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TRICHOME DENSITY DIFFERENCES AND BEAN LEAF BEETLE, *CEROTOMA TRIFURCATA* (FORSTER), FEEDING BEHAVIOR ON SOYBEAN PODS

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ABSTRACT: The pod trichome densities of eight soybean lines and one public variety were determined, and the associated aspects of bean leaf beetle, *Certoma trifurcata* (Forster), feeding behavior on soybean pods were investigated. Three-seeded soybean pods were removed from the top and the bottom of the plants of selected lines. The pods were divided into seven sections, starting from the peduncle and ending at the pod tip. Circular areas within each section were delineated, and the number of trichomes in each circle was determined. Data were analyzed for differences in trichome numbers among lines, within plant regions, and among sections of pods. The trichome density for different lines ranged from 495 to 924 trichomes/cm^2. Pods from the top of the plant had higher trichome densities than pods from the bottom. Soybean pod sections nearest the pod tip had the highest trichome densities, and the sections nearest the peduncle had the lowest. Free choice feeding assays were conducted in the laboratory with three-seeded pods from all lines. Field-collected adult bean leaf beetles were allowed to feed for forty-eight hours. The percentage of the surface damaged per pod section was estimated. Bean leaf beetles showed a stronger tendency to feed on pods at the peduncle end and the sections nearest it. These pod sections had significantly lower numbers of trichomes. Areas with the highest trichome densities had the lowest percentage of beetle damage. Lines HC83-193-5 and HC83-123-9 and the experimental cultivar "Anderson Velvet" had the greatest resistance to overall pod damage.

KEYWORDS: Bean leaf beetle, feeding behavior, host-plant resistance, pods, pubescence, soybeans, trichomes.

INTRODUCTION

Soybean, *Glycine max* (L.) Merrill, is attacked by many foliar and pod feeding insects (Kogan, *et al.,* 1988). The bean leaf beetle, *Cerotoma trifurcata* (Forster) (Coleoptera: Chrysomelidae), causes pod injury that predisposes the seeds to injury by secondary pathogens (Shortt, *et al.*, 1982) such as *Alternaria tenuissima* (Kunze ex Pers.), resulting in yield and seed quality reductions (Smelser and Pedigo, 1992a). The feeding behavior of first and second generation beetles is different. Second generation adults prefer to feed on soybean pods instead of leaves (Sims, *et al.*, 1984). The larvae feed on roots, root hairs, and *Rhizobium* nodules (McConnell, 1915). Bean leaf beetles are also important vectors of bean pod mottle virus in the southern United States (Hopkins and Mueller, 1983).

Bean leaf beetle management relies mainly on the use of insecticides. Despite their effectiveness, insecticides can create environmental problems. Research on alternative management strategies that minimize insecticide application has focused on the use of resistant plant material. This approach also has the potential to delay the development of insecticide resistance in the bean leaf beetle. Trichomes on foliage and/or pods can act as a physical barrier to inhibit insect feeding (Norris and Kogan, 1980).

Trichome density, the number of trichomes per unit area, has been shown to influence the behavior of several chrysomelid beetles. Lamb (1980) found that the trichomes on the pods of the mustard plant inhibited feeding by the flea beetle, *Phyllotreta cruciferae* (Goeze). Flea beetle feeding increased on pods whose trichomes were removed. Baur, *et al.* (1991) demonstrated through the use of dual-choice laboratory assays that trichome density influenced *Agelastica alni* L. oviposition and feeding on the gray alder, *Alnus incana* (L.). Palaniswamy and Bodnaryk (1994) showed that wild *Brassica* species having a leaf trichome density greater than 2,172 trichomes/cm^2 were highly resistant to flea beetle feeding. *Brassica* species with less than 30 trichomes/cm^2 suffered significant damage. Behavioral observations showed that high trichome densities act as a physical barrier to flea beetle feeding. A notable case of the influence of trichome density on a chrysomelid beetle is the effect of wheat leaf trichome density on the behavior of the cereal leaf beetle, *Oulema melanopus* (L.). Trichome density influenced cereal leaf beetle oviposition (Gallun, *et al.*, 1966; Casagrande and Haynes, 1976; Lampert, *et al.*, 1983), egg viability (Lampert, *et al.*, 1983), and larval survival (Ringland and Everson, 1968; Hoxie, *et al.*, 1975). Schillinger and Gallun (1968) found that pubescence deterred adult cereal leaf beetle oviposition on wheat leaves and resulted in abnormal behavior (*e.g.,* movement). Fewer eggs hatched on highly pubescent leaves, suggesting that the eggs may have become desiccated. In addition, trichome density reduced early larval stage survival. The larvae have to eat through the trichomes to reach the leaf surface. The composition of the trichomes ingested (*e.g.,* lignin and cellulose) caused an imbalance in the larval diet (Schillinger and Gallun, 1968).

Minimal information exists on trichome density and its effects on soybean pod feeders. The major objectives of this study were to (1) determine if differences exist in soybean pod trichome density and to (2) examine any relationship between trichome density on soybean pods and feeding behavior by adult bean leaf beetles.

MATERIALS AND METHODS

Trichome Density. Eight soybean lines (MBB80-169, MBB83-190, MBB80-133, MBB83-368, HC83-193-5, HC83-19-2, HC83-123-9, and L76-0038) known to demonstrate foliar resistance to the Mexican bean beetle, *Epilachna varivestis* (Mulsant) and one susceptible cultivar, "Williams 82," were planted on 28 May 1993 at the Purdue University Agronomy Research Center, West Lafayette, Indiana. Each line and cultivar was sampled and analyzed using a completely

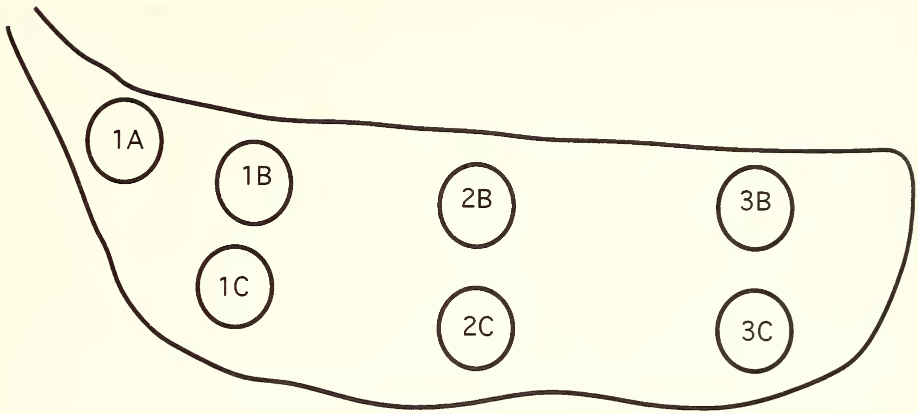

Figure 1. A diagram of a three-seeded soybean pod showing the areas where trichomes were counted.

randomized experimental design. The experimental area was 222.8 m^2 (12.1 m x 18.2 m) and previously had been planted to corn. Each line was planted in two-row plots 154.9 cm long and 76.2 cm wide, oriented north to south. Plots were separated by a 30.4 cm east to west alley. Blocks were separated on the ends with alleys 121.9 cm wide. Sixty-four seeds of each entry were planted per row with a Planet Junior® Sample Plot Planter (Swanson Machine Co., Champaign, Illinois) at a depth of 0.63 to 1.2 cm. Plants of "Anderson Velvet" were planted in a single row by themselves in the same area.

On 24 June 1993, a 18 x 14 mesh polyethylene screen (Lumite Co., Gainesville, Georgia 30503) was placed on a metal frame over the entire area to prevent insects such as the Japanese beetle (*Popillia japonica* Newman), bean leaf beetle, and grasshoppers (various species) from feeding on the foliage.

On 9 September 1993, approximately 30 pods were randomly collected from the top and 30 from the bottom of 5 randomly selected plants in the R6 growth stage (Ritchie, *et al.*, 1992). Pods were collected and placed into polyethylene bags (15.2 x 7.6 cm), transported to the laboratory, and stored at 2.8 ± 2° C.

Laboratory Evaluation. In the laboratory, 5 three-seeded pods per line were randomly selected from the 30 pods collected from the top and bottom of the plants from each line. Pods were divided into seven sections starting at the peduncle and ending at the apex of the pod (Figure 1). The section between the peduncle and the first seed was represented by the letter "A." Each of the three sections of the pod containing a seed were divided into an upper and lower section (nearest the dorsal and ventral sutures) represented by the letters "B" and "C," respectively. Circular areas within each section were delineated with a 0.5 cm cork borer (0.2 cm^2). The number of trichomes in each circle was counted with the aid of a 20x dissecting microscope. Data were analyzed by ANOVA (SAS Institute, 1988). The Student-Newman-Keuls Sequential Range Test (SNKS Range Test) was used to separate significant differences ($P \leq 0.05$) among lines, plant regions, and pod sections.

Table 1. The mean pod trichome density among selected soybean lines. Within column means followed by the same letter do not differ significantly (Student-Newman-Keuls test: $P \leq 0.05$, $n = 70$).

Line	No. of trichomes / cm^2
HC83-193-5	924.3 a
MBB80-169	831.7 a b
MBB83-190	803.7 a b
HC83-19-2	794.0 a b
MBB83-368	747.0 b
HC83-123-9	669.0 b c
MBB80-133	598.2 c d
L76-0038	548.5 c d
Williams 82	495.2 d

Bean Leaf Beetle Feeding Behavior Assays, 1993. Adult feeding preference assays were conducted on 9, 18, and 27 September and 7 October. Pods used for the assay were collected within 24 hours of the assay. Thirty three-seeded pods were collected from the top and 30 from the bottom of each line. Three-seeded pods of approximately the same size from seven of the lines plus "Anderson Velvet" were randomly placed on filter paper moistened with distilled water. The pods were placed equidistant around the perimeter of a Petri dish (2.5 x 15.2 cm). Fifteen field-collected adult bean leaf beetles of unknown sex and age were placed in each Petri dish and allowed to feed for 48 hours. The Petri dishes were placed on a laboratory bench at 22.2 ± 5° C at a 14:10 (L:D) photoperiod with a relative humidity of 85 ± 5% inside the Petri dishes. Three Petri dishes, each representing a replication, were evaluated each day.

Each pod was divided into 7 sections (see above). Both surfaces of the pod were evaluated. Feeding damage was visually estimated as the percentage of pod surface damaged per pod section. Average damage per section was determined by dividing the mean values by two, since both surfaces of the soybean pod were evaluated for damage. Average damage per pod was determined by summing the means of the percent damage per section for each line and dividing by the number of sections ($n = 7$). Pod section means for each line were determined by summing all the percent damage per section means for each section and dividing this value by the number of lines ($n = 8$). Due to the irregularity and roundness of the soybean pod, the actual area damaged by the bean leaf beetles was not measured. Because the data from the feeding assay studies were based on subjective visual observations on non-standard experimental units, formal statistics were not applied. However, the results were consistent for both years of the study, and a distinct range of feeding by the adult bean leaf beetles was noted in all assays (Tables 3-5). This information suggests that a feeding pattern exists.

Bean Leaf Beetle Feeding Behavior Assays, 1994. Adult feeding preference assays were conducted on 9, 12, 14, and 21 September. Pods used for this study were collected within 24 hours of the assay from the Purdue University Agronomy Research Center and the Environmental Entomology Laboratory. Identical lines were included in each assay. The experimental cultivar "Anderson Velvet" and the glabrous line D88-5320 were also included in the 1994 assay. The bioassay method was identical to that described above.

Table 2. The mean trichome density of pod sections averaged over soybean lines/cultivars. Within column means followed by the same letter do not differ significantly (Student-Newman-Keuls test: $P \leq 0.05$, $n = 90$).

Section	No. of trichomes / cm^2
3B	971.0 a
2B	831.0 b
3C	811.9 b
2C	671.8 c
1B	650.5 c
1A	544.8 d
1C	505.6 e

RESULTS AND DISCUSSION

Trichome Density Study. Significant differences ($P \leq 0.05$) occurred in trichome densities among lines ($F = 12.0$, $df = 8, 72$), plant regions ($F = 7.2$, $df = 1, 72$), and pod sections ($F = 365.9$, $df = 6, 432$). HC83-193-5 had the highest trichome density, while "Williams 82" had the lowest (Table 1). Significantly ($P \leq 0.05$) higher trichome densities were found on the pods at the top of the plant (759.8 trichomes/cm^2) than at the bottom (684.8 trichomes/cm^2). Trichome densities also varied significantly ($P \leq 0.05$) among sections of the soybean pod (Table 2). Section 3B had a significantly higher trichome density than other sections, followed by sections 2B and 3C, 2C and 1B, 1A, and 1C. Section 1C had a significantly lower trichome density than all other sections.

Differences in trichome density among lines may be the result of genetic variation. Bernard and Weiss (1973) reported that genetically controlled variation in leaf trichome density occurs in some exotic soybean germplasm. Zaiter, *et al.* (1990) demonstrated that trichome density is under genetic control and that differences in leaf trichome densities exist among soybean cultivars.

Differences in trichome density among plant regions is not unusual. Yapp (1912), working with *Spiraea ulmaria* L., and Stober (1917), working with herbs, reported that leaves on the upper part of the plant have more trichomes than leaves located toward the base. Ehleringer and Mooney (1978) reported that leaf pubescence reduces light absorptance and lowers heat loads. Reflection of solar radiation maintains the leaf temperature below the air temperature resulting in lower transpiration rates. Because the upper region of the plant receives higher amounts of direct solar radiation, trichomes may act as a barrier to reduce the amount of light reaching the pod surface, thus reducing moisture loss and desiccation. In addition, as demonstrated with soybean leaves, trichomes reduce wind movement which lowers transpiration rates from leaf surfaces (Woolley, 1964). Pods in the top region of the soybean plant are exposed to wind, thus increased trichome density would presumably reduce water loss. The plant canopy reduces wind movement among pods at the bottom of the plant creating a microenvironment in which trichome density is less important for reducing transpiration from the pod.

The differences in the trichome density on many plants could result from surface area expansion. Some young organs, such as leaves, fruits, and stems,

Table 3. The percent adult bean leaf beetle damage per pod section corresponding to 1993 and 1994 assay dates.

Section	9/18/93	9/27/93	10/7/93	9/9/94	9/12/94	9/14/94	9/21/94
1A	23.0	26.9	8.3	25.8	25.9	32.8	19.4
1B	11.5	13.0	1.9	11.4	12.9	18.0	9.0
1C	17.2	15.9	5.8	15.7	15.7	18.7	13.3
2B	0.7	1.1	0.10	2.5	6.0	4.6	2.5
2C	3.4	4.9	0.60	6.6	4.4	5.7	5.2
3B	5.8	0.72	0.95	3.9	4.8	5.0	4.2
3C	7.9	3.7	3.1	8.2	9.8	8.5	7.4

Table 4. The percent adult bean leaf beetle damage per pod (= line) corresponding to 1993 assay dates.

Line	9/18/93	Line	9/27/93	Line	10/7/93
Williams 82	21.7	L76-0038	28.5	HC83-19-2	5.0
L76-0038	13.6	MBB80-133	14.5	MBB80-133	4.7
Anderson Velvet	9.2	MBB80-169	13.1	MBB83-190	4.3
MBB80-133	9.0	HC83-19-2	9.5	MBB83-190	3.4
MBB83-190	8.9	Williams 82	4.4	Williams 82	2.9
MBB83-368	8.2	MBB80-190	2.9	L76-0038	2.7
HC83-193-5	5.9	MBB80-169	2.2	HC83-193-5	0.71
HC83-123-9	2.8	Anderson Velvet	0.71	Anderson Velvet	0.0

have a dense covering of trichomes. As the organ grows, the trichomes become spaced further apart, and, if new trichomes are not produced, growth results in lowered trichome densities (Johnson, 1975). With soybean, the continued expansion of the pod surface (the number of cells increases, and these cells elongate) moves the trichomes further apart and reduces trichome density (Jackai and Oghiakhe, 1989). At the time of sampling, the pod sections nearest the peduncle (1A, 1B, and 1C) had undergone more expansion than those farther from these sections, resulting in the gradient of trichome density over the length of the pod. Because expansion was less at the apex of the pod, sections closer to the apex (2B, 2C, 3B, and 3C) had higher trichome densities.

Bean Leaf Beetle Feeding Behavior Studies. Adult bean leaf beetles demonstrated a strong preference for feeding at the pod's peduncle end and the sections nearest it (Table 3, columns 2-4 and 5-8). The greatest damage occurred in sections 1A, 1C, and 1B, which had the lowest trichome densities (Table 2). The least damage occurred in sections 2B and 3B, which had the highest trichome densities. Field observations have shown that adult bean leaf beetles tend to feed on the peduncle end of soybean pods (L. Bledsoe, pers. comm.). The results of

Table 5. The percent adult bean leaf beetle damage per pod (= line) corresponding to 1994 assay dates.

Line	9/9/94	9/12/94	9/14/94	9/21/94	Percent Damage Per Pod (Ave./Year)
Williams 82	22.6	34.8	7.1	11.6	19.0
D88-5320	16.6	19.2	28.1	18.7	22.6
L76-0038	18.2	15.9	12.8	7.0	13.5
MBB83-368	9.9	15.9	10.6	9.9	11.6
HC83-19-2	17.9	12.8	6.4	7.1	11.0
MBB80-169	5.6	7.9	19.1	0.22	8.2
MBB80-133	11.8	6.3	31.0	18.2	16.8
Anderson Velvet	2.9	4.9	6.5	5.1	4.8
MBB83-190	7.1	4.5	16.5	10.3	9.6
HC83-193-5	3.7	1.7	4.9	1.8	3.0
HC83-123-9	0.11	1.1	3.7	6.0	2.7

these laboratory studies suggest that bean leaf beetles feed on the peduncle end and the sections nearest it because these sections have the lowest trichome densities. In addition, bean leaf beetles may be able to "mow" down the trichomes in these sections, making it easier to reach the pod's outer surface. Hulley (1988) demonstrated this behavior with the caterpillar, *Pardasena* sp. nr *diversipennis* Gaede, on *Solanum coccineum* Jacq.

Lines HC83-123-9 and HC83-193-5 as well as "Anderson Velvet" demonstrated the greatest resistance to adult bean leaf beetle pod feeding (Table 4 and 5). "Anderson Velvet" is highly pubescent. The high number of trichomes made it difficult to obtain reliable counts, so trichome density was not determined. The unsuitability of the various lines to bean leaf beetle feeding might also result from nutritional deficiencies or disproportionalities, biophysical deterrence, or physiological inhibitors (Barney and Rock, 1975). In addition, other genetically controlled factors might influence the degree of resistance (Clark, *et al.*, 1972).

Although more studies have been conducted to investigate the interaction of soybean leaf trichome density than pod trichome density with insect resistance (Chiang and Norris, 1983; Zhan, *et al.*, 1986; Gunasinghe, *et al.*, 1988; Lambert, *et al.*, 1992), research with other agricultural crops has demonstrated that pod trichome density is associated with reduced feeding by some insects. Chiang and Singh (1988) found that trichomes on the pods of cowpea, *Vigna vexillata,* contributed to resistance against the pod-sucking bug, *Clavigralla tomentosicollis* Stal. Jackai and Oghiakhe (1989) reported that trichomes on the pods of two cowpea varieties interfered with pod feeding and development of the legume pod-borer, *Maruca testulalis* (Geyer), as well as *C. tomentosicollis*. They found that the insects were restless and had difficulty positioning their legs on the pod wall. Oghiakhe, *et al.* (1992) determined that greater trichome density on *Vigna unguiculata* pods reduced larval damage from *M. testulalis* (Geyer), and they concluded that trichome density was the major factor controlling resistance.

While some studies have demonstrated the effectiveness of soybean pod trichomes in reducing insect feeding damage, other studies show that increased pubescence is not always associated with resistance. Morse and Cartter (1937) found that glabrous soybeans were highly resistant to the soybean pod borer, *Laspeyresia glycinivorella* Mats., whereas pubescent varieties were highly susceptible. Broersma, *et al.* (1972) reported that soybean strains with 2,969 to 3,100 trichomes/cm^2 had significantly higher potato leafhopper populations than strains with 610 to 810 trichomes/cm^2. Turnipseed (1977) observed that potato leafhopper populations were less affected by trichome density than trichome length.

Very little information was found in the literature on the interaction of pod trichome density and bean leaf beetle feeding damage. Previous studies have only investigated the effect of pod pubescence on reducing seed quality loss due to bean leaf beetle feeding and subsequent invasion by *Alternaria tenuissima* (Shortt, *et al.*, 1982) and in relation to yield and quality reduction (Smelser and Pedigo, 1992a, b).

The existence of an inverse relationship between increased trichome density and feeding preference by bean leaf beetles for both soybean lines (Tables 4 and 5) and pod sections within the lines (Table 3) was found in this study. HC83-123-9 was a notable exception to this trend. This line showed a high level of resistance to bean leaf beetle feeding at a much lower pod trichome density (Table 1). HC83-123-9 is highly resistant to Mexican bean beetle and adult Japanese beetle foliar feeding (Cooper and Hammond, 1988), suggesting that factors other than trichome density may contribute to host plant resistance. Nevertheless, high trichome densities may inhibit adult bean leaf beetles from reaching the pod surface and feeding. Additional studies should be conducted to evaluate this behavior further.

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