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CEREAL LEAF BEETLE (COLEOPTERA: CHRYSOMELIDAE) AND WINTER WHEAT: HOST PLANT RESISTANCE RELATIONSHIPS[1]

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ABSTRACT

The cereal leaf beetle was introduced into North America from Europe prior to 1960. An overview of the control of the insect in North America is presented with major emphasis on host plant resistance. The length and density of the adaxial trichomes (pubescence or leaf hairs) convey resistance to wheat, and the amount of resistance can be estimated mathematically without the insect being present.

As the number of travelers between continents grows and the time in transit decreases, the probability of accidentally moving plant or animal pests from one continent to another increases. The probability of accidental introduction of a foreign pest necessitates that we maintain good communication and international relationships so that previously used and successful control measures can be rapidly implemented to assist in the suppression and control of a recently introduced pest.

The cereal leaf beetle (CLB), *Oulema melanopus* (L.), is a Eurasian pest that was first identified from southwestern Michigan in 1962. Fortunately, the beetle became established in the eastern rather than the western United States where greater acreages of small grains occur. Control of the CLB was deemed necessary initially when CLB moved from winter wheat to spring oats. The beetles prefer oats to wheat, and typically move to oats as soon as the seedlings are a few inches tall. Since there were about 10 times more acres of winter wheat than oats in southern Michigan, the movement to fewer acres of oats caused a widely dispersed population to become concentrated in oats and required control.

The CLB damages small grains by skeletonizing the leaf surfaces, thus reducing yield. This introduced pest had been treated by farmers with insecticides for three years before it came to the attention of entomologists. Shortly after its identification, federal and state resources were allocated to cope with this potential threat to North American small grains. Haynes and Gage (1981) deduced that the insect may have been introduced between 1947 and 1949, giving it ample time to reach damaging populations in the late 1950's. Since its introduction, it has spread primarily with prevailing southwesterly winds and now is present in 22 states and two Canadian provinces. Today about 23% of the small grain acreage in North America is within the range of the beetle.

Federal and state cooperative programs were initiated with the intent of suppressing and controlling the insect. Products that might harbor the insect were quarantined, inspected, and often fumigated. These included grain, hay, fodder, and straw, and, later, Christmas trees, when beetles were discovered overwintering on the trunks. Concurrently, a large

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scale aerial control program was initiated in 1963 in Michigan, Indiana, and Illinois, using malathion and carbaryl. The intent was to suppress the CLB population so that further studies might be conducted and the most economically effective pest management system could be adopted. Research was initiated on all aspects of the basic biology of the insect: European parasitoids were identified with the intent of establishing some of them in North America; effective insecticides for all life history stages were evaluated; possible alternative methods to insecticidal control using radiation or microbial agents were evaluated; and the possibility of using host plant resistance to help suppress the population was studied.

Since the CLB originated in Eurasia, a close liaison developed between scientists in North America and Europe, especially in France, Poland, Switzerland, West Germany, and Yugoslavia. Throughout these studies, many individuals and agencies cooperated to suppress and control the CLB. The cooperative effort in the mid-1960's included the federal government (USDA-ARS and APHIS), state departments of agriculture (from Michigan, Indiana, Illinois, and Ohio), university and foreign scientists, extension personnel, and farmers. There were annual CLB meetings where problems and new findings were discussed in depth.

This paper will discuss the interaction of the CLB with its hosts, especially those found to possess host plant resistance, and the interactions between organizations to bring about a successful CLB control program.

HOST PLANT RESISTANCE

From 1965 to 1981 cereal nurseries with thousands of cultivars and germplasm lines were planted in Michigan and Indiana, and became infested naturally with the CLB. These small grains were evaluated to find differences between lines relative to feeding, oviposition, or CLB survival. In 1966, Gallun et al. found that wheat leaves were not oviposited or fed upon as much if the leaves were highly pubescent. Also, cereal grains with the greatest pubescence, that is, having leaf hairs or trichomes, came from southern Russia, from an area not too distant from the presumed origin of the beetle in southern Asia. A review of literature revealed that Megalov (vide Vavilov 1951:147) reported in 1926 that blade pubescence was detrimental to the CLB. Schillinger and Gallun (1968) noted that pubescent wheats (Fig. 1) deterred adult feeding and oviposition, and Schillinger (1969) and Wellso (1973) reported on decreased larval feeding and survival.

The deterrent effect of pubescent wheat initially was ascribed to the density of the leaf hairs on the adaxial surface of the leaf. Cooperatively, plant breeders and entomologists rated the cultivar entries in their nurseries to determine which cultivars were more resistant. Cereals were grown in the field in locations with ample beetle populations, and CLB feeding damage was visually rated on a scale from 0 (no damage) to 5 (with severe damage, over 75%) on each line. To further quantify resistance, a technique to clear leaf tissue was used, and the density of leaf hairs on the upper surface of the leaf was determined. The more promising lines were regrown and retested.

DEVELOPMENT OF RESISTANT CULTIVARS

The development of a new, resistant cultivar depends upon selecting genotypes in the field that had less feeding damage or fewer eggs than adjacent cultivars. Unfortunately, this technique, highly successful when insect numbers are ample, was utilized at a time when the CLB population was small and declining. During this period (1971–1980), the beetles were not always present in large numbers where the nurseries were located in southwestern Michigan, and Drs. D. H. Smith, Jr. (plant geneticist) and J. A. Webster (entomologist) moved their nurseries several times to areas with greater beetle numbers. Some years, existing CLB populations were implemented by collecting beetles elsewhere and releasing them in their nurseries (Webster and Smith 1983).

Fig. 1. Adaxial surface of C.I. 8519, a highly resistant winter wheat blade (130×).

During this period the beetle was rapidly spreading eastward across the U.S. and into Canada. Five European species of hymenopterous parasitoids of the CLB were introduced. Four became established, and two of these, *Testrastichus julis* (Walker) and *Anaphes flavipes* (Foerster), caused a significant decrease in CLB numbers.

A significant research finding was the discovery that insecticides could be applied when the parasitoid, *Tetrastichus julis*, was in the soil and would be affected minimally (Gage and Haynes 1975). The time of application can thus be critical to successful biological control of the CLB.

Federal and state scientists at Purdue University decided it was appropriate to develop a wheat variety with beetle resistance. Germplasms called 'Vel,' for velvet, and 'Fuzz,' for fuzzy, that were somewhat resistant to the CLB, were being bred and evaluated. 'Fuzz' was the resistant germplasm utilized initially in a federal pilot program (by Gallon and Roberts, 1975–1980) to evaluate "The effects of pubescent wheats on the population dynamics of the cereal leaf beetle." This program was jointly conducted by federal and state scientists at Purdue and Michigan State universities on the border between Indiana and Michigan. 'Fuzz' was utilized in the pilot test for only one year, as some fields of 'Fuzz' had greater numbers of beetles and sustained more damage than expected. A third germplasm, 'Downy,' developed as a commercial variety at Purdue University by state and federal scientists, was utilized for the next four years in the pilot program.

Hoxie et al. (1975) evaluated the relationship of trichome length and density on wheat blades relative to CLB larval survival and oviposition. The length was found to be more important than the density of trichomes relative to CLB resistance. Trichomes of 'Fuzz' were found to have an adequate density, but they were too short to provide adequate resistance.

EFFECTS OF TRICHOMES

Interaction of the CLB with cereal grains is very broad and all life history stages are affected by the presence of trichomes on wheat (Table 1). Since adults and larvae feed on

Table 1. Influence of wheat trichomes on the cereal leaf beetle.

Developmental stage	Trichome effect
Adult:	—Interference with movement on the blade surface
	—Reduction in quality and quantity of food consumed
	—Reduction in number of eggs produced
	—Reduction in number of eggs laid on the pubescent blade
Egg:	—Increase in mortality due to desiccation, dislocation, and being punctured
Larva:	—Increase in mortality because of orientation and feeding difficulty (some larvae die because the trichomes actually perforate the alimentary canal) on pubescent surface of the blade
	—Decrease in food consumed
Pupa:	—Decrease in size due to less food consumed by larva
Adult:	—Decrease in size due to reduced food consumption by the previous larval stage

cereals, both would be directly affected when feeding on a pubescent, resistant wheat. Eggs are affected indirectly in that the number of eggs per female depends upon the amount and quality of food consumed, and successful hatch depends upon the eggs being affixed firmly to the blade (trichomes interfere with this). The egg stage is directly affected by the trichomes as about 7% of the eggs are physically punctured by the sharp-pointed trichomes (Wellso 1979). Larval feeding is reduced on resistant wheat seedlings, and newly emerged adults from these larvae are smaller (Wellso 1973). In fact, first instar larvae bite the trichomes into three nearly equally sized fragments before reaching the nutritious cytoplasm, while fourth instar larvae consume about 72% of the 200 μm trichomes whole. An analysis of the alimentary canal of a cleared fourth instar larva showed that it had the basal portion of about 100 trichomes in its alimentary canal. Some of the trichomes penetrate the alimentary canal and kill the larvae. Hence, the number of pupae and adults depends upon the host quality and quantity at the time of larval development.

The main effect of pubescent wheat is to deter CLB oviposition (Gallun et al. 1966). A question is often posed; can an insect adapt to the resistance and thus render it useless? To obtain information about the adaptability of the CLB, a no-choice test was designed to determine whether the behavior of beetles feeding on pubescent wheats could be altered (Wellso 1979). To accomplish this, ovipositing females that were feeding and ovipositing on barley at a rate of 10 eggs/day, were transferred into a screen cage with a highly resistant wheat seedling (CI 8519). The seedling was changed daily, and feeding and oviposition decreased daily until after 9.1 days oviposition ceased. The beetle again was provided susceptible barley seedlings and within 3.2 days was again ovipositing at a rate equal or greater than 10 eggs/day. Beetles treated in this manner went through seven cycles of 10 or more eggs/day on susceptible barley to 0 eggs/day on resistant CI 8519 wheat.

About 40% of the eggs were haphazardly laid on pubescent seedling leaves with ca. 60% laid on the screen cage. Since the CLB is so responsive to trichomes, it was decided to find out what would happen if the beetles were placed in a cage "more resistant" than the resistant seedling host plant. To accomplish this, the sides of the screen cage were covered with white velvet (200 cut fibers/mm^2 with an average length of 1.5 mm). Beetles in these cages fed and oviposited nearly twice as long for each cycle on resistant wheat than the beetles that were confined in the normal screen cages (Table 2). This showed that the beetle can adapt to the pubescent wheat leaves and, if it were confronted with large acreages of pubescent wheat, it probably would feed and oviposit more eggs on the resistant grains than previously suspected. In fact, if the CLB were completely deterred

Table 2. Average duration and feeding of CLB transferred from 'Lakeland' barley (B), after reaching a daily oviposition of 10 or more eggs per day, to resistant C.I. 8519 wheat (W), until no eggs were laid. Beetles were then transferred back to barley and the cycle repeated.

	Host plants															
	B	W	B	W	B	W	B	W	B	W	B	W	B	W	B	W
Test 1[a]																
No. of females	40	39	20	18	13	13	7	7	4	4	3	3	2	2	1	1
Days	6.4	9.1	3.2	5.0	3.4	4.5	3.0	5.3	5.0	3.5	3.0	3.0	3.0	7.0	3.0	4.0
Daily feeding (mm)[b]	235	254	367	218	351	234	301	152	287	139	310	143	184	195	227	72
Test 2[c]																
No. of females	31	31	22	22	13	12	5	5								
Days	7.1	12.5	4.1	9.9	3.0	8.2	5.0	3.6								
Daily feeding (mm)[b]	247	398	257	228	276	234	283	162								

[a] Test conducted in screen cages.
[b] Since CLB feeding is about the same width and depth on a cultivar, for comparative purposes one need only compare the length of the feeding scars.
[c] Test with barley in screen cages; test with wheat in velvet-lined cages.

from feeding and ovipositing on winter wheat seedlings in spring, it is possible that it might feed on native grasses in the fence rows or even on bluegrass in lawns.

POPULATION DYNAMICS

Utilizing all of the information from field and laboratory studies, a model depicting the survival and development of a hypothetical CLB population confined for one generation with either a susceptible barley or a highly resistant wheat was developed (Table 3). This model shows that in one year the CLB would increase about 4.6-fold on barley, while on resistant wheat it would decrease about 1/5 to 1/20 of its initial number. The amount of reduction due to host plant resistance in an area would be dependent primarily upon the level of resistance in the host, and the availability of alternate hosts.

The pilot program to study the population dynamics of the CLB on resistant wheats was mentioned previously. This study was undertaken in a 16-square-mile region of southern Michigan and northern Indiana. 'Downy,' a field-selected cultivar resistant to the CLB, was developed by federal (USDA-ARS) and state (Purdue University) scientists located at West Lafayette, Indiana. The trichome length and density of 'Downy' were evaluated in the laboratory, and the cultivar was labeled as resistant to the CLB. To everyone's surprise, the beetle fed and oviposited on this cultivar in some fields much more than had been predicted.

A study was initiated to determine the length and density of trichomes on the base, mid-region, and apex of each blade of 'Downy' as it grew in the field in spring (Wellso and Hoxie 1981). This provided a trichome profile (trichome length and density) of this cultivar under natural conditions, and might explain why it did not deter oviposition and feeding as much as had been predicted from laboratory studies.

CLB, in a field of 'Downy,' fed and oviposited selectively on those plants that had trichomes that were shorter in length. Trichome profiles were found to differ significantly between years for the same leaf-number and between different leaves the same year. The procedure of counting the density of trichomes in a given area that had helped quantify resistance in wheat to the CLB for ca. 10 years was not as accurate a method as desired. The length and the density both had to be determined to give an accurate resistance rating to the plant. The flag leaf, usually stated as the most important photosynthetic site during grain filling, was found to be significantly less resistant than the three blades below it. The

Table 3. A model depicting the survival and development of a hypothetical CLB population confined for one generation with either a susceptible barley or a highly resistant wheat. Data have been extrapolated from various field and laboratory experiments.

	Barley		C.I. 8519 wheat			
	Screen cage		Velvet-lined cage		Screen cage	
	No.	%	No.	%	No.	%
Initial population (1:1: ♂:♀)	100		100		100	
Oviposit	47	94	23	46	23	46
Avg. eggs per female	225		72		38	
Total eggs	10,575		1,655		874	
Eggs on plant	10,258	97	1,341	81	341	39
Total hatched (70% RH)	7,694	75	912	68	232	68
Survival to pupae	3,847	50	182	20	46	20
Survival to adult	1,923	50	91	50	23	50
Aestivating adults	1,154	60	55	60	14	60
Overwintering mortality	577	50	28	50	7	50
Survival to oviposition	462	80	22	80	6	80

overall trichome profile could best be estimated by samples from the mid-region of the leaf. Trichome density of the first blade was positively correlated with blade length and negatively correlated with soil moisture in the laboratory. Trichome profiles of the first seedling blade were positively correlated with temperature. Seedlings grown under higher temperatures (26.7°C) in the laboratory had longer trichomes than seedlings grown at 20°C. It was for this reason that 'Downy,' a cultivar with moderate resistance, was given a higher resistance rating when evaluated in the laboratory.

In the field, the quality of resistance was determined by comparing germ lines with each other and selecting those exhibiting less damage or fewer eggs. If the CLB population pressure is great, the resistance may appear to have failed as the beetles tend to disperse more uniformly throughout the nursery and attack all hosts. The relationship between trichome length on various blades and temperature has not been studied. The flag leaf also is very important in the synthesis of nutrients that are translocated from the blade to the filling seeds. Perhaps the flag leaf expends less energy for protection than for nutrient production and translocation.

These studies have shown that development of wheat blades is variable respecting trichome length and density. The resistance to the beetle is of a physical nature. Another question posed is whether the trichomes interfere with the searching ability of parasitoids. It appears that the trichomes do not decrease the number of CLB that are parasitized (Lampert et al. 1983). Thus, host plant resistance and biological control can be implemented concurrently. These methods bring about a reduced CLB population and the need for insecticidal control is greatly reduced.

ESTIMATION OF RESISTANCE

The quality of wheat resistance to the CLB can be estimated from the density per unit area and the length of trichomes on the adaxial blade surface. The mechanical resistance of wheat is influenced by temperature and soil moisture. A standardized procedure for determining the resistance rating of wheat in the laboratory or field is now available to make host ratings or selections of resistance. The amount of resistance (RS) can be calculated using the formula:

$$RS = 0.001 \text{ X length X density } 1/3$$

with length = mid-leaf trichome length (μm) on the adaxial surface, and density = number/mm^2.

Thus, it is possible to ascribe CLB resistance ratings based on trichomes to all of our wheats, even without the CLB being present. However, great care must be taken in evaluating material in the field under natural conditions. Soil moisture and temperature in a given year may modify the findings.

Host resistance as described in this paper is a most effective and ideal method to control phytophagous insect pests. The method is very specific in that only those insects that attack the plant are affected. We are all aware of the recent contamination of the environment with various chemical pesticides. This type of insect control is certainly needed, but only after all of the other available, alternative methods have proven inadequate. Host resistance is one of the very best alternative pest-control methods and reduces the overall cost of control as well as environmental contamination. This method is also adaptable to genetic engineering in that chromosome fragments with the codon for specific physical or chemical resistant traits may be duplicated and inserted into plant cells to further increase the effectiveness of host plant resistance.

Whether the cereal leaf beetle or wheat gains an evolutionary advantage depends upon whether the pest or the host plant has more mutable genes that can be used to overcome corresponding genes in the other life form.

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