

Characterization of Lesser Cornstalk Borer Injury to the Root-Hypocotyl Region of Peanut Plants¹

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ABSTRACT

Lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller) (Lepidoptera: Pyralidae), larval injury to the root-hypocotyl region of greenhouse-reared 'Florunner' peanut, *Arachis hypogaea* L., plants was investigated by determining the size and distribution of feeding sites. The percent injury to periderm, cortex, phloem, and xylem tissues also was estimated. Tissue loss due to insect feeding was measured for only the most prominent of several wound sites on each stem axis. Percent injury to principal tissues was estimated by planimetric methods.

The lesser cornstalk borer caused significant injury to the periderm, cortex, and the phloem on mainstems of peanut plants. Mean percent injury was 31.67% for the periderm and cortex, 16.78% for phloem, and only 0.19% for the xylem. Approximately 91% of all feeding sites occurred on the mainstem or were contiguous with the mainstem and a branch. The frequency of plants with feeding sites declined linearly with increasing number of sites. These data support the hypothesis that root growth declines with increasing larval injury to phloem and xylem (food and water conducting tissues, respectively) in the root-hypocotyl region.

Key Words: Economic injury level, insect injury, phloem and xylem destruction

The lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller) (Lepidoptera: Pyralidae), is a key pest of peanuts grown in the New World and the most economically damaging insect pest of peanuts in the southeastern U.S. (20). Population outbreaks occur during periods of hot, dry weather (10, 12, 20), and in sandy soils (7, 11). Outbreaks of *E. lignosellus* caused over \$43 million in damage to peanuts in Alabama, Georgia, Oklahoma, and Texas in 1980 alone, and yield losses can exceed 70% following severe outbreaks (20).

Several descriptive accounts of *E. lignosellus* damage to peanuts have been published (1, 10, 11). First- and second-instars feed on vegetative buds, axillary buds in leaf axils, leaves, and plant stems at ground level. Older larvae feed on the stem and taproot at the root-hypocotyl region (13), and on pegs (gynophores) and pods (11). Smith and Holloway (21) reported that 28- to 58-day-old Spanish peanuts may be

more severely injured by larval feeding on young flower buds concentrated in the plant crown before gynophore and pod formation.

Few studies have measured *E. lignosellus* injury to peanuts. Smith and Holloway (21) showed that yield in Spanish peanuts decreased in a curvilinear manner with increasing *E. lignosellus* density, and Berberet *et al.* (2) stated that yield declined linearly at 60-110 days after planting from *E. lignosellus* larval injury to Spanish peanuts. Mack *et al.* (13) found that uninjured pod, seed, and root dry weight declined linearly with an increase in *E. lignosellus* density. Uninjured pod (with seeds) weight decreased by 0.54 g per larva, which is a 5.82% loss per insect per plant. Mack *et al.* (13) also reported that both phloem and xylem tissue were injured by *E. lignosellus* feeding to root crowns and lower stems. According to King *et al.* (10), the presence of *E. lignosellus* is indicated by the scarring of young roots. Injury to phloem and xylem tissue may decrease root growth and development, thereby reducing conduction of water from the roots and the translocation of photosynthates to the roots. It is important to understand what a stem-feeding insect such as the *E. lignosellus* does to water- and nutrient-conducting tissues, because injury to these tissues can indirectly decrease reproductive potential and lessen a plant's ability to withstand other stresses, such as vascular diseases (e.g.: 18) and drought. Consequently, studies were begun to characterize the amount of injury to the peanut root-hypocotyl region caused by *E. lignosellus* feeding. This report quantifies *E. lignosellus* injury to periderm, phloem, and xylem in the peanut root-hypocotyl region, and proposes a hypothesis for the effects of this injury on plant growth.

Methods and Materials

Methods employed in this study were similar to those used in Mack *et al.* (13). Larvae of *E. lignosellus* were reared in 30-mL plastic cups in the laboratory on an artificial diet (5) at 27 ± 1°C with a photoperiod of 14:10 (L:D). Third instars (length range: 5 to 10 mm) were used to infest peanut plants, because smaller larvae could not be handled without significant mortality.

Plant Culture. Peanut plants were grown in a fiberglass greenhouse. Certified Florunner seeds were planted in 1-liter plastic pots filled with autoclaved Dothan fine sandy loam soil at a pH of 5.9 and containing <0.5% organic matter. Natural light was supplemented with fluorescent "gro" lights over each plant. Plants at the V7 stage (3) were transplanted into 11.3-liter pots. All transplants were bottom-watered with sufficient water to prevent wilting while allowing the top 2.5 cm of soil to remain completely dry. Thus, the soil near the root-hypocotyl region was dry throughout the experiment, simulating the conditions associated with damaging *E. lignosellus* populations.

Two spotted spider mites were managed by releasing the predaceous

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mite, *Metaseiulus occidentalis* (Nesbitt). Weeds were removed manually within 7 days after their germination.

Infestation and Injury Evaluations. Plants were infested with eight *E. lignosellus* larvae per plant at the V11 plant growth stage. Both the number of larvae per plant and the plant growth stage were chosen because they were within the range of 0 to 8 larvae per plant and the V9 to R7 growth stages examined by Mack *et al.* (13). Plants were infested with larvae by transferring individuals to the soil surface at the base of a plant with a camel's-hair brush. Each plant was covered with a 61-cm tall cone-shaped 1.5-mm mesh aluminum screen to prevent newly emerged adults of *E. lignosellus* from escaping.

Larval injury to the root-hypocotyl region was examined by sectioning injured stems and determining percent injury to protective and nutrient-conducting tissues (the epidermis was being replaced by a relatively undifferentiated periderm). Measurement of tissue loss due to larval feeding was determined for only the most prominent of several wound sites on each stem axis. Plants were harvested for these measurements immediately after adult emergence. Tissue loss was determined planimetrically. Fresh sections of the root-hypocotyl region were removed from plants and used for slide preparation. Samples were placed in a beaker containing distilled water, and were aspirated in a vacuum chamber at 172 kPa for 30 min. Samples were then refrigerated for 2 h, and free-hand cross sections were made through injured areas. Sections were placed in a 0.5% toluidine blue staining solution for 5 s, rinsed in water, and placed on standard microscope slides for viewing.

Photomicrographs were prepared of all sections. Prints were photocopied and tissue boundaries of the injured areas were drawn in using the photomicrograph of each cross section as a guide to estimate missing tissue regions (Fig. 1A). The cross-sectional area of a photocopy of each cross section before and after each injured tissue was cut out of the photocopy was calculated with an electronic planimeter. Each measurement was made three times on the planimeter, and the mean area of each injured tissue was calculated for each cross section. Percent injury was defined as the mean cross sectional area removed by feeding of *E. lignosellus* larvae. This technique allowed us to measure the percent injury to the periderm and underlying cortex, phloem, and xylem.

The number and location of feeding sites on each plant was determined in a separate experiment. Plant and insect rearing and handling procedures were identical to those previously described. The number of feeding sites per plant, and the size and location of each feeding site was determined at harvest (R8) for 23 plants that were infested at the V11 stage with eight larvae per plant. Each feeding site was classified as being on the mainstem or on a branch. The vertical distance of the feeding site from the soil surface was measured with calipers for each site on the mainstem. The distance from the mainstem was measured for those feeding sites that were on a branch. The maximum length (vertical dimension) and width (horizontal dimension) of each site was also measured.

Analysis. Means were calculated for the percent injury to periderm and cortex, phloem, and xylem tissues. The percentage of feeding sites at a given distance from the soil surface was calculated, and regression analysis (19) was used to relate the number of feeding sites per plant to the frequency of plants with a given density of sites.

Results

Periderm, cortex, phloem, and xylem tissues were all injured by *E. lignosellus* feeding. The periderm and cortex were injured significantly more than any other tissue region, with xylem sustaining the least amount of injury (Table 1). Percent injury to principal tissues was 31.67% for the periderm and cortex, 16.78% for phloem, and only 0.19% for the xylem. Larvae usually ate into the stem until more differentiated cells of the xylem were contacted (Fig. 1B), and then extended the feeding site by feeding vertically or horizontally instead of penetrating deeper into the stem.

Approximately 91% of all feeding sites occurred on the mainstem, or were contiguous with the mainstem and a branch. Only 4 to the 44 feeding sites occurred on branches, and were located 4.5 ± 2.2 mm from the mainstem ($x \pm$ std. error mean).

Approximately 48% of all feeding sites on the mainstem occurred at the soil surface, with no more than 4.7% located at any other height (Fig. 2). The average feeding site occurred

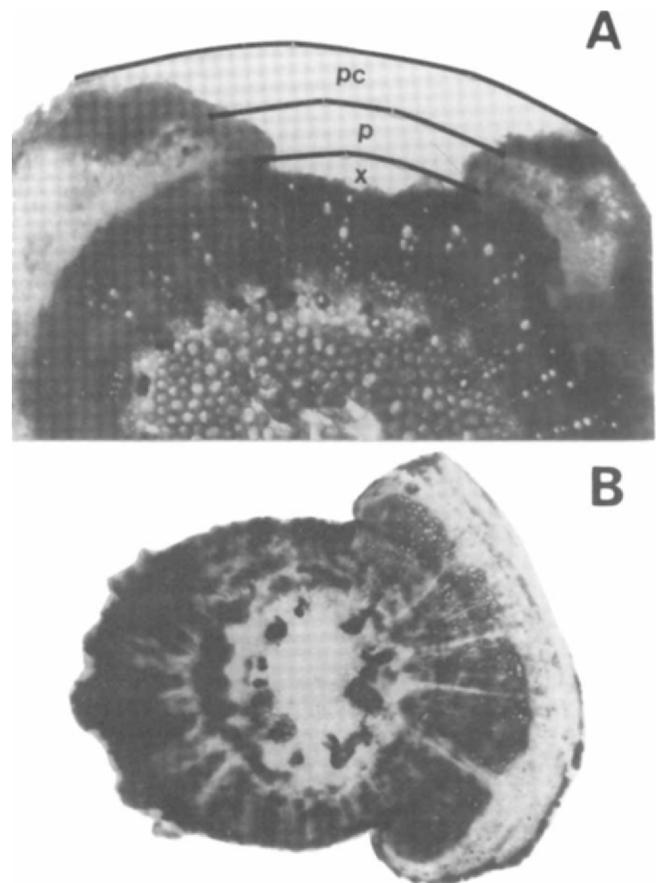


Fig. 1A. Cross section of peanut stem, illustrating the method of calculating the percent damage to various tissues. PC represents the periderm and cortex, and P is the phloem. Areas were estimated with a planimeter by sequentially removing the labeled areas from a photocopy of the cross section. **B.** *E. lignosellus* damage to the root-hypocotyl region. Note extensive damage to periderm, cortex, and phloem tissues.

0.20 ± 0.94 mm below the soil surface. Thus, most feeding sites occurred on the mainstem at the soil surface.

Most feeding sites were as long as they were wide. The average maximum length of a feeding site was 4.94 ± 0.26 mm, and the width was 4.72 ± 0.29 mm. The number of plants with a given number of feeding sites declined linearly with increasing number of sites (Fig. 3). More than 75% of the plants that were examined had ≤ 3 feeding sites.

Discussion

The lesser cornstalk borer caused significant injury to the periderm, cortex, and phloem on mainstems of peanut plants. Injury to phloem in the root-hypocotyl region of mainstems could affect nutrient transport to roots and possibly reduce turgor pressure due to injury to the outer cells of the xylem. Wilting of peanut plants that were severely injured by lesser cornstalk borer larvae has been observed in the field. Injury to phloem tissues in the root-hypocotyl region should lead to a reduction in root dry weight due to decreased availability of carbohydrates available for root production, unless an injured plant could compensate for the loss of nutrient-conducting tissues by increased translocation of carbohydrate in phloem tissues adjacent to feeding sites. A

Table 1. Mean percent injury to stem tissues caused by lesser cornstalk borer larvae.

Tissue	N ^a	% Injury ^b
Total Area	22	19.53 ± 2.77 b
Periderm and Cortex	22	31.67 ± 3.72 a
Phloem	22	16.78 ± 2.70 b
Xylem	22	0.19 ± 0.13 c

^aNumber of mainstem cross sections examined.

^bMean ± std. error mean. Means followed by the same letter are not significantly different according to a Waller-Duncan K-ratio mean separation test (K=100). Actual means are shown, but mean separations are from arcsine transformed data, as recommended in Steel and Torrie (1960).

decrease in root dry weight from *E. lignosellus* feeding has already been reported (13). In our current study, feeding injury to the root-hypocotyl region was so extensive in some cases that it is unlikely that adequate translocation of carbohydrates in remaining phloem cells could have compensated for tissue loss (Fig. 1B).

Our working hypothesis is that root growth declines with increasing larval injury to phloem and xylem in the root-hypocotyl region. The decline is due to: a) reduction in assimilates translocated from the shoot to the root system caused by insect injury to phloem tissues which limits carbon allocation to the roots, and thus the overall size of the root system, and b) a reduction in net carbon fixation in the leaves caused by stomatal closure due to reduced water conduction from roots as a consequence of direct and indirect insect injury to xylem tissue that limits water absorption and conduction. Parts "a" and "b" of the hypothesis assume that the plant cannot adequately compensate for loss of phloem or xylem by increasing translocation of photosynthates or conduction of water in vascular tissues adjacent to injured areas. This is a reasonable assumption because nutrient-conducting tissue in the root-hypocotyl region is the only pathway in this region by which photosynthates and water can be conducted. Thus, injury to phloem and xylem in this

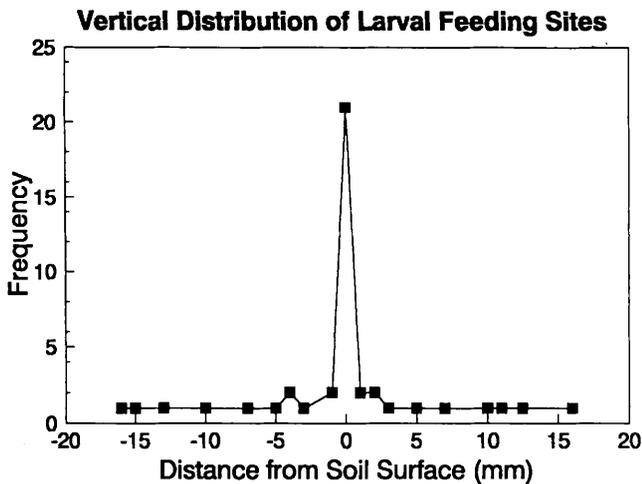


Fig. 2. Vertical distribution of *E. lignosellus* feeding sites on peanut plant mainstems. Negative numbers denote sites below the soil surface. Frequency refers to the total number of sites examined that were at a given distance from the soil surface.

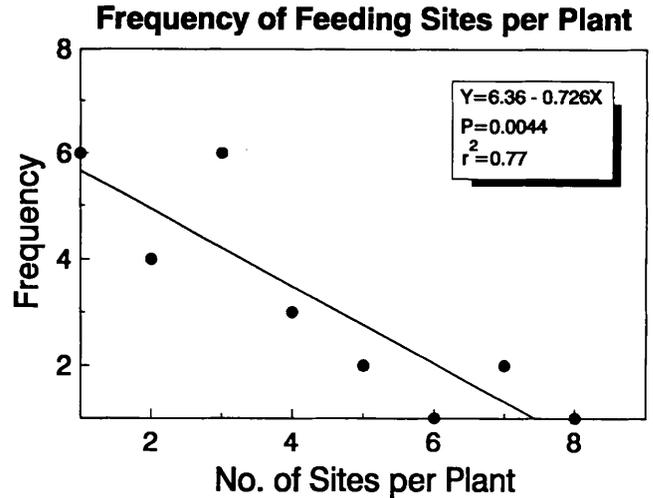


Fig. 3. Distribution of the number of feeding sites per plant caused by *E. lignosellus*, and regression equation relating number of plants with a given number of sites to the number of sites per plant. Frequency refers to the total number of plants examined that had a given number of feeding sites.

region should affect water and photosynthate movement to the rest of the plant. Part "a" assumes that root growth is proportional to the amount of fixed carbon or photosynthate available for growing new tissue, and that less carbon is available for storage and growth when translocation is reduced by loss of functional phloem. Part "b" assumes that the conductive efficiency of the root system is limited due to the change in cross-sectional area of functional xylem in the root-hypocotyl region available for water movement and that the absorptive capacity also declines as root growth is limited by reduced assimilate flow to the roots. This is a less likely effect than the effects described in part "a", because of the small amount of observed injury to xylem tissues. However, a small amount of injury could lead to the formation of an embolism, which could block water movement.

Wound depth has been used as an indicator of the physiological impact of insect feeding to stems or taproots (17), with greater depth indicating greater injury. Larvae almost always ate down to or into the xylem in our study, disrupting phloem cells, destroying the vascular cambium that produced additional phloem and xylem cells, and exposing the xylem to infection and/or desiccation. A portion of the xylem that was exposed to the air was often discolored and necrotic. This was not included in the estimates of percent injury that were calculated for larval feeding, because we estimated only the tissue that was removed. However, it is still injury resulting from larval attack, and the inclusion of the necrotic tissue in a calculation of injury to xylem would increase the injury by several percentage points. These results, when coupled with the crop loss study (13), indicate that *E. lignosellus* feeding is a physiologically-damaging stress that reduces primarily food-conducting capacity of the plant.

Unlike plant injury from leaf-feeding insects, injury from root- or stem-feeding insects usually involves the disruptive of tissues that are important in nutrient conduction or protection from diseases. Plant responses to root- or stem-feeding injury have included stunting (14), decreasing leaf area production (9), diminished root, pod, and/or seed dry weight (6), reduced xylem sap pressure (16), a decline in

photosynthate flow in phloem tissues (9), and decreased nitrogen-fixing activity (9). Wilting of plants attacked by stem- or root-feeding insects is a common symptom of injury to the stem or root (e.g.; 4, 8), strongly suggesting a decline in water transport within the plant. Observed wound-healing mechanisms in herbaceous plants include the production of adventitious roots and partial to complete production of bark tissue (cork) over the injured sites (23, 15). However, we have not observed any appreciable wound healing responses to *E. lignosellus* injury in peanuts. Periderm can act as a deterrent to fungal penetration and colonization, so the removal of periderm could expose plants to infection by secondary pathogens, such as whitemold, *Sclerotium rolfsii* Sacc.

This study delimited the vertical and horizontal distribution, and the average length and width of *E. lignosellus* feeding sites on greenhouse-grown peanut plants. These results provide a basis for additional studies simulating *E. lignosellus* injury to the root-hypocotyl region by experimentally removing tissue regions of the same length and width as the feeding sites in this study. Artificial injury studies will permit separation of pod injury from root-hypocotyl injury and determine the number of feeding sites on the root-hypocotyl region that cause economic losses in yield. It seems likely that several sites on a stem should increase percent injury. However, an additional site may not simply double the percent damage, due to the proximity of sites to each other in the horizontal and vertical planes on the stem. For example, a second feeding site located in the same horizontal location but in a different vertical location may have little or no effect, because only one might block the vertical movement of photosynthates to the root. With the size and depth of each feeding site measured, the number and location of feeding sites can now be manipulated to determine the plant's response to one or more sites, and whether increases in the rate of carbohydrate translocation occur in phloem tissues adjacent to the feeding site(s).

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