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# FEEDING HABITS OF THE TOMATO BUG, *CYRTOPELTIS (ENGYTATUS) MODESTUS* (DISTANT) WITH SPECIAL REFERENCE TO THE FEEDING LESION ON TOMATO

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## INTRODUCTION

The present study concerns the feeding habits of the tomato bug, *Cyrtopeltis (Engytatus) modestus* (Distant), and the unusual feeding lesions produced on tomato plants (fig. 1). Existing information on the feeding habits and the taxonomic status of this insect have been incorporated in this bulletin. During the five-year period of this study, 1940–1945, the tomato bug was a serious pest of tomato in Hawaii and was difficult to control with the insecticides available at that time. At present it is effectively controlled by DDT.

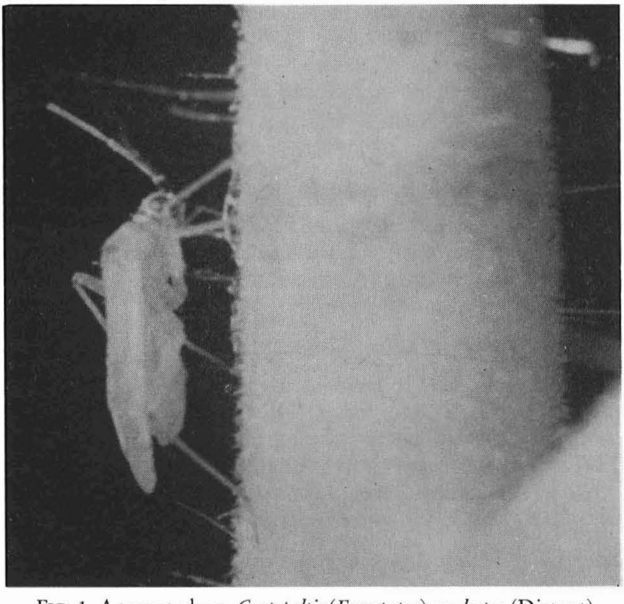

FIG. 1. A tomato bug, *Cyrtopeltis (Engytatus) modestus* (Distant), feeding at site of young lesion on tomato stem.

### *Taxonomic Status*

There has been much confusion in connection with the scientific name of the tomato bug. It was first described by Reuter (*65*) in 1875 as *Engytatus geniculatus*. In 1909, however, he placed it in the genus *Cyrtopeltis*, which he believed to be synonymous with *Engytatus* (*46, 18*). According to Knight (*46*) and China (*18*), however, the epithet *geniculatus* Reuter could not be used because it is preoccupied in *Cyrtopeltis* by *geniculata* Fieber. Since Uhler (*87*) had stated that *Neoproba varians* Distant was a synonym of *Engytatus geniculatus* Reuter, *varians* Distant was the next available name for the species. The problem became further involved when Reuter in 1910 reversed his viewpoint of 1909. Knight (*46*), after a careful comparison of *Cyrtopeltis geniculata* Fieber and *Engytatus geniculatus* Reuter, concluded that *Cyrtopeltis* and *Engytatus* were congeneric. In 1946 Usinger (*88*), in his study of the insects of Guam, came to the conclusion that *Cyrtopeltis* (type: *geniculata* Fieber) and *Engytatus* (type: *geniculatus* Reuter) were distinct genera. However, Carvalho (*15, 16*) in 1947 and 1952 placed *Engytatus* as a synonym of *Cyrtopeltis* in his publications on the classification of the Miridae.

Recently China and Carvalho (*19*) conducted a thorough study of the genitalia of this group and concluded that the genital characters would necessitate establishing a number of new genera. They decided to include all very closely related groups other than *Dicyphus* and *Macrolophus* as subgenera under *Cyrtopeltis* Fieber. Furthermore, after examining the type specimen, they found that Distant's species, *varians*, is quite distinct from "*geniculatus*." On this basis, they gave *Cyrtopeltis* (*Engytatus*) *luridus* (Gibson) as the name of the tomato bug. However, due to a curious *lapsus*, China and Carvalho placed *Neosilia modesta* Distant, 1893, in synonymy under *luridus* Gibson, 1917, on page 160. Usinger (*in litt.*) reports that he called this inconsistency to the attention of Dr. China in conversations in London in 1953 and that Dr. China agreed that *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) is the correct name.

*Cyrtopeltis* (*Engytatus*) *modestus* (Distant) is commonly known in Puerto Rico as the large tobacco suck-fly (*51*), in California as the tomato suck-fly (*23*), and in Hawaii as the tomato bug (*30, 33, 34*).

### *History and Importance of the Tomato Bug in Hawaii*

In 1924 Swezey (*76*) first reported the presence of *C. modestus* on tomato in Manoa Valley, Oahu, and in 1925 reported it from widely scattered regions on Oahu (*77, 78*). Between 1927 and 1935, the tomato bug was collected from Kauai (*80*), Molokai (*83*), Maui (*79*), Hawaii (*81*), and Rabbit Island (*10*). Holdaway and Look (*33, 34*) reported the tomato bug abundant in hot, dry regions but not in cool, moist regions.

From 1937 to 1947, the tomato bug became increasingly more important to tomato production in Hawaii. It reached its peak of importance soon after 1941 when the Hawaii Agricultural Experiment Station (*75*) introduced a tomato variety which was found suitable for production at low elevations and high temperature (31). When DDT became commercially available in 1947, this insecticide was found to be highly toxic to the tomato bug, and the extensive use of DDT has practically eliminated the tomato bug from tomato plantings (32).

### *Distribution and Feeding Habits Mentioned in the Literature*

*C. modestus* has been reported also as a pest of tomato from Cuba (*8, 9*), Puerto Rico (*22*), southern California (*23*), South Carolina (*66*), Delaware (*52*), Arizona and Texas (*44*), and Georgia and Mississippi (*47*). It is a pest on tobacco in Brazil (*56*), Puerto Rico (*51, 8*), and Cuba (*8, 9*).

The tomato bug has been reported on many plants in addition to tomato and tobacco: *Jatropha gossypifolia* L. (*22*); squash vines (*40, 33, 91*); *Heterotheca grandiflora* Nutt.(*82*); potatoes and eggplant (*30, 33*); ornamental geraniums and a species of ornamental *Plumbago* (*33, 91*); watermelon, dishcloth gourd, and the hairy morning-glory (*Merremia aegyptia* (L.) Urban = *Ipomoea pentaphylla* (L.)) (*34*); garden bean (*35*); *Lagenaria* sp. (gourd) (*91*); *Gynandropsis pentaphylla* (L.) De

Candolle (*48*); *Bougainvillaea* sp., *Solanum sisymbrifolium* Lam., a type of marigold (*Calendula* sp.), and pumpkin leaf.* According to Uhler (*87*), the tomato bug in the West Indies lives on various kinds of weeds growing on roadsides and in neglected gardens.

The tomato bug attacks chiefly the younger growing parts of tomato plants (*44, 66*), and its feeding results in a type of injury reported by various workers as girdles (*44*), feeding scars (*33*), and feeding rings or red rings (*41, 66, 23*). Apparently these workers are referring to the same type of injury or lesion, which is described most appropriately by the term "feeding ring." The stem or petiole is weakened at the site of the feeding injury, and when bent breaks readily. Later the injured portion becomes swollen and quite resistant to breakage (*44, 41, 66*). The bug produces feeding rings also on the morning-glory, dishcloth gourd (*34*), and tobacco (*85*).

According to Illingworth (*37, 38, 39*), the feeding of the tomato bug on tomato blossoms results in blossom drop. Fullaway (*28*) observed that feeding on flower stems causes shedding of blossoms. Reynard (*66*), however, reported that in South Carolina the tomato bug attacks only the stems and leaves of tomato and not the flowers.

Holdaway and Look (*33*) observed that tomato plants infested with tomato bugs produce more flower-buds than uninfested plants, but flower production is retarded, the flowers are reduced in size and number, and flower shedding is more marked than in uninfested plants. The infested plants are bushy and have swollen nodes and short internodes. Moreover, the date of first fruiting is later in bug-infested plants and the yield is reduced.

Illingworth (*41*) reported that tomato plants infested with tomato bugs develop abnormal fruits with rings of scars that appear to be egg-punctures.

For tobacco, Moreira (*56*) reported that *C. modestus* feeds on the leaves, which turn yellow and dry prematurely. Leonard (*51*) and Bruner and Scaramuzza (*9*) reported that the feeding of the bug on tobacco flower-buds causes them to absciss and thereby reduces the number of potential seed capsules. Thomas (*85*), however, stated that the principal economic damage is caused by breakage of the tobacco flower stalks at the sites of feeding rings, and observed that there appears to be no permanent injury caused by the feeding of tomato bugs on tobacco leaves or stems in the early stages of plant growth. On young tobacco, the adults and nymphs are usually found feeding on petioles and leaf veins, whereas on maturing plants they are found also on seedstalks, buds, blossoms, and seed clusters.

The tomato bug, besides being herbivorous, is carnivorous on aphids, mealy bugs, *Dicyphus minimus* Uhl., hornworm eggs, newly hatched hornworms, eggs and young larvae of *Heliothis* spp., and other small insects (*22, 69, 42, 53, 9, 33, 34, 17, 85, 91*).

## THE FEEDING LESION

*Procedure*

The development of lesions on tomato by the feeding of *C. modestus* was observed on plants under three different conditions: (1) plants enclosed within cloth-celluloid cages, (2) parts of tomato stems and petioles within glass-tubing cages, and (3) plants growing in the field. The cloth-celluloid cage, developed in Hawaii by the Pineapple Research Institute, consisted of a sheet-metal framework covered on the sides with organdy cloth, and on the top and front with celluloid (fig. 2A). Two openings, one on each side, permitted handling the insect on the plant. The cage

* Data on the last four plants are unpublished records of the Department of Entomology, Hawaii Agricultural Experiment Station.


FIG. 2. *A.* Tomato plant covered with cloth-celluloid cage. *B.* Glass-tubing cages fastened to stems and petiole of tomato plant.

measured 15 x 15 x 27 inches and fitted directly into 10-inch clay pots by means of a circular extended rim.

The glass-tubing cage was a modification of the type used by Ewing (*25*), King and Cook (*45*), and McGarr (*55*). Instead of a vial with a closed end as was used in their studies, a piece of glass tubing with open ends was held in place with cellulose tape on the stem or petiole (fig. 2B). The end of the tube placed on the plant was ground to fit the round stem. Before the cage was attached to the stem, a piece of cloth (flannelette) with a hole in it was placed between tube and stem to make a close fit and to prevent injury to the stem. The open end of the tube was plugged with cotton after the insect had been introduced into the tube.

Observations on the formation of feeding lesions were made on three series of plants in cloth-celluloid cages. The plants were germinated in an insect-proof greenhouse. Except for the first series, the plants were transplanted to 10-inch clay pots and covered directly with cloth-celluloid cages. In the first series the plants were hardened for several days in a large outdoor screen cage. Since the tomato bug was able to enter the screen cage, the plants were examined carefully for any visible lesions before they were used. In Series I, the bugs were introduced one to each cage when the plants were 12–18 inches high, 7–18 inches in Series II, and 6–10 inches in Series III. The bugs were starved about 3 hours prior to introduction so that feeding would take place soon after caging. Half of the bugs were males, the other half, females. Bugs that died during the first 2 days of the study were replaced.

The plants were observed three times daily: morning, noon, and late afternoon. At each observation, records were taken of the feeding of the bug on the particular region of the plant and also of the development of lesions at that site. The observations were discontinued when the plants grew to the top of the cages. This occurred in 12, 15, and 21 days, respectively, for the three series.

The maximum and minimum temperatures varied widely within the cages. The temperature ranged from 14° to 35° C. in Series I, from 16° to 36° C. in II, and from 16° to 37° C. in III.

The formation of feeding lesions by tomato bugs enclosed within glass-tubing cages was studied on plants that were 10–15 inches in height. The cages were attached to stems and petioles on the upper halves of the plants. In one of the series in which 36 cages were placed 6 each on six plants, observations were made once in the morning and once in the afternoon, to follow the development of the feeding lesion. In two other series, in which 176 cages were used on 36 plants, the area within the cages was marked with India ink, and the portion of the stem attacked was preserved for sectioning. One group of stems was preserved immediately after exposure to feeding for 1 hour, 6 hours, 12 hours, 24 hours, 48 hours, and 5 days; another group was collected after 48 hours exposure to feeding for 12 hours, 24 hours, 48 hours, and 5 days.

Plants of another series were pierced to a depth of approximately 1 millimeter with *minuten nadeln* to compare the lesions thus formed with the feeding lesions of the bug. Some of the pins were unsterilized, while others were sterilized by boiling in distilled water for a half-hour. In one series the plants were pricked in definite regions of the stems and petioles ten times daily, and the regions were preserved for histological examination after intervals of 24 hours, 48 hours, 3 days, and 5 days.

*External Characteristics.*

In South Carolina, Reynard (*66*) observed that *C. modestus* girdles the stem with punctures approximately 1 millimeter in depth. Soon after injury, marks are barely discernible, but they later turn reddish brown and are usually raised above the normal surface of the stems. Holdaway and Look (*33*) reported that feeding scars appear approximately 40 hours after the beginning of the attack.

In the field and in cages the tomato bug has been observed to form complete or incomplete brown feeding rings by sucking in a series of punctures that partly or entirely encircled the stem or petiole.* The bug may feed on the same region for as long as one or two days. The injury is at first a faint yellow or yellowish brown spot, which on further feeding develops into a fine brown streak encircling the stem. The brown streak then collapses below the surface of the stem to form a sunken ring. Later, usually after the bug has ceased feeding, this region swells to form a small tumor. When the injury is severe the lesion may split and expose internal tissues.

The period from the first signs of discoloration to the collapse of the epidermis has been designated as the young lesion stage; the period when the epidermis sinks below the surface has been designated as the mature lesion stage; and the development of the tumor-like growth as the old lesion stage (fig. 3A, B, C). Whether or not an injury passes through all three stages depends upon the length of time the bug feeds at that region. A bug feeding for a short period produces only a young lesion, which may not collapse or form a tumor, and which may disappear entirely. Ewing (*25*), however, stated that the length of feeding time of mirids seemed to have little if any effect upon the extent of injury.

The first sign of a feeding lesion usually appeared within 24 hours after the tomato bug was introduced into the cage. In several instances, lesions were observed within 12 hours, especially on the petioles and leaf blades. Feeding spots were observed after the plant was exposed to the feeding of the bug for 3 to 8 hours. In one instance, in which an insect was left in a glass-tubing cage for only 1 hour, a very faint spot developed 24 hours later.

The feeding lesion on the stem usually develops in the manner previously described. When the brown ring is formed, the stem is weakened at this region, and snaps readily when bent (fig. 4). However, in the old lesion in which the tumor-like growth is produced, the plant apparently has recovered and has become resistant at this point to bending. These characteristics have been reported also by Jones (*44*), Illingworth (*41*), and Reynard (*66*).

The development of the lesion on the petiole is similar to that on the stem, but feeding is usually confined to the upper half of the petiole. If feeding extends around the petiole, the lower portion usually collapses, and the leaf bends downward and grows at an angle. The leaf later recovers and straightens out. On the blades, the tomato bug usually feeds on the large veins, where feeding lesions may be formed. Occasionally, it feeds on the smaller veins or veinless areas, where clear transparent spots are formed. These spots turn yellow or brown, and may drop out of the leaf, forming "shot holes."

On flowers, the bug feeds most frequently on the base of stamens, where brown feeding spots are produced. When feeding is severe, the entire group of stamens shrivels and dries.† The style, except for its tip, and the ovary are injured infrequently and usually do not show any discoloration. The bug may also feed on the

* A similar type of injury or girdling is produced by the three-cornered alfalfa hopper, *Stictocephala festina* (Say), on alfalfa and cotton (*26, 29*), and by the buffalo treehopper nymphs (*Ceresa bubalus* (Fab.)) on potatoes (*27*). The senior author has observed *S. festina* (Say) feeding on a brown ring on the stem of pole beans at Waipahu, Oahu.

† A midge, *Contarinia* sp., feeds on tomato blossoms and probably causes shriveling of stamens also.

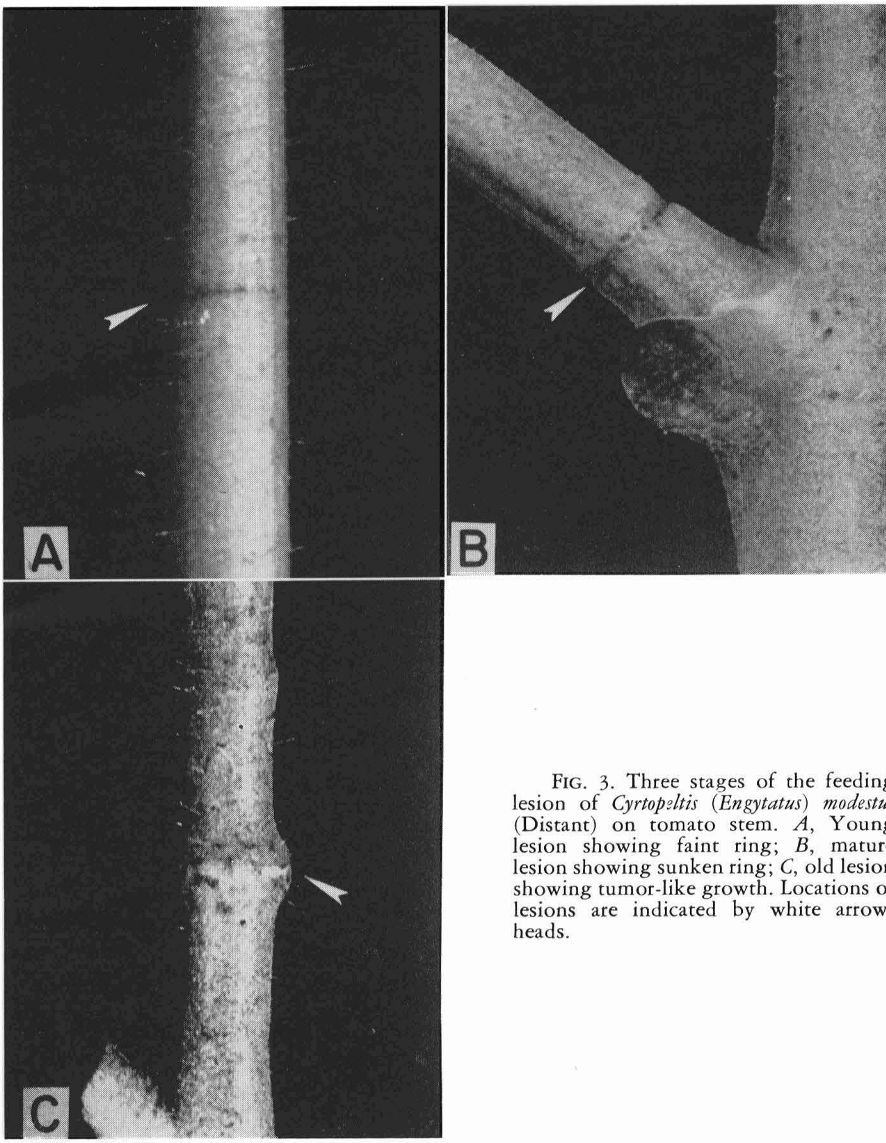


FIG. 3. Three stages of the feeding lesion of *Cyrtopeltis (Engytatus) modestus* (Distant) on tomato stem. *A*, Young lesion showing faint ring; *B*, mature lesion showing sunken ring; *C*, old lesion showing tumor-like growth. Locations of lesions are indicated by white arrowheads.

peduncle and form brown feeding rings. It occasionally feeds on the fruits and produces small brown spots.

The external appearance of lesions produced artificially by puncturing with *minuten nadeln* was somewhat similar to that of the feeding lesions. The artificial lesions became brown and discolored, and later were seen to swell. The injured area was also weakened and snapped readily when bent. These lesions differed from the feeding lesion in showing minute holes where the pins, which are much larger than the insect's stylets, had pierced the tissues.

*Internal Characteristics*

The plant material on which the bugs were permitted to feed for different lengths of time and that on which lesions were produced artificially with needles, were fixed in medium chrom-acetic acid solution. Feeding lesions representing the different stages were also collected from the field and preserved for histological study. Some of the latter tissues were fixed in formol-aceto-alcohol solution. The tissues were dehydrated by Johansen's tertiary-butyl alcohol method and embedded in paraffin (*43*). The infiltration process with paraffin was much more gradual than directed by Johansen, since his method resulted in shrinkage of the tissues and rupture of the epidermis. Serial sections were cut at 10 to 14 microns, and stained with safranin-fast green.

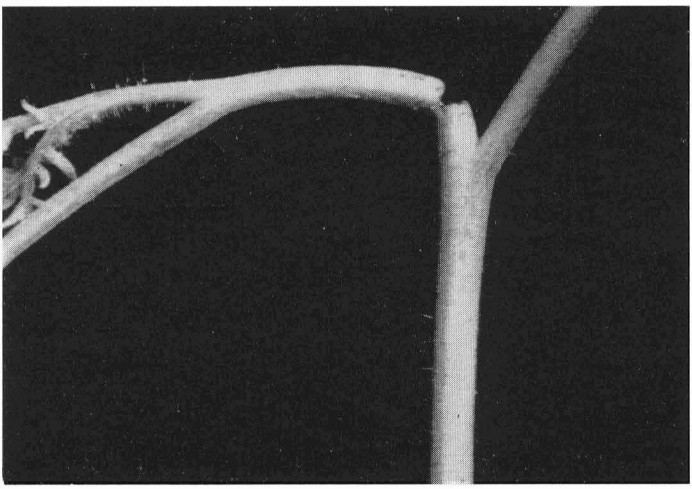

FIG 4.. Tomato stem broken at site of feeding lesion of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant).

So far no thorough histological examination has been published on the feeding lesion produced by *C. modestus*. Illingworth (*41*) has reported that sections through the rings showed dead, corky cells with no suggestion of egg punctures. Jones (*44*) observed brownish discoloration in cortical tissues.

The reaction of tomato tissues to the feeding of the tomato bug was found in this study to follow closely the stages presented by Bloch (*6*, *7*) in the wound healing in higher plants. The stylets of the tomato bug penetrate intracellularly through the tomato tissues (fig. 5A). The pierced cells die. The nuclei of the cells bordering the feeding puncture tend to lie on the side of the cells nearest the puncture. Horsfall (*36*) and Smith (*72*) have observed a similar tendency in the nuclei of the cells lying beside punctures made by aphids. Bloch (*6*) stated that some of the earliest visible effects of wounding are "traumatotactic" movements of nuclei and plastids toward the sides of the cells facing the wound. In the feeding lesion of the tomato bug, the nuclei of cells adjacent to the feeding puncture are large with one or two prominent nucleoli, and the chromatin granules take a darker stain than those of other cells. The cells bordering the puncture enlarge and divide in

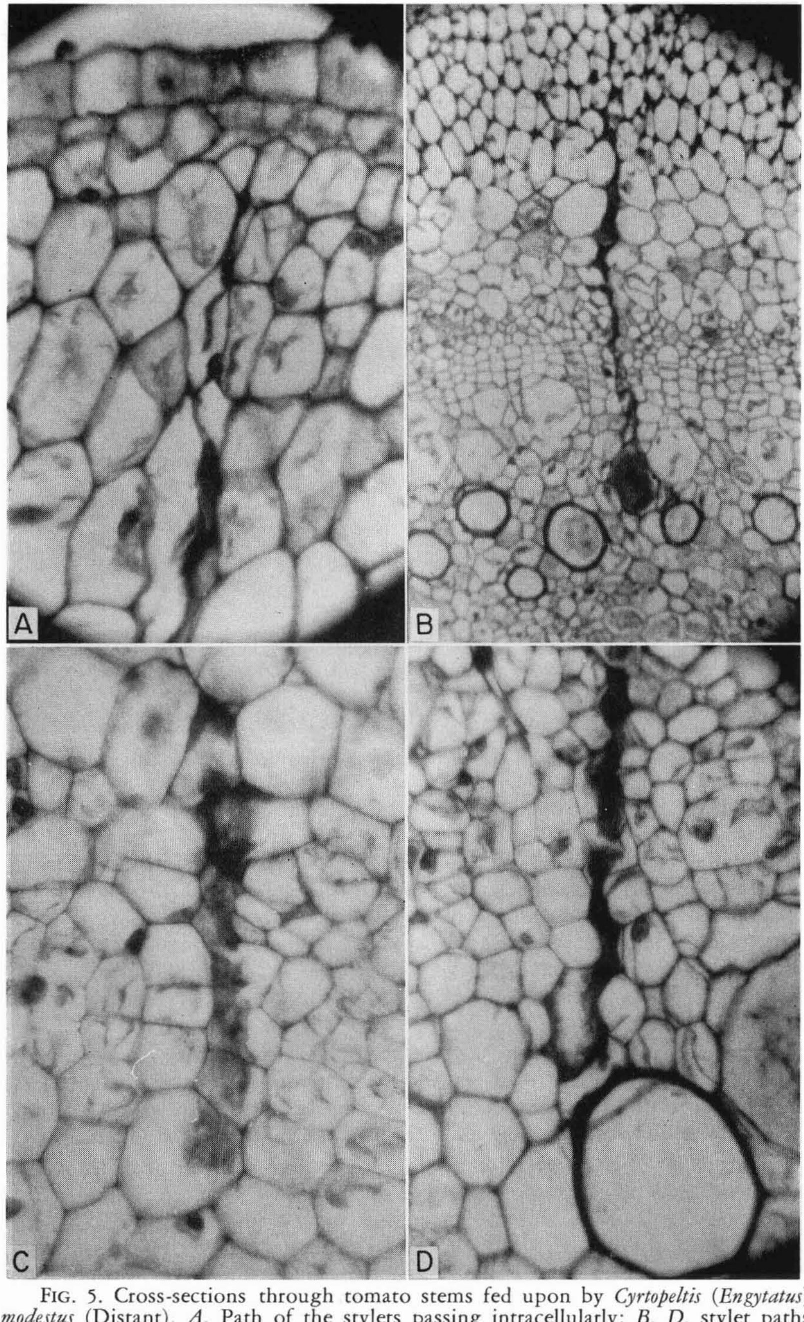


FIG. 5. Cross-sections through tomato stems fed upon by *Cyrtopeltis* (*Engytatus*) *modestus* (Distant). *A*, Path of the stylets passing intracellularly; *B*, *D*, stylet paths extending directly to xylem vessels; *C*, stylet path indicated by collapsed cell contents within row of cells of vascular bundle. Sections stained with safranin and fast green.

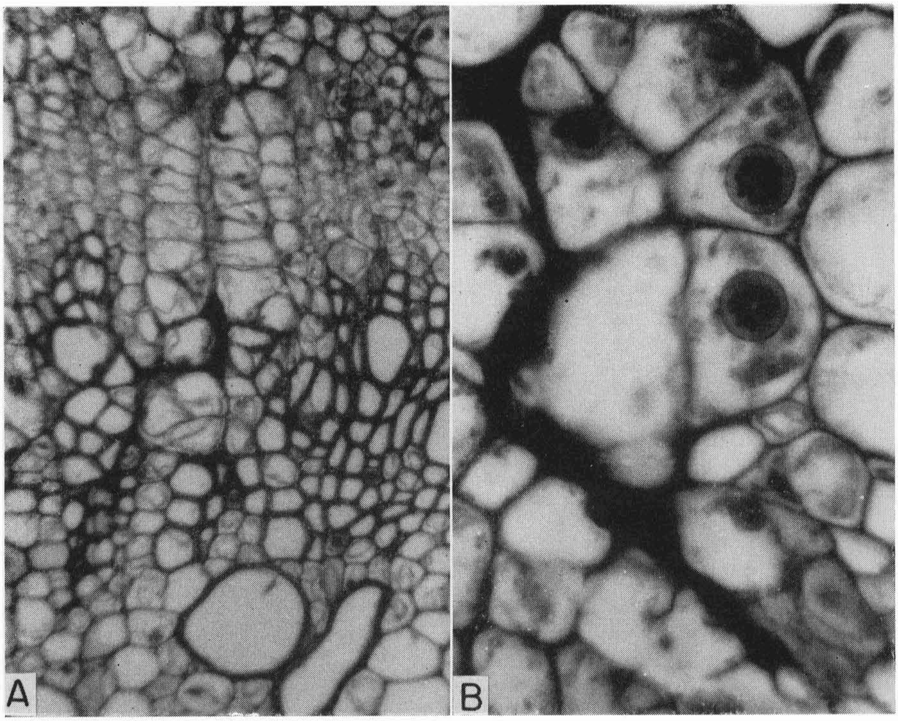


FIG. 6. Cross-sections through tomato stems showing reaction of cells to injury by the feeding of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant). *A*, Enlarged cells and newly-formed cells along stylet path; *B*, wound reaction products within cells. Sections stained with safranin and fast green.

a plane parallel to the stylet path. The pressure exerted by enlarging and dividing cells presses the walls of dead cells together, forming a reddish-brown streak of cell walls and dead protoplasm extending inward from the epidermis (fig. 5B). This brown streak superficially resembles the stylet tracks that have been observed in tissues fed upon by aphids and other Homoptera (*36*, *72*, *45*, *70*, *5*, *84*, *64*). King and Cook (*45*) have occasionally observed brownish streaks in cotton tissues injured by mirids.

In certain sections exposed to the feeding of the tomato bug for 12 to 48 hours, a collapsed mass of cell contents formed a line along the path of the stylets (fig. 5C, D). The line of cell contents was found most frequently within the vascular bundle. This cellular reaction may have resulted from a mild toxic secretion.

The cytoplasm of the pierced cells collapses within 6 hours after feeding. After 12 hours, the cells neighboring the stylet path begin to enlarge. Within 24 to 48 hours, the dead cells have collapsed to a thin brown line (fig. 5B, 7A). The cells adjacent to the injury, particularly those of the vascular bundle, are stimulated in growth and a few newly-formed cells may be found (fig. 6A). Within the cells, there are small spherical bodies which stain with safranin and are apparently wound reaction products.* Painter (*60*) has reported glistening oval or round particles,

* Fresh free-hand sections failed to give a positive test for tannin with ferric chloride solution.

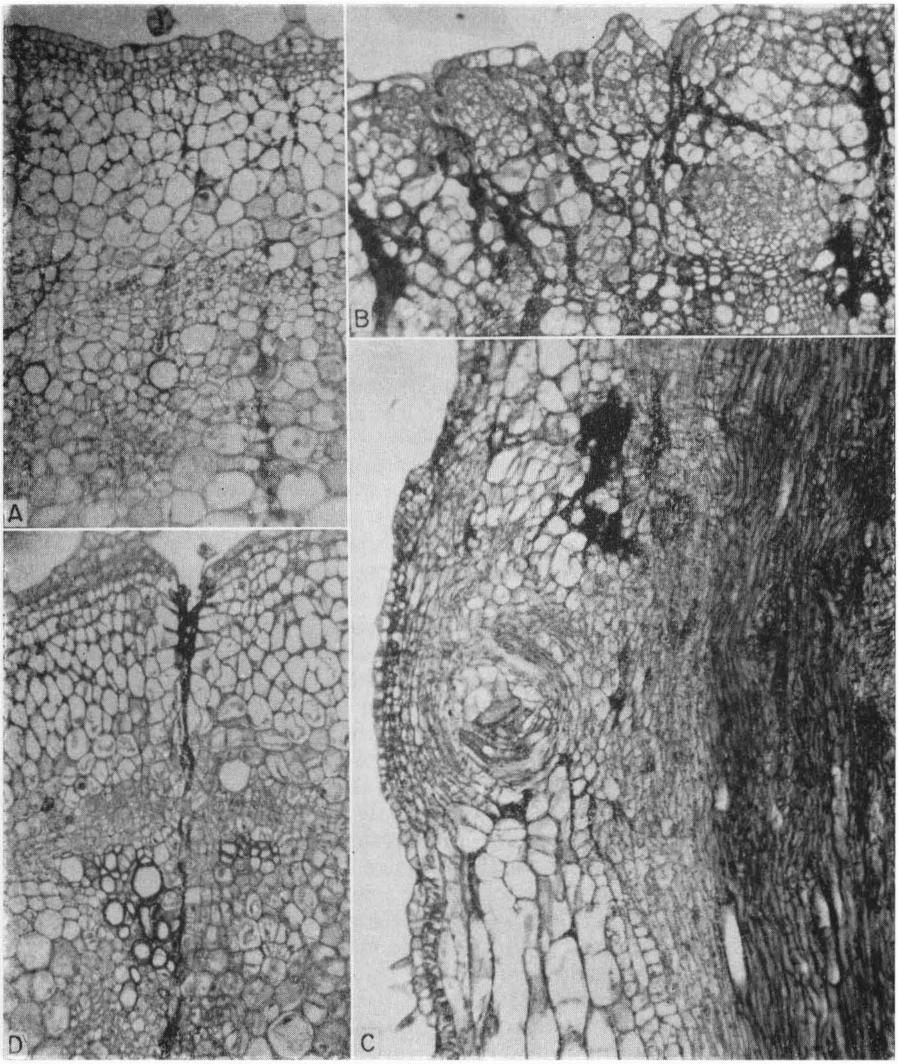


FIG. 7. Sections through tomato stems at sites of lesions produced by *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) and by puncturing with *minuten nadeln*. *A*, Cross-section through young feeding lesion; *B*, cross-section through mature feeding lesion; *C*, longitudinal section through old feeding lesion, showing distorted stele and wound tracheids in cortex; *D*, path of *minuten nadeln* three days after stem was pierced. Sections stained with safranin and fast green.

often with a darker rim, in the injury of *Psallus seriatus* Reut. on cotton. These particles, according to him, resembled spores of fungi. King and Cook (45) found peculiar, deeply stained, granular material which they reported as being purely secondary or accidental in occurrence and not likely a fungus.

Longer feeding by the tomato bug results in an increased number of feeding streaks and an increase in the size of such streaks within the feeding lesion (fig. 7B). Numerous cells become enlarged, and cell division is intense. The red-stained bodies within the cells increase in size, and range from a mass of minute particles to large glistening bodies with a dark center (fig. 6B). Some of these bodies also stain yellow in color. The wound parenchyma replaces the injured elements of the vascular bundle, and the stele becomes perforated by rows of newly-formed irregular parenchyma cells.

The majority of the stylet tracks end in the vascular tissue, pith, and internal phloem. Several of the tracks ended in a xylem vessel that was sometimes filled with a coagulated mass (fig. 5B). Smith (*73*) stated that occasionally the xylem vessel in tissues fed upon by mirids becomes clogged by a dark-staining material.

Binucleate cells were seen occasionally in the sections. Bloch (*6*) stated that in wound tissue the apparent binucleate cells are often the result of daughter nuclei at telophase appearing in one plane; accordingly, not a multi-nucleate condition. Within the feeding lesion, no cell plate was observed in the binucleate cells.

The histology of the young feeding lesion is similar to that of tissues exposed to 24 hours feeding (fig. 7A). The mature lesion presents a pathologic histological picture (fig. 7B). Numerous reddish-brown streaks pass through the tissues; enlarged cells and newly-formed cells are evident; the vascular stele is separated into scattered bundles by wound parenchyma and appears reduced in size. The epidermis appears normal except for the cells pierced by stylets. In severe injury, however, portions of epidermis are destroyed and are later replaced by cork cambium developing in the cortex. Part of the dead cells and cell walls within the tissue have been reabsorbed, especially in the region of vascular tissue.

In old lesions, the vascular ring is continuous but very distorted at the region of severe injury (fig. 7C). Nearly all the dead protoplasm and cell walls within the stele have been reabsorbed, but a few discolored areas may remain in the cortex and pith. Within the cortex, spherical bundles of lignified cells or wound tracheids are produced. Bloch (*6, 7*) stated that tracheid and phloem bridges are later phases of wound tissue development. Tate (*84*) reported the formation of abnormal tissues resembling pseudovascular tissues in leaves heavily infested with aphids. Gall wood or wound wood formation in the stem canker caused by *Helopeltis bergrothi* Reut. on mango has been reported by Leach and Smee (*50*), and on tea by Leach (*49*).

The internal characteristics of lesions in the petiole appear to be similar to those of the stem. However, most of the stylet paths are found on the upper half of the petiole where the cortical layer is thin and the vascular elements lie nearer to the epidermis than on the lower part (fig. 8A).

On flowers, the stylet paths occur chiefly near the vicinity of vascular traces within the stamen. Some stylet paths run completely through the stamen (fig. 8B). In severely injured stamens, the cells around vascular elements become a disorganized mass of protoplasm and cell walls (fig. 8C).

Within the artificially produced injury the punctures appear, after 24 hours, as wide fissures lined with dead collapsed cells. There is little or no cell division, but the nuclei of cells adjacent to the injury are similar in appearance to those adjacent to the path of stylets in the feeding lesion. After 48 hours, cell division begins to take place, and minute red bodies appear in the cells. After 72 hours, the fissure has closed to a narrow line which resembles the brown streak in the feeding lesion (fig. 7D). Accordingly, the histological characteristics of the artificial lesion are similar to those of the feeding lesion in the initiation of cell enlargement, cell division, absorption of dead cells, and the production of wound reaction products in the cells. They seem to differ mainly in the size of puncture.

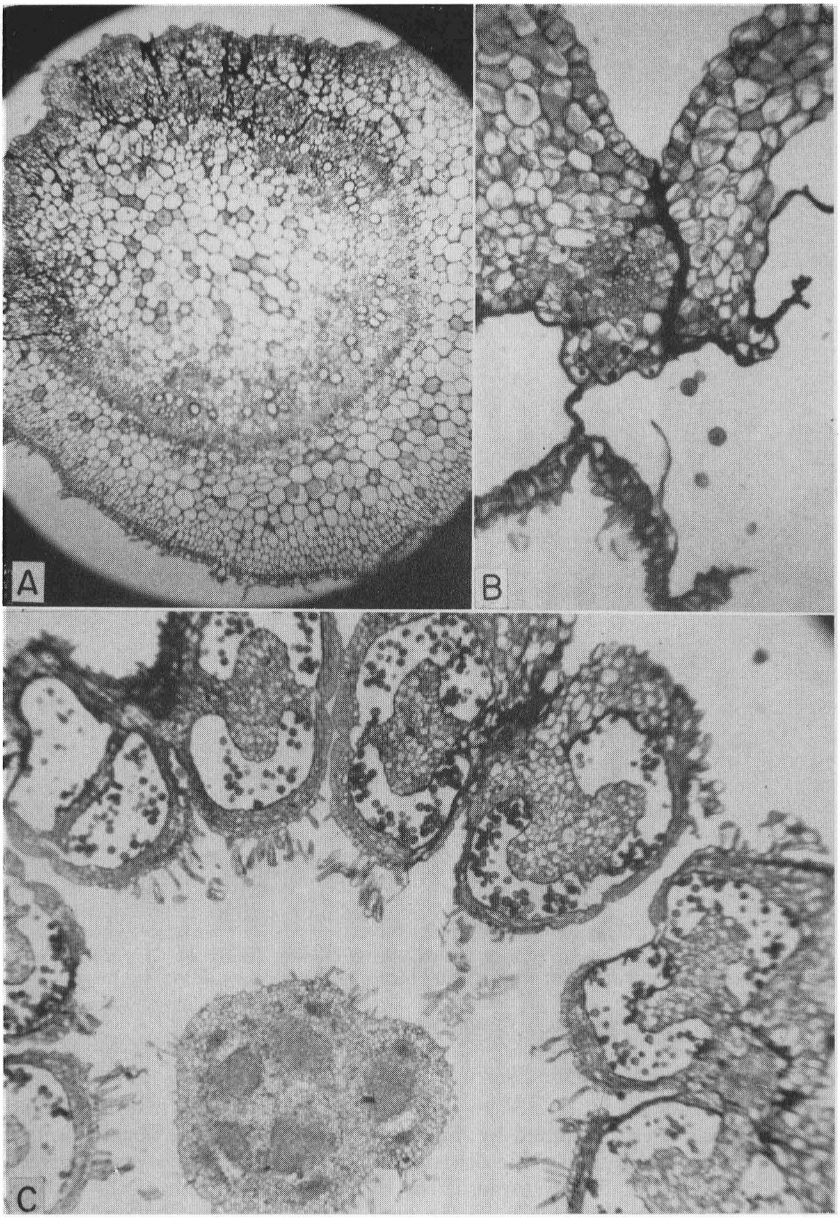


FIG. 8. *A*, Cross-section through young feeding lesion of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) on tomato petiole. Note presence of feeding punctures mainly on upper half of petiole. *B*, Stylet path extending completely through stamen of tomato flower. Note lateral path leading to vascular bundle. *C*, Severe feeding injury on stamens of tomato flower. Note absence of feeding punctures in pistil.

FIG. 9. Tomato stem whose young leaves above feeding lesion of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) have wilted but whose older leaves below feeding lesion are turgid.

## FEEDING ON VASCULAR TISSUES

### *Observations in Cages and in the Field*

The histological evidence indicates that the tomato bug feeds mainly on vascular tissues. This has been confirmed by the following field and cage observations. The feeding of the tomato bug in a ring occasionally causes structures beyond the feeding lesion to wilt (fig. 9). For example, if the bug girdles the base of the leaflet, the leaflet may wilt; if the bug feeds on the petiole, the entire leaf beyond the site of feeding may wilt. Usually the plants are able to recover from such wilting.* In the morning when root pressure is high, plants often "bleed" through the feeding lesions. Furthermore, water of guttation appeared as clear droplets at the margins of

* Puncturing the stem in a ring with *minuten nadeln* also caused wilting.

all leaf blades except those whose petioles had been recently girdled by the feeding of the tomato bug.

These observations indicate that the xylem tissue was pierced by the stylets and the water column consequently broken. Other workers also have reported the penetration of the xylem tissue by mirids (*72, 60, 45, 50, 49, 73*). It appears likely, therefore, that the tomato bug ingests substances from the xylem. To determine this, the following experiment was devised.

*Ingestion of Dyes from Xylem Tissue*

The tomato bugs were collected in the late afternoon, starved for 1 hour, and then caged individually in glass-tubing cages on stems that were placed in dyes or in tap water. The stems were cut under water to prevent air from entering and clogging the xylem. The following dyes were used in dilute aqueous solutions: acid fuchsin, 0.05 and 0.1 percent; eosin Y, 0.025 and 0.05 percent; safranin O, 0.025 and 0.05 percent; and congo red 0.1 percent. Stronger concentrations were avoided because the dyes at higher concentrations tended to diffuse into the phloem. The dyes reached the top of the stems within a few hours.

The bugs were left on the stems overnight, then anesthetized with chloroform and dissected under a dissecting microscope using natural light. The presence or absence of dyes in the digestive tract was noted.

In order to determine whether the dyes had been confined to xylem tissue, sections were cut from the stems at three different regions. The first region was about ½ inch above the topmost cage, the second about ½ inch below the lowest cage, and the third region approximately halfway between the two. The sections were cut free-hand with a razor blade that was rinsed in tap water after cutting each section.

The results (table 1) show that the tomato bug ingests substances from the xylem. Out of 40 bugs, 10 (25 percent) had dyes within the digestive tract. With the exception of the stems in the 0.05 percent safranin, none of the sections of the stems had dye outside the xylem tissue, although a negligible amount of eosin

TABLE 1. Ingestion of dyes by *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) from the xylem tissue of tomato plants after 15 hours of feeding.

| DYES USED | CONCENTRATION OF DYE | SEX OF BUG | | | |
|---|---|---|---|---|---|
| | | *Male* | | *Female* | |
| | | Dye present | Dye absent | Dye present | Dye absent |
| | *percent* | | | | |
| Acid Fuchsin | 0.05 | 3 | 3 | 0 | 0 |
| | 0.1 | 2 | 0 | 0 | 3 |
| Eosin | 0.025 | 1 | 4 | 1 | 0 |
| | 0.05 | 0 | 2 | 0 | 2 |
| Safranin | 0.025 | 0 | 2 | 0 | 3 |
| | 0.05 | 0 | 2 | 0 | 3 |
| Congo Red | 0.1 | 2 | 2 | 1 | 4 |
| Total | | 8 | 15 | 2 | 15 |
| Control | | 0 | 3 | 0 | 2 |

was found in the phloem. Of the dyes used, acid fuchsin gave the best results, and safranin was the least satisfactory.

It is unlikely that starving the bugs caused them to seek the xylem for water, since most of them did not feed at once when placed in the cages. Moreover, on some plants, nymphs that happened to be on the stems, and an adult that had escaped, had some red dye within their abdomens.

## FORMATION OF FEEDING LESIONS BY NYMPHS

Since adults of *C. modestus* produced feeding lesions readily, it appeared likely that nymphs also were capable of producing them. Other investigators have reported that nymphs of certain mirids produced injuries similar to those of adults (*71, 45, 50, 55*). The five nymphal instars of the tomato bug were placed on young tomato plants, 4 to 5 inches high, which had been germinated and grown in an insect-proof greenhouse. The observations were made in an outdoor screened cage. Since adult bugs were able to enter the screened cage, five plants were grown in cloth-celluloid cages and first instar nymphs, which appeared to be the least likely of instars to produce lesions, were placed on them.

The first instar nymphs were reared from eggs laid by females which had been caged on a tomato plant for 1 day. The plant was examined daily for emergence of the first instar nymphs. As soon as the nymphs emerged, they were placed one each on the young tomato plants. The other instars were obtained by rearing the earlier instars on pieces of petiole or stem which had been placed with the nymphs in vials. The nymphs were observed carefully each day until they molted, then transferred to the plants.

When feeding lesions developed on the plants, the plants were examined closely for molted skins which would indicate whether the insects were still in the same stage as at the beginning of the study. The instar was further verified by head measurements, which were compared with the measurements reported by McAfee.* Any injury from a faint white streak to a brown ring is reported as a feeding lesion.

All five instars were found capable of producing lesions on young tomato plants (table 2). Apparently the fourth and fifth instars produced lesions as readily as the adults, while the first three instars, especially the first instar, produced lesions less frequently. The first instar nymphs produced three of the six lesions on plants in cloth-celluloid cages. These plants were much more succulent than those outdoors.

## RETURN OF BUGS TO FEEDING LESIONS

### *Cage Observations*

During observations on the formation of feeding lesions in the cloth-celluloid cages, the tomato bug was observed to possess an unusual feeding habit of returning several times to feed at the same region. In many instances the bug moved a considerable distance from its feeding site, and yet returned the following day to the former site. Since the bug has a habit of investigating the tissues with short stabs of its proboscis, it apparently locates former feeding sites in this manner.

The 18 bugs under observation returned in at least 31 instances to their former feeding sites (table 3). In 19 of these instances, the bugs returned once to their former feeding sites, and in one instance a bug returned 7 times.

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* Unpublished report by Mrs. Ethel Lucas McAfee, formerly with the Department of Entomology, Hawaii Agricultural Experiment Station.

TABLE 2. Formation of feeding lesion by the five nymphal instars of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant)

| INSTAR | NUMBER OF PLANTS | PLANTS WITH LESIONS | PERCENT WITH LESIONS | PERIOD IN WHICH LESION DEVELOPED |
|---|---|---|---|---|
| | | | | *days* |
| 1 | 25* | 6 | 24 | 2½–5 |
| 2 | 15 | 8 | 53 | 1–6 |
| 3 | 15 | 9 | 60 | 1–2 |
| 4 | 11 | 11 | 100 | 1–2 |
| 5 | 11 | 11 | 100 | 1–2 |
| Control....... | 9 | 0 | 0 | |

* Five plants were grown in cloth-celluloid cages and first instar nymphs produced feeding lesions on three of them.

### *Field Observations*

This peculiar behavior of returning to a former feeding site was further investigated. For this study, 55 tomato plants were planted in 11 rows of 5 plants each. When the plants were 2 feet high, 40 each of the three stages of feeding lesion, 20 on petioles and 20 on stems, were tagged and subsequently examined. All except the old lesions had bugs feeding on them when they were tagged.

Lesions produced artificially by pricking 30 times in a ring with sterilized *minuten nadeln* were tagged also. In the first series of artificial lesions, the pricking was done only once. In the second series, the regions were pricked with the same number of punctures 48 hours later. Each series had 40 artificial lesions, 20 on petioles and 20 on stems.

TABLE 3. Number of occasions that adults of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) returned to their former feeding sites. Each adult was placed singly on a caged tomato plant.

| PLANTS | NUMBER OF OCCASIONS | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| A–1 | | | | | | | |
| B–1 | | | | | | | 1 |
| C–1 | | 1 | | | | | |
| D–1 | 1 | | | | 1 | | |
| E–1 | 1 | | | | | | |
| F–1 | 2 | | | | | | |
| A–2 | | | | | | | |
| B–2 | 3 | | | | | | |
| C–2 | | | | | | | |
| D–2 | 1 | | | | | | |
| E–2 | | 1 | | | | | |
| F–2 | 1 | | | | | | |
| A–3 | 2 | 2 | 1 | | | | |
| B–3 | 1 | | | 1 | | | |
| C–3 | 2 | 1 | | | | | |
| D–3 | 1 | | | | | | |
| E–3 | 4 | 1 | 1 | | | | |
| F–3 | | 1 | | | | | |
| Total.... | 19 | 7 | 2 | 1 | 1 | | 1 |

The tagged regions on the plants were scattered as widely over the plot as possible. Observations were made on 5 different days. There were two observations each day: 9:00 A.M. and 4:00 P.M. At each observation, bugs found feeding on the lesions were deliberately frightened away; hence, any bug found feeding on them at the following observation, although not necessarily the same bug, must have been attracted by the lesion.

Results of the observations (table 4) show that, under field conditions, the bugs repeatedly return to feed on the same feeding lesion and on artificial lesions. There were 10 adults and 48 nymphs attracted to feeding lesions, and 3 adults and 35 nymphs to artificial lesions. Most bugs were attracted to mature lesions, and very few to old lesions. Lesions on the stems attracted more bugs than those on the petioles. Nymphs were the predominant form that returned to the lesions, probably because adults, when frightened away from the lesion, often flew away from the plant.

Wounding plants with *minuten nadeln* in the second series of pricking 48 hours later did not increase the attractiveness of the lesions to the bugs.

*Feeding on Fresh Injury*

Since the previous experiment indicated that the tomato bug was attracted to wounds, the question arose as to whether this preference was caused by the injury itself or by the physiological changes that develop later in the tissues. The following experiment was designed to determine whether or not the bugs were attracted to newly-formed artificial lesions. Ten tomato plants, 12–22 inches high, were used. Lesions were made by pricking the stem or petiole about 30 times in a ring with sterilized *minuten nadeln*. On each plant there were five lesions on the petioles and five on the stems. A line was drawn with India ink about a half-inch below each lesion to mark its locality. After the lesions were made, the plants were enclosed in cloth-celluloid cages and about 10 tomato bugs were introduced into each cage. The bugs were collected the day before, and fed overnight on a piece of petiole. The first observation was made 1 hour after introducing the insects, and four subsequent hourly observations were made.

The tomato bugs were attracted to freshly made wounds (table 5). Within 1 hour, 3 bugs were found feeding on the lesions, and in 2 hours, 18 bugs were feeding on them. It appears that the bugs were attracted by the exuded sap and the tender wounded tissues, which could be pierced much more easily than unwounded tissue.

TABLE 4. Number of tomato bugs, *Cyrtopeltis* (*Engytatus*) *modestus* (Distant), returning to feeding and artificial lesions.

| STAGE OF BUG | STAGE OF FEEDING LESION | | | | | | ARTIFICIAL LESION | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Young* | | *Mature* | | *Old* | | *One series of puncture* | | *Two series of puncture* | |
| | Stem | Petiole | Stem | Petiole | Stem | Petiole | Stem | Petiole | Stem | Petiole |
| Adult | 0 | 3 | 2 | 5 | 0 | 0 | 1 | 0 | 0 | 2 |
| Nymph | 13 | 5 | 23 | 4 | 3 | 0 | 17 | 4 | 10 | 4 |
| Total | 13 | 8 | 25 | 9 | 3 | 0 | 18 | 4 | 10 | 6 |

TABLE 5. Feeding of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) on fresh artificial lesions on tomato plants.

| BUGS | HOURS AFTER LESION WAS MADE | | | | | | | | | NUMBER OF PLANTS | NUMBER OF LESIONS | NUMBER OF BUGS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 18½ | 27 | 42½ | 51 | | | |
| Number seen feeding.... | 3 | 18 | 22 | 23 | 19 | 10 | 21 | 9 | 21 | 10 | 100 | 100 |

## MICROCHEMICAL ANALYSIS OF LESIONS

Although the previous experiment showed that tomato bugs were attracted to fresh wounds, field observations indicated that the majority of bugs were attracted to mature feeding lesions and not to young or old lesions. It appears likely, therefore, that the physiological condition of lesions may also be a factor in causing bugs to feed on them. Accordingly, the three different stages of the feeding lesion were analyzed microchemically for reducing sugars, dextrin, starch, and protein. The feeding lesions were obtained from the field and sectioned, while fresh, at 150 microns. The knife was rinsed in distilled water after each tissue was sectioned. Sections were rinsed in distilled water before the different microchemical tests were applied. Sections were cut also from regions about a half-inch above and below the lesions, and the average reading from these two regions, whose tissues were assumed to be unaffected by the feeding of the bug, was called the control.

Readings were based on an arbitrary scale: one, two, three times, etc., that of the control reading of unaffected tissues. These readings, although not quantitative, were necessary to bring out the proportionate difference of the various substances within the tissues. Readings were taken from all tissues except the chlorenchyma and pericycle. The presence of chlorophyll made it difficult to take readings from the chlorenchyma.

The presence of reducing sugars was determined with Flückiger reagent. The sections were rinsed quickly in 5 percent tartaric acid to remove the sugars present on their surfaces. The sections were than rinsed in distilled water and placed on slides in a drop of alkali in which a knife-point of copper tartrate had been dissolved. The sections were warmed gently for 5 minutes on a slide warmer and then examined.

The presence of starch and dextrin was determined by the iodine-potassium iodide test.

Protein was detected with a 0.1 percent aqueous solution of eosin Y (protein stains red with eosin). The freshly cut sections were placed in this dye for 10 minutes, then cleared in glycerine and mounted on slides. Confirmatory tests were made in one series with Millon's reagent and the Biuret reaction.

Eight series of determinations for the three different stages were made, and the average readings from these determinations are plotted in figures 10A, B, C, D.

There was a difference in the carbohydrate and protein contents within the three different stages of feeding lesion. The quantity of reducing sugars decreased as the lesions developed (fig. 10A). The difference in the amount of sugars in the control and in the young lesion was greater than that between the control and the mature or old lesions. The old lesion differed the least from the control. It was difficult to localize the sugars in the different tissues, but the trend appeared to be the same for all tissues. Within the old lesion, the tissues that were chiefly injured by the feeding of the bug had less sugars in them than the controls. There appeared to be slightly more sugar below the lesions than above them. In the swelling caused by *Psallus seriatus* on cotton, Painter (60) reported the presence of larger amounts of reducing sugars.

All three stages had greater quantities of dextrin than the controls (fig. 10B). The amount of dextrin, with respect to the controls, was most abundant in the mature lesion. There was about an equal quantity of dextrin above and below young and old lesions, but there appeared to be more dextrin below the mature lesion.

In the tomato plant, starch is stored chiefly in the endodermis and pith, and, therefore, observations were recorded only for these two tissues. The amount of starch in all three stages was less than the amount in the controls (fig. 10C). The endodermis, which was affected much more by the feeding of the bugs than was the pith, had the lowest starch content at the mature lesion stage. There appeared to be a slight accumulation of starch below the old lesions, but apparently none in the young and the mature lesions.

The quantity of protein was greater in the lesion than in the control (fig. 10D). There was a positive trend in the protein content with respect to the control in the three different stages, except in the pith, where larger amounts of protein were found in mature lesions than in the other two stages. The greatest amount appeared in tissues that were affected mainly by the stylets: namely, the cortex, endodermis, phloem, and xylem. There was very little difference in the protein content above and below the lesions. The tests made with Millon's reagent and Biuret reaction confirmed the results obtained with eosin. Because these tests are more specific in their reactions, they indicate less than the total quantity of protein.

## DISTRIBUTION OF BUGS ON TOMATO PLANT PARTS IN THE FIELD

### *Procedure*

The distribution of tomato bugs on the different regions of tomato plants in the field was observed on a row of tomato plants about 120 feet long. Twenty-five alternate plants were examined on alternate days. The plants ranged from 20 to 36 inches in height when the first observation was made.

Each plant was divided into six major divisions: apical meristem, which included terminal 1 inch of all stems; first division, which included region 6 inches below terminal 1 inch; third division, which included region on stem 10 inches above soil; second division, which was located between first and third divisions; flowers; and fruits. The apical meristem and the first three divisions were separated into stems, petioles, and leaf blades. The flowers and fruits were separated into peduncle or pedicel and flower proper or fruit proper. Six counts were made of the number of adults and nymphs on the different divisions of the plant. The number of feeding lesions or scars on the plants was recorded in the last observation.

### *Results*

The majority of adults and nymphs was found on the first 7 inches of the apex of the stems; that is, on that portion of the plant represented by the apical meristem and the next 6 inches (table 6). The 10 inches at the base of the plants had only 1 percent of the total adults and 0.8 percent of the total nymphs. The insects were abundant also on the flowers. Adults and especially nymphs were most abundant on petioles of the growing point, whereas in the second division, they were more abundant on stems than on petioles. In the first division, the number of adults was equally divided between stems and petioles, while the nymphs were more abundant on stems in this region than on petioles. The total number of adults or nymphs on the stem or petiole was greater than the number on the leaf.

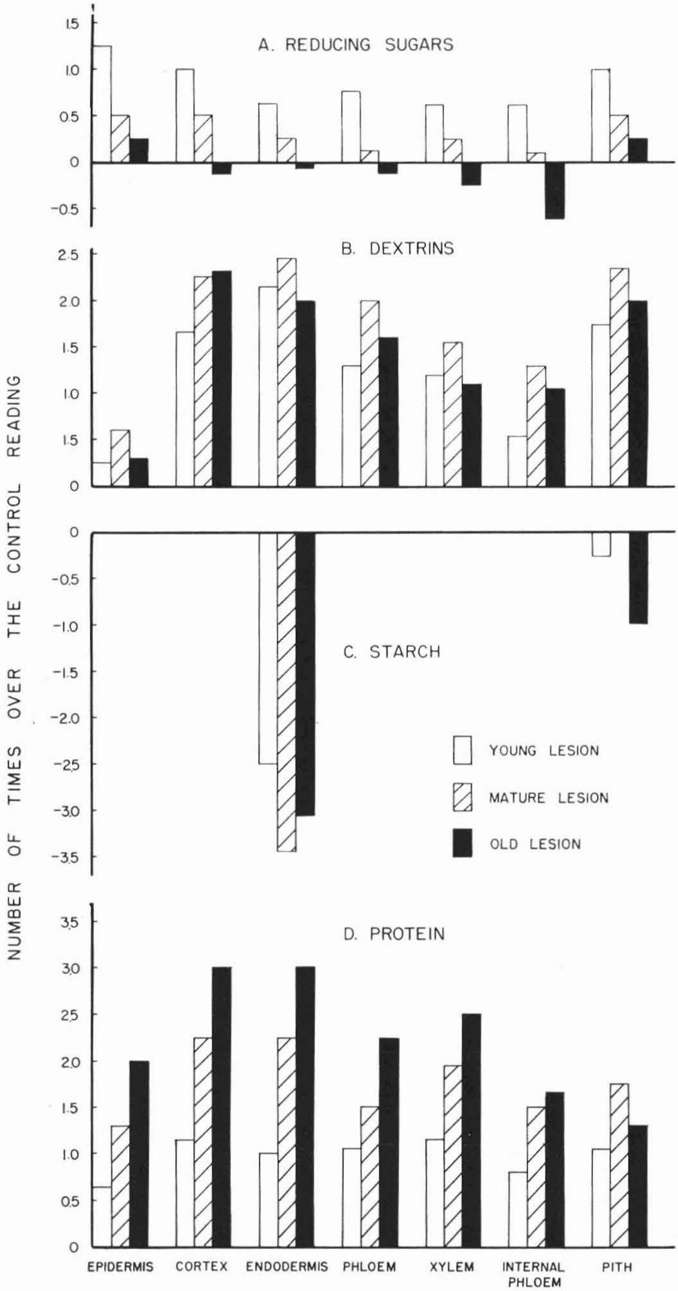


FIG. 10. Average estimate obtained from microchemical tests for carbohydrates and protein within young, mature, and old feeding lesions of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant). *A*, Reducing sugars; *B*, dextrins; *C*, starch; *D*, protein.

TABLE 6. Distribution of adults and nymphs of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) on different regions of tomato plants in the field. Total of six counts.

| PLANT PARTS | APICAL MERISTEM | | FIRST DIVISION | | SECOND DIVISION | | THIRD DIVISION | | FLOWER | | FRUIT | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Adult* | *Nymph* | *Adult* | *Nymph* | *Adult* | *Nymph* | *Adult* | *Nymph* | *Adult* | *Nymph* | *Adult* | *Nymph* |
| Stem | 35 | 311 | 140 | 387 | 59 | 147 | 1 | 4 | | | | |
| Petiole | 125 | 589 | 141 | 202 | 39 | 37 | 2 | 2 | | | | |
| Leaf | 58 | 95 | 58 | 94 | 50 | 295 | 6 | 13 | | | | |
| Peduncle | | | | | | | | | 14 | 62 | 10 | 29 |
| Flower or fruit proper | | | | | | | | | 128 | 127 | 18 | 28 |
| Total | 218 | 995 | 339 | 683 | 148 | 479 | 9 | 19 | 142 | 189 | 28 | 57 |
| Percent of total adults and total nymphs | 24.7 | 41.1 | 38.4 | 28.2 | 16.7 | 19.8 | 1 | 0.8 | 16.1 | 7.8 | 3.2 | 2.4 |
| Total of all bugs | 1213 | | 1022 | | 627 | | 28 | | 331 | | 85 | |
| Percent of all bugs | 36.7 | | 30.9 | | 19.0 | | 0.9 | | 10.0 | | 2 6 | |

On the flowers, both adults and nymphs were found mainly on flower parts and less on peduncles; while on the fruits they were found about equally distributed on the fruit proper and peduncle.

Distribution of feeding lesions on the plants was similar to that of the bugs (table 7). Over 68 percent of lesions were on the apical 7 inches (apical meristem plus the first division), whereas, the third or basal division had only 0.2 percent of the lesions.

TABLE 7. Distribution of feeding lesions of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) on different parts of 25 tomato plants in the field.

| PLANT PARTS | NUMBER OF LESIONS IN THE DIFFERENT DIVISIONS | | | | | |
|---|---|---|---|---|---|---|
| | *Apical meristem* | *First division* | *Second division* | *Third division* | *Flower* | *Fruit* |
| Stem | 41 | 121 | 36 | | | |
| Petiole | 222 | 311 | 173 | | | |
| Leaf | 10 | 28 | 64 | 2 | | |
| Peduncle or pedicle | | | | | 5 | 21 |
| Flower or fruit proper | | | | | 34 | |
| Total | 273 | 460 | 273 | 2 | 39 | 21 |
| Percent in each division | 25.6 | 43.1 | 25.6 | 0.2 | 3.7 | 2.0 |

## DISTRIBUTION OF BUGS ON PLANTS GROWN AT DIFFERENT NITROGEN LEVELS

### *Procedure*

Since the tomato bug feeds mainly on young and tender growths and on lesions that are rich in soluble carbohydrates and proteins, a study was undertaken to determine if there was a variation in the abundance of bugs on plants at different internal levels of nitrogen. Tomato seeds were germinated in tap water on a germinating frame. The seedlings were planted in a mixture of equal parts of sterilized soil and black cinder sand in clay pots (9¾–10 inches in diameter). When the plants were 6 inches high, 60 of uniform appearance were arranged on tables outdoors. Later, 15 plants (5 plants for each different treatment) were taken into the greenhouse to obtain a more luxuriant growth. The remaining plants outdoors were designated as the Outdoor Series, and the plants in the greenhouse as the Greenhouse Series.

Each week the lateral branches, except for two or three near the growing point, and all the flower buds were removed. The plants were kept pruned to the last 2 weeks before harvest.

The plants were separated into three groups of 20 each: nitrogen deficient, nitrogen moderate, and nitrogen high. The plants of the different treatments were distributed throughout the plot in such a manner that no two similar treatments were opposite or adjacent to each other.

When the plants began to show signs of nitrogen deficiency, the following nutrient solutions were added to the different treatments.

| | *N High* | *N Moderate* | *N Deficient* |
|---|---|---|---|
| | *M* | *M* | *M* |
| $Ca(NO_3)_2$ | 0.005 | 0.005 | |
| $MgSO_4$ | 0.002 | 0.002 | 0.002 |
| $KH_2PO_4$ | 0.002 | 0.002 | 0.002 |
| $NH_4NO_3$ | 0.001 | | |
| $CaCl_2$ | | | 0.005 |

Toward the end of the experiment, the amount of $NH_4NO_3$ given to the nitrogen high plants was increased to 0.002 M and still later to 0.004 M. The nutrients were applied at intervals of 3 to 4 days during the first part of the experiment, but later, on alternate days. About 8 days after nutrients were added, the plants which received no nitrogen began to show nitrogen deficiency.

Since the infestation of bugs on the plants was light at the early stage of the experiment, 240 bugs were liberated among the plants on the sixteenth and on the eighteenth day after the first bug count when the plants began to show variations in nitrogen. The bugs were scattered over the plot from three widely separated regions. When the plants of the Greenhouse Series were taken into the greenhouse, 100 bugs were liberated among them.

About a week before the nutrients were added, counts of the adults and nymphs were made on two different days. Each plant was divided into three major divisions. The upper or first division included the first 6 inches of the apical meristems of all stems. The remainder of the plant was equally divided into two parts, the middle or second division, and the lower or third division. Each division was separated into stems, petioles, and leaves.

Eight counts were made on the plants of the Outdoor Series over a period of 39 days, and 10 counts on the Greenhouse Series over a period of 42 days. The average number of adults and nymphs on the plants of different nitrogen levels was plotted against time. The significance between means of the adults and of the nymphs of the different series was tested by the method of Fisher and "Student" (*4*).

At the end of the experiment, the number of shoots over 1 inch in length was counted, and the abundance of bugs at the last count was expressed as number per shoot.

About 42 days after the first bug count, the plants were harvested and separated into the three different divisions. The plant material was chopped into small pieces and dried for 3 to 4 hours at 70°–90° C. in a forced-draft drying oven. The material was ground to a fine powder. Duplicate samples weighing 1 gram each were analyzed for total nitrogen by the Gunning method modified to include the nitrogen of nitrates (*1*). Results of the analysis are expressed as the percent of nitrogen in a gram of dried sample.

*Results*

More tomato bugs were found on plants with high nitrogen content than on those with low nitrogen content (tables 8, 9). Distribution of adults and nymphs within the three divisions was always greatest in the first division. The different divisions of higher nitrogen plants nearly always had a greater number of adults and nymphs than those of lower nitrogen plants.

TABLE 8. Distribution of adults and nymphs of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) on the three divisions of tomato plants at different levels of nitrogen (Outdoor Series).

| PLANTS AT DIFFERENT N LEVEL | AVERAGE NUMBER IN THE DIFFERENT DIVISIONS* | | | | | |
|---|---|---|---|---|---|---|
| | *1st division* | | *2nd division* | | *3rd division* | |
| | Adult | Nymph | Adult | Nymph | Adult | Nymph |
| N Deficient | 2.6 | 3.1 | 1.2 | 1.4 | 0.2 | 0.2 |
| N Moderate | 6.9 | 8.2 | 1.9 | 1.6 | 0.3 | 0.4 |
| N High | 9.7 | 8.2 | 2.1 | 1.5 | 0.5 | 0.9 |

* Average number of bugs per plant from the last three observations.

During the early stage of the experiment, the plants were uniform in growth and appearance, and had nearly an equal number of bugs on them. However, when the plants began to show differences in nitrogen, the population of bugs began to vary among the three different treatments (figs. 11, 12). The average number of adults on nitrogen high plants increased at a faster rate than on the nitrogen moderate and nitrogen deficient plants. On the nitrogen deficient plants, there was at first a gradual increase in number of bugs, but during the last few conuts the number decreased. The average number of bugs on nitrogen moderate plants was between the levels of nitrogen high and nitrogen deficient plants. The difference in the population levels of the three treatments increased greatly during the last four or five readings which were made over a period of 14 to 20 days.

Results of the Greenhouse and Outdoor series were similar. Although the difference in the number of bugs between the treatments in the Greenhouse Series was greater than in the Outdoor Series, the significance of the differences was less because of the smaller number of plants that had been used.

The statistical difference between means of adults of nitrogen high and nitrogen deficient plants was consistently above the 1 percent level (*t*-value) during the last four readings in the Outdoor Series and during the last five readings in the Greenhouse Series. The difference between means of adults of nitrogen high and nitrogen moderate plants was above the 1 percent level in the last reading of the Outdoor Series and in the last two readings of the Greenhouse Series. Means of adults of the nitrogen moderate and nitrogen deficient treatments differed significantly (1percent level) in the last three readings in the Outdoor Series, but showed no significant difference in the Greenhouse Series.

The average number of nymphs on the three types of treated plants followed a pattern similar to that of the adults (fig. 11A, 12A). There was, however, a lag,

TABLE 9. Distribution of adults and nymphs of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) on the three divisions of tomato plants at different levels of nitrogen (Greenhouse Series).

| PLANTS AT DIFFERENT N LEVEL | AVERAGE NUMBER IN THE DIFFERENT DIVISIONS* | | | | | |
|---|---|---|---|---|---|---|
| | *1st division* | | *2nd division* | | *3rd division* | |
| | Adult | Nymph | Adult | Nymph | Adult | Nymph |
| N Deficient | 3.5 | 4.6 | 1.0 | 1.6 | 0.1 | 0.1 |
| N Moderate | 6.1 | 6.3 | 2.7 | 2.4 | 0.8 | 0.6 |
| N High | 11.3 | 14.0 | 4.7 | 3.2 | 0.6 | 0.7 |

* Average number of bugs per plant from the last four observations.

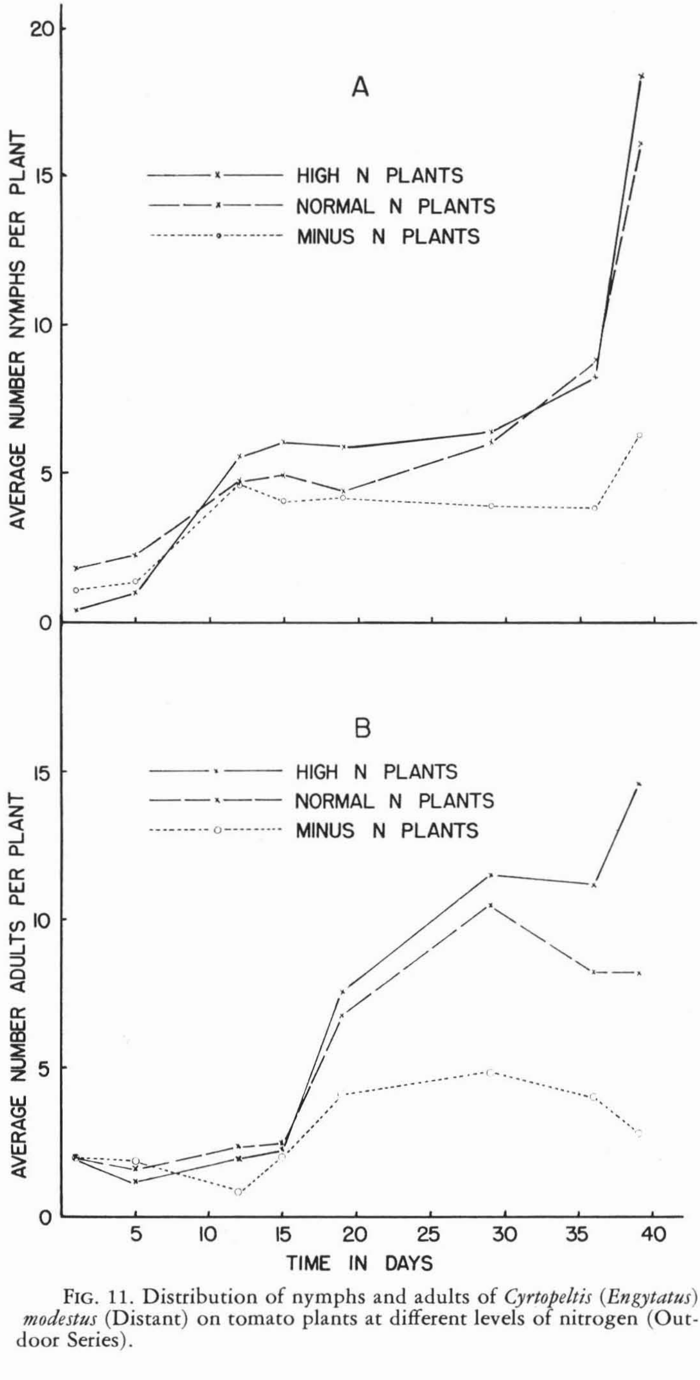


FIG. 11. Distribution of nymphs and adults of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) on tomato plants at different levels of nitrogen (Outdoor Series).

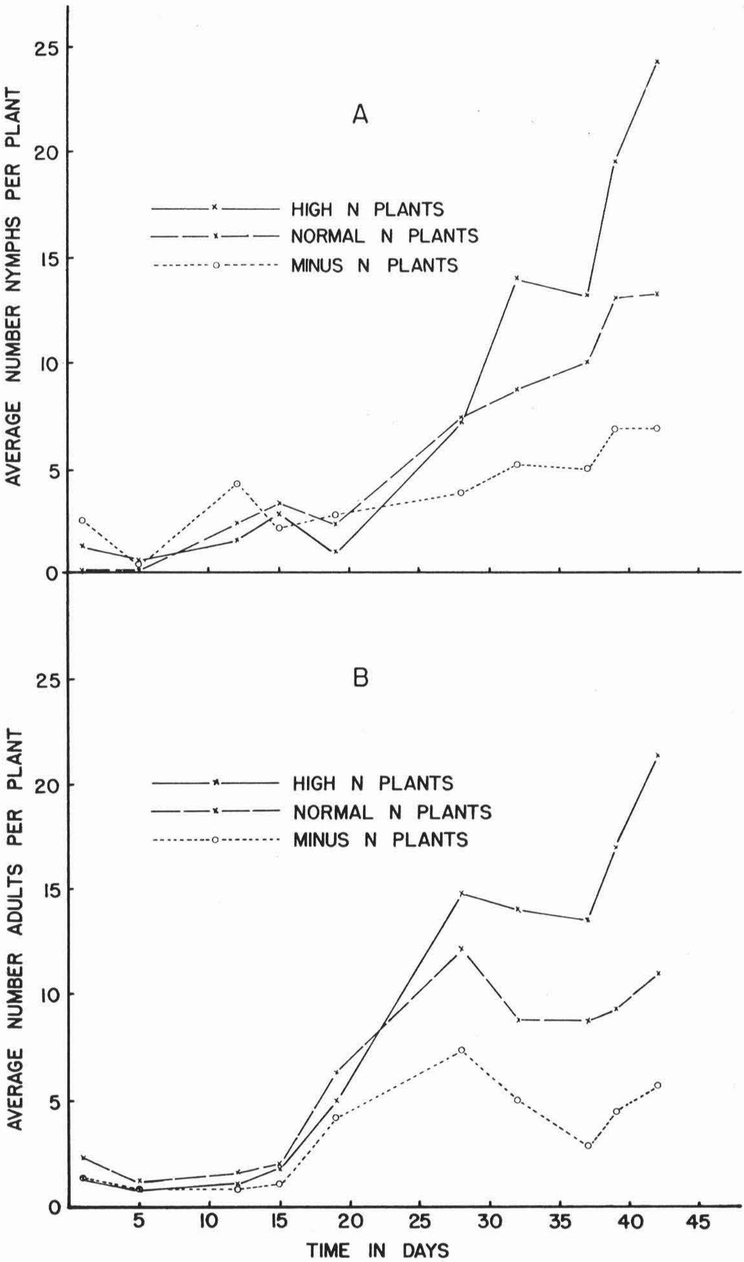


FIG. 12. Distribution of nymphs and adults of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) on tomato plants at different levels of nitrogen (Greenhouse Series).

TABLE 10. Number of adults and nymphs of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) per shoot on tomato plants at different levels of nitrogen (Outdoor Series).

| PLANTS AT DIFFERENT N LEVEL | TOTAL NUMBER OF SHOOTS | TOTAL NUMBER OF ADULTS* | ADULTS PER SHOOT | TOTAL NUMBER OF NYMPHS* | NYMPHS PER SHOOT | ADULTS AND NYMPHS PER SHOOT |
|---|---|---|---|---|---|---|
| N Deficient | 56 | 34 | 0.6 | 76 | 1.4 | 2.0 |
| N Moderate | 90 | 91 | 1.0 | 177 | 2.0 | 3.0 |
| N High | 108 | 146 | 1.4 | 184 | 1.7 | 3.1 |

* Figures are from the last observation.

and the difference between the treatments became marked at a later period.

In comparing the number of adults and nymphs of the Outdoor Series on a shoot or growing point basis, there were more adults and nymphs per shoot on nitrogen high plants than on nitrogen deficient plants (table 10). In the Greenhouse Series, however, there was only a slight difference between nitrogen high and nitrogen deficient plants in the total number of bugs per shoot, and there were fewer adults and nymphs per shoot on nitrogen moderate plants than on nitrogen deficient plants (table 11).

The amount of nitrogen in the plants varied in proportion to the different treatments (table 12). Throughout the different divisions, total nitrogen was greater in plants given nitrogen than in the nitrogen deficient plants. The greatest amount of nitrogen occurred within the first 6 inches of the shoots, and the least amount was present in the third division. The amount of nitrogen in plants of the Greenhouse Series was slightly greater than the amount in the Outdoor Series.

## DISCUSSION

The development of the feeding lesion of *Cyrtopeltis* (*Engytatus*) *modestus* on the tomato plant has been separated into three stages: young, mature, and old lesions. The feeding lesion is formed by the tomato bug feeding in a series of punctures which frequently encircle the stem. The lesion does not necessarily pass through the three different stages, because this is dependent on the length of time the bug feeds on the lesion. Short feeding may result in very faint discoloration of a young lesion, from which the plant recovers without any other external symptom. After frequent and more intensive feeding in the same region, lesions of the second or mature stage develop. When the bug feeds less frequently or ceases to feed on the mature lesion, the lesion develops a small tumor-like growth, and this stage has been designated as the old lesion stage.

The external symptoms appearing in the development of the feeding lesion

TABLE 11. Number of adults and nymphs of *Cyrtopeltis* (*Engytatus*) *modestus* (Distant) per shoot on tomato plants at different levels of nitrogen (Greenhouse Series).

| PLANTS AT DIFFERENT N LEVEL | TOTAL NUMBER OF SHOOTS | TOTAL NUMBER OF ADULTS* | ADULTS PER SHOOT | TOTAL NUMBER OF NYMPHS* | NYMPHS PER SHOOT | ADULTS AND NYMPHS PER SHOOT |
|---|---|---|---|---|---|---|
| N Deficient | 19 | 28 | 1.5 | 37 | 2.0 | 3.4 |
| N Moderate | 45 | 55 | 1.2 | 66 | 1.5 | 2.7 |
| N High | 56 | 107 | 1.9 | 121 | 2.2 | 4.1 |

* Figures are from the last observation.

TABLE 12. Nitrogen and moisture contents of plants of the three different treatments (Outdoor and Greenhouse series).

| SERIES | PERCENT NITROGEN AND MOISTURE | PLANTS AT DIFFERENT NITROGEN LEVELS | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | *N Deficient* | | | *N Moderate* | | | *N High* | | |
| | | First div. | Second div. | Third div. | First div. | Second div. | Third div. | First div. | Second div. | Third div. |
| Outdoor..... | nitrogen | 2.25 | 1.45 | 1.16 | 3.04 | 2.22 | 1.92 | 3.91 | 2.79 | 2.60 |
| | moisture | 83.7 | 81.0 | 80.3 | 86.3 | 83.9 | 83.0 | 86.7 | 85.4 | 84.0 |
| Greenhouse... | nitrogen | 2.40 | 1.42 | 1.20 | 3.23 | 2.11 | 1.93 | 4.16 | 2.99 | 2.69 |
| | moisture | 85.2 | 82.3 | 81.1 | 87.4 | 85.1 | 82.7 | 86.9 | 86.2 | 85.3 |

apparently are the result of the histological changes within the lesion. In the young lesion, the brown discolored areas are caused by dead protoplasm, wound products, and collapsed cell walls. In the mature lesion, the longer feeding results in many dead cells, especially in the cortex. These cells collapse and the epidermis sinks below the surface of the stem. The vascular tissue is pierced at many points and weakened. The newly-formed wound parenchyma which replaces the elements of the vascular bundle is tender and brittle. Consequently, the stem breaks off easily when bent at this region. In the old lesion, cell proliferation is very marked; the lesion swells to form a small tumor; dedifferentiation and redifferentiation have taken place. The wound parenchyma in the xylem has become lignified. Although the stele is distorted, the elements are continuous with each other. In the cortex some of the parenchyma cells become lignified to form wound tracheids. Such anatomical changes result in strengthening the stem, and old lesions are strong and resistant to bending.

Within several of the feeding lesions, an occasional collapsed mass of cell contents was found in the paths of the stylets. This cellular mass is apparently different from the stylet sheaths reported for aphids and other Homoptera. The feeding of the tomato bug on 3 and 4 percent agar left no visible sheath material along paths of feeding punctures. Other workers have also reported the absence of stylet sheaths or make no mention of such sheaths in tissues fed upon by mirids (*63, 71, 72, 25, 45, 55*).

The feeding lesion of mirids is usually the result of traumatic injury from stylet punctures and the injection of toxic substances into the plant tissues. Smith (*73*) stated that the toxic effect of injected saliva is most pronounced in Miridae. There appears, however, a variation in toxicity of the saliva among the toxicogenic species (*14*).* Petherbridge and Husain (*63*) and Smith (*71*) have noted differences in the ability of species of mirids to produce injury to apples. But others have found that all species of mirids which they studied produced similar injury (*25, 45, 26, 55*).

The tomato bug very likely secretes toxic saliva into the plant. The toxic effect of the saliva, however, appears mild, and the feeding lesion seems to be caused mainly by the stylets piercing, sucking, and killing the cells. Within the feeding lesion, there are no intense cellular reactions that may be associated with a strong toxic saliva. There is also a likelihood that the tomato bug produces rapidly diffusible

* Carter (*12*) introduced the term *toxicogenic* and defined it as referring to species which have the inherent capacity to produce toxins.

toxic saliva which may affect the general physiology of the plant.

In general, the reaction of tissues within the feeding lesion was similar to that of the lesions artificially produced by sterile needles. In the feeding and the artificial lesions, the pathologic stimulus resulted in tissue changes that take place in the wound-healing of higher plants (*6, 7*).

The mirid bugs feed on a number of tissues within the plant. Leach and Smee (*50*) and Leach (*49*) have reported that *Helopeltis bergrothi* Reut. feeds on the cortex, xylem, and especially the parenchyma of the pericycle. Smith (*73*) has stated that mirids tap the vascular bundle. Smith (*72*) and King and Cook (*45*) have found that the mirids they studied tap any part of the internal tissues. The tomato bug feeds primarily on the vascular bundle as indicated by our following observations. Feeding of the bug may result in the wilting of organs beyond its region of feeding. "Bleeding" from the feeding lesion has been observed, and water of guttation is absent on leaves that have been girdled by feeding lesions. These observations indicate that the stylets puncture the vascular bundle and disrupt the movement of solutes. This has been confirmed by the histological study of the feeding lesion in which the stylets ended chiefly in the vascular bundle. Furthermore, on the petioles of large leaves, the bugs feed mainly on the upper half where vascular bundles are nearer to the epidermis than on the lower half. It is likely, however, that other tissues such as the cortex, endodermis, pericycle, and pith may also serve as sources of food, since protein and soluble carbohydrates were found in high concentration in these tissues in the feeding lesion.

Of the tissues within the vascular bundle, the xylem appeared to be tapped as often as phloem and cambium. The tomato bug apparently obtains most of its organic nutrients from the phloem. It is also possible that the tomato bug obtains food from xylem parenchyma cells or from developing xylem vessels. It was found, however, that the bug ingests dyes from xylem tissue, and many of the stylet paths ended in a xylem vessel, in which occasionally a coagulated mass, very likely injected by the bug, was present. Clements (*20*), Clements and Engard (*21*), and Stout and Hoagland (*74*) have shown that the upward movement of inorganic solutes takes place chiefly in the xylem. Nightingale (*58*) stated that in tomato the reduction of nitrates and the synthesis of amino acids occur predominantly in the tops of the plant. There is little organic material moving within the xylem vessels. The tomato bug, apparently, obtains chiefly water and inorganic salts from xylem. Wigglesworth (*90*) and Trager (*86*) have pointed out the importance of inorganic salts, especially potassium and phosphorus, in the nutrition of certain insect species.

The tomato bug was found to return to the young and the mature lesions, its former sites of feeding. It is attracted to newly-formed wounds probably because of their tenderness and the exuded sap from injured cells. Since it has the habit of selecting the feeding site by probing the stem with its proboscis, it is able to locate such regions. Other workers have also observed this exploring feeding habit in other mirids (*72, 60, 68*). Painter (*61, 62*), however, stated that hardness of tissue as a cause of resistance of plants to sucking insects is open to question. The physiological relationship, according to him, may be of greater importance.

In the feeding lesion of the tomato bug, the quantities of protein, reducing sugars, and dextrin were nearly always greater than in the uninjured tissues. This region is unquestionably a good source of food for the bugs.

The young shoots of plants in the field and in pots had the largest number of tomato bugs on them. The bugs were found distributed in a gradient along the stems, with the largest number occurring on the top 7 inches of stem. Total nitrogen was higher at the top of plants than at the bottom. Murneek (*57*) and Nightingale *et al.* (*59*) have reported that assimilated nitrogen, especially protein, is much higher at the top than at the base of tomato plants.

A preliminary study on tomato plants containing different levels of nitrogen indicated that nitrogen high plants were more attractive to adult tomato bugs than nitrogen deficient plants. The difference in the total number of bugs became apparent when the plants began to react to the different nitrogen levels. The effect of the different levels was not as evident on nymphs as it was on adults. It appears, therefore, that the nitrogen condition or the succulence of the plants is influential in the distribution of tomato bugs on tomato plants. The importance of nitrogen for growth and reproduction in insects has been discussed by Uvarov (*89*), Wigglesworth (*90*), Trager (*86*), and Auclair (*3*). Evans (*24*) found a positive correlation between the rate of reproduction of the aphid, *Brevicoryne brassicae* L., and the nitrogen content, especially protein in the host plant. Maltais (*54*) has reported that varieties of peas susceptible to the pea aphid, *Macrosiphum pisi* (Kltb.), have higher total, water-soluble, and amino nitrogen than resistant varieties. The preference for a high nitrogen diet by the tomato bug is further indicated by its carnivorous habit. Illingworth (*42*) has found difficulty in rearing the tomato bug on a vegetable diet, but found that it thrived on an animal diet.

At present, DDT is very effective for the control of tomato bug on tomato. Possibly a second method of control may be based on the fact that the tomato bug feeds on xylem tissue. Repellent or toxic substances could be introduced into the xylem through the root system or by injecting them directly into the tissue. Such toxic substances could be safely used on tomato or tobacco that are grown for seed production. Andrews (*2*) has prevented the attack of *Helopeltis theivora* Waterh. on tea plants by supplying potash directly to the fine roots of the plants. W. Carter (*13*) stated that Andrews also accomplished the same result by direct injection of tea bushes with potash. R. H. Carter (*11*) and Roark (*67*) have summarized the literature on the treatment of trees by injections. In recent years, the systemic organic insecticides have been used against sucking insects.

A third possible method of reducing the tomato bug population may be based on the plant physiological manipulation of the nitrogen level of tomato plants. The high nitrogen plants appear much more attractive to the tomato bugs than the low nitrogen plants. Obviously good productive plants cannot be grown under conditions of nitrogen deficiency. Hence the nutrition of the plants would need to be controlled carefully so that the plants are maintained at their optimum level of nitrogen.

## SUMMARY

1. External and internal characteristics in the development of the feeding lesion of the tomato bug on tomato plants have been described. Development of the lesion has been separated into three stages: young, mature, and old lesions.

2. The lesion is the result of numerous feeding punctures made in a complete or incomplete ring around the stem or petiole. Toxic salivary secretions of the tomato bug are mild and do not produce intense cellular reactions within the feeding lesion. External and internal characteristics of the feeding lesion were, in general, similar to those of lesions produced artificially with sterile needles.

3. The path of stylets is intracellular. A collapsed mass of cell contents, apparently different from the stylet sheath of Homoptera, is occasionally found indicating the path of stylets. The brown streak formed by collapsed dead cells also has a superficial resemblance to the stylet track of Homoptera.

4. Vascular tissue appears to be the major site of feeding by the tomato bug, but the cortex, endodermis, pericycle, and pith also may be fed upon, since protein and soluble carbohydrates are also abundant in these tissues in the feeding lesion.

5. The tomato bug has been found to take up dyes from xylem tissue.

6. All five nymphal instars have been found to produce feeding lesions. The fourth and fifth instars produce feeding lesions readily, while the other three instars, especially the first, produce them less frequently.

7. The tomato bug has an unusual habit of returning to its former regions of feeding, especially to mature lesions. It is also attracted to freshly made wounds.

8. Tissues within young and mature feeding lesions have a greater quantity of protein, dextrin, and reducing sugars, and much smaller quantity of starch than the uninjured tissues. The presence of this large amount of nutritive organic substances makes the feeding lesion a suitable site of feeding.

9. The tomato bug feeds mainly on young shoots and flowers. In the field, distribution of the bugs on the tomato plant was in a gradient along the stem, with the majority of adults and nymphs being found on the first 7 inches at the top of stems.

10. The bugs were found in greater abundance on plants with higher nitrogen content than on those with lower nitrogen content.

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