at time of testing, were given top priority for inclusion in an oviposition preference test. Parents were placed on either side of the F_1. The three plants were randomly assigned a position together in a row. The cage was then filled with assorted plants that were available. The additional plant material gave the beetles more selection and greater leaf surface area to feed on. The purpose was to test the difference between parents and progeny within each cross not to distinguish between crosses.

A total of 196 plants were included in the test. Nineteen were complete crosses, 57 were plants to be used for parent progeny comparison. A border row of Mariner was included.

On 31 January 100 laboratory reared adult beetles were introduced into the cage. Due to cloudy weather, feeding and oviposition activity was poor. On 1 February fifty additional beetles were introduced. The beetles were removed on 2 February. Egg number and plant height in cm. were recorded.

The third leaf of each plant was sampled for pubescence evaluation. Parents and progeny of crosses were retained for transplant and seed collection.

The mid-parent, the mean of male and female parents, was calculated. A "t" test of the variance of the difference between mid-parent and F_1 was negative for egg counts. The variance of the difference was not significant by "t" test. The F_1 plants had fewer eggs than the parental mean.

Plants tested for oviposition preference were evaluated for pubescence density. The mean difference of trichome counts when parental mean was subtracted from progeny was positive but not significant by "t" test. The F_1 plants exhibited a slight increase over the parental mean. Genes for trichome expression are believed to be dominant. Crosses may be successful due to increased gene dosage.

The correlation between parent and progeny trichome counts was .911. The correlation coefficient between parent and progeny egg counts was -.055.

5. Arkansas-11 Segregates

The oat line Arkansas-11 typifies the effect that leaf pubescence has on host plant-beetle interaction. Arkansas-11

segregates All-1 and All-3 originated from the same cross. Segregate All-1 is glabrous as are all its progeny. Segregate All-3 and progeny are highly pubescent. Pubescence density is variable. Total trichome counts for five microscopic fields per leaf range from sixteen to ninety-four. While lines isogenic for the gene or genes controlling trichomes are not available, two random isolates of an F_3 line, originating from the cross Nora × NCCR-3 (one of which has trichomes and one of which does not) are available. Phenotypically the lines are alike.

Glabrous All-1 averaged 8.23 eggs per plant in the oviposition line test conducted during the winter of 1979. The mean egg count of All-3 was 4.86 eggs per plant. When offered seedlings of the same size, the female beetles preferred glabrous plants for oviposition over pubescent plants.

Five replications of All-1 and All-3 were planted in each field cage for larval feeding damage evaluation during the summer of 1979. An analysis of variance separating the two segregates was calculated for each trait observed.

Differences between cages was not significant for growth habit and maturity. The plant height in cages 1 and 3 was not significantly different. However, plants in cage 2 were taller because height measurement was made at a later date.

Egg count, larval count and egg + larval count or "Count" were not significantly different between All-1 and All-3. There were more eggs and larvae on All-1 than All-3 but not significantly more. Adults did not distinguish between the two segregates for oviposition

preference in the field. Yet, the larval feeding damage scores on All-1 were significantly higher than on All-3. All-3 is a poor food source. The larvae may experience an antibiosis effect as the result of feeding on pubescent All-3. Less larval feeding damage resulted. Thus two isogenic segregates had significantly different larval feeding damage scores due solely to differences in pubescence density.

Glabrous and pubescent segregates of other lines have not been compared for oviposition preference or larval feeding damage.

The results of this comparison justify oat plant selection based on trichome density. Pubescence is biologically significant in the determination of larval feeding damage in oats.

DISCUSSION

The exact combination of plant characteristics which impart resistance in oats to the cereal leaf beetle is not known at this time. Plant height, growth habit and maturity were evaluated in addition to egg and larval counts and larval feeding damage to observe plant growth rate and size relationship with the beetle. Differences in plant size and growth habit appear to be more important in the determination of oviposition preference and larval feeding damage than the differences in germplasm. The beetle interacts with the whole plant.

Germination percent and rate of germination affect the number of plants and consequently insect contact with that particular line. An abundance of seedlings early on, when plant material is scarce, may render those lines more vulnerable to insect attack. On the other hand, adults prefer young succulent tissue. Newly emerged plants and leaves may be more susceptible. Plant height and number of leaves at the time of infestation may be important. Additional evaluation of seedlings could reveal the influence of plant growth stage on insect attack. If plant height affects oviposition preference, differences in seedling height may be disguised by differential growth rate at maturity.

Differences in oviposition preference for vernalized and non-vernalized wheat seedlings have been observed. The internal physiological change from vegetative to reproductive condition occurs after infestation. Such a change may affect larval feeding rate and damage.

All comparisons of larval feeding damage and oviposition preference made in these tests are relative between lines tested. Painter (27) states that preference may exist when susceptible and resistant varieties are grown together. But that resistance may be lacking when the "non-preferred" variety is grown alone.

Differences in height and growth habit exhibited between lines are important when beetle reaction is evaluated in a heterogeneous situation with various lines. Identification of the effects of these morphological differences are important. Selection must be made with regard to, but in spite of, growth habit, height and maturity. Field crops grown in monoculture are uniform in height and maturity. Beetle preference is then, not a choice between lines, but, whether to feed or not, to oviposit or not, to remain in the oat field or to find alternate hosts for oviposition and feeding. Selection is based on discouraging feeding and oviposition within the field and severe antibiosis to reduce larval growth and feeding damage should adult feeding and oviposition occur. Resistance of decumbent or late maturing types based solely on avoidance in the presence of taller types is not effective when plants are grown in monoculture.

Methods of testing prospective plant material under monoculture have been developed by Dr. J.A. Webster. Several lines are tested in individual cages with equal levels of infestation. Cages with a resistant or susceptible check in addition to the test line are used to compare relative beetle activity of lines in separate cages. Selection of resistant lines based on monoculture tests

project a more accurate estimate of beetle reaction to the plants under field conditions.

Pubescence was evaluated concurrently with other plant characters in an attempt to identify the role of leaf pubescence in oat plant cereal leaf beetle resistance interactions.

Isogenic segregates of one line which differ only in presence of leaf pubescence were compared for three levels of beetle infestation. The pubescent segregate had fewer eggs and larvae than the glabrous segregate. Mean larval feeding damage feeding scores were significantly lower for pubescent plants when compared to glabrous plants for each level of infestation.

This was the first solid evidence that pubescence affects the cereal leaf beetle reaction to oats. Further exploration will indicate which phases of the insect life-cycle are most affected by dense pubescence.

The presence of leaf pubescence has been shown to affect all aspects of adult and larval interaction with the plant material. Many insect species have sensors on the legs, antennae or ovipositor which sense the presence of pubescence upon landing on the plant (27). Leaf blade pubescence is a deterrent to the adults indicating a poor food source and oviposition site. Gravid females confined to pubescent wheat plants appear to be nervous (32). Many refuse to oviposit on the leaves. Eggs placed on the leaves are haphazardly attached. Eggs on pubescent leaves have a high frequency of desiccation and drop off rate (52). The pubescence is distressful to the female. Either the female cannot reach the leaf surface

or is unable to find enough non-pubescent leaf surface to attach the egg firmly.

Oviposition and eclosion take place over an extended period of time in field tests. A single count of eggs and larvae gives no indication of the total number of eggs oviposited nor the drop off rate. Hatch percent and dropoff rate would give more insight into ovipositional preference and plant characters affecting the size of the larval population prior to initiation of larval feeding. Evaluation of hatch percent and dropoff rate would require observations of field plants several times during the oviposition and larval feeding period rather than once in the growing season.

Pubescence density differs between plants grown in the greenhouse, growth chamber and in the field. Fedak (12) found that high light intensity decreased pubescence length and density of barley plants relative to plants grown in low light conditions. Sarkarung (30) found that field and greenhouse growth conditions differed in light intensity and quality, particularly blue, red, far red and ultra violet quantity. Low light may cause etiolation of leaf cells including trichomes. Low light conditions may be cooler, not drying the plants as rapidly permitting more water for cell expansion. High light and consequently higher tempreature may cause smaller, thicker cells.

Plants treated with gamma irradiation experienced erratic changes, increase and decrease, in pubescence density. Changes in pubescence density were not inherited suggesting a physiological change in the epidermal cells rather than mutation of the germ cells.

Altered growth conditions may be used when growing plants for selection. Extreme light conditions may affect trichome expression of test lines differently. Adverse conditions may be used to distinguish lines with genetic potential for high pubescence density from those with potentially less pubescence. Selection based on low light conditions could distinguish lines that appear identical under "normal" light regime. Selected segregates returned to normal growth conditions may exhibit increased pubescence density due to elimination of excess material that is less pubescent.

Distance between vein spacing in leaves may affect suitability for larval feeding. Older larvae with wider mouth parts are unable to feed between the veins and have poor weight gain due to ingestion of high fiber leaf vein tissue (54). Webster (44) indicated that vein spacing and leaf curl may influence larval feeding damage.

Esau (9) observed bulliform cells, "cells shaped like bubbles", between veins of the Gramineae. These highly vacuolated cells are poor in solids content but rarely contain tannins or crystals. Bulliform cells control unrolling of new leaves and hygroscopic opening and closing of mature leaves. By description, larvae feed on bulliform cells and the parenchyma and mesophyll layers below. Selection for smaller, tougher bulliform cells could discourage feeding. Smaller cells could result in slightly curled leaves which Webster (44) proposed to discourage larval feeding.

The initial segregate selection was based on both larval feeding damage scores and trichome density. Subsequent selection has emphasized trichome density more so than larval feeding damage.

Lack of increased resistance of selected segregates may be attributed to lack of selection for host-plant interaction components. Simultaneous selection for high density and low larval feeding damage scores retains resistance in the next generation.

Within line crosses between selected segregates were made. Progeny tests were made using one or two F_1 plants and four to ten F_2 plants. Due to small population size, the probability of recombination and reassortment to produce wide differences between progeny was reduced. Differences found between parents and progeny may be due to chance alone. The F_1 data indicate that pubescence and ovipositional non-preference are dominant. Segregation in F_2 progeny make conclusions difficult but possibly more accurate due to larger population size.

Selection of segregates for use in crosses was based on F_3 and F_4 data of each parental line. Selected segregates exhibited high pubescence counts and low larval feeding damage. Segregates may not differ in genes for trichome expression and oviposition preference. Transgressive segregation occurs with complementation of different genes. The desired increase in trichome number may not be possible through within line crosses.

Sarkarung (30) found pubescence was due to gene dosage of one or two partially dominant genes dependent on the line tested. Nora X NCRR-3 segregated 3:1 for leaf pubescence with an additional gene for sheath pubescence. Nora X Tam 0-301 also segregated 3:1 for leaf blade pubescence but contained only recessive genes for a glabrous leaf sheath. Glabrous plants had only glabrous progeny.

Highly pubescent F_2 plants had only highly pubescent progeny. Lightly pubescent F_2 plants segregated into highly pubescent and lightly pubescent plants in the F_3.

Possibly the population size was too small to observe glabrous segregates.

Modifying genes were found in Tam O-301 and NCRR-3. These progeny were more pubescent than the A. sterilis from which pubescence was derived.

CONCLUSION

These tests exhibited that improved resistance to the cereal leaf beetle can be achieved through hybrization and selection.

Oviposition preference tests adequately determined adult preference for plants of nearly the same size and age. Egg and larval counts in the field were dependent on differences of trichome density but also confounded with plant height and other characteristic gross morphological traits.

Further study of plant characters affecting oviposition preference and larval feeding damage should be made.

Trichome density varied with environmental conditions under which the plants were grown. This variation was consistent for all lines tested.

Trichome density was quantitatively inherited, and may be increased through recurrent selection.

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