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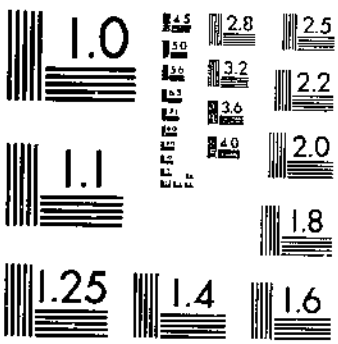


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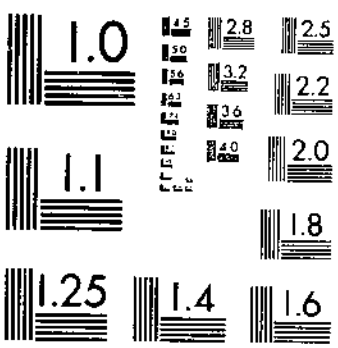


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# LIFE HISTORIES AND BEHAVIOR OF FIVE INSECT VECTORS OF PHONY PEACH DISEASE



UNITED STATES DEPARTMENT OF AGRICULTURE

Technical Bulletin No. 1188

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# LIFE HISTORIES AND BEHAVIOR OF FIVE INSECT VECTORS OF PHONY PEACH DISEASE

By WILLIAM F. TURNER[1] and HERSCHEL N. POLLARD, *entomologists, Entomology Research Division, Agricultural Research Service*

The incrimination of four species of leafhoppers—*Homalodisca coagulata* (Say),[2] *Oncometopia undata* (F.), *Graphocephala versuta* (Say), and *Cuerna costalis* (F.)—as vectors of phony peach was announced in 1949 (*8*).[3] Since then at least two other cicadellids—*Homalodisca insolita* (Wlk.) and *Draeculacephala* sp.—have been shown to transmit the disease. *H. insolita* is as effective experimentally as the first four species, but apparently *Draeculacephala* sp. is not an efficient vector (*9*).

The first two species are primary natural vectors. *G. versuta* is next in importance. Whether *costalis* and *insolita* induce natural spread, except rarely, is doubtful.

The search for vectors of phony peach was begun in 1936 with both extensive and intensive surveys of the insect fauna associated with peach orchards in the Southeastern United States. In conjunction with these surveys, the habits of the first four vectors, together with those of many other species of Homoptera, were observed incidentally. By 1942, when circumstantial evidence pointed more and more strongly to a small group of Tettigellinae as suspects, additional attention was devoted to observations on the habits and behavior of this group. Once the four members of this subfamily were actually incriminated as potential vectors, a more concerted effort was made to study their life histories and to determine definitely the nature of their association with peach orchards. Studies based on direct observations in the field have been supported by data obtained through the use of sticky-board traps (*3*), and the field work has been supplemented by limited studies conducted in an insectary at Fort Valley, Ga., on the life histories of the different species.

Field observations of *insolita* were begun in 1952 and have also been supported by limited life-history studies in the insectary. This species is native to Mexico and the Southwestern United States, including Arizona, New Mexico, and western Texas, and it has recently extended its range across the Gulf States. It was observed for the first time at Fort Valley in September 1950, and since then it has

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[1] Retired May 31, 1957.

[2] Until recently the species of *Homalodisca* commonly found in the Southeastern United States has been designated as *triquetra* (F.). Current studies by D. A. Young, North Carolina State College, demonstrate that *triquetra* is a South and Central American species that is not found within the limits of the continental United States. The species described in this bulletin is *coagulata* (Say).

[3] Italic numbers in parentheses refer to Literature Cited, p. 28.

increased in numbers so rapidly that it is now as abundant as any of the other potential vectors with the exception of *versuta*.

Because of the marked inefficiency of *Draeculacephala* sp. in transmission experiments, its habits and behavior have not been studied in detail. The members of this genus that occur in the Southeast are typically grass feeders. In our surveys and studies they have never been found associated with peach trees. Although they can live for a considerable time when confined on peach, it appears certain that they rarely, if ever, feed on this host by choice.

All the insects that have demonstrated ability to transmit phony peach belong to one subfamily of the Cicadellidae—the Tettigellinae. Four of the six species are members of the same tribe—the Proconiini. None of these leafhoppers have ever been given common names, but members of the subfamily as a whole are commonly called sharpshooters.

## DESCRIPTIONS

The adults of *coagulata* (fig. 1, *J*) are large, rather slender leafhoppers, measuring from 11 to 13 mm. in length. The males are slightly smaller than the females. The head is bluntly angled and the crown nearly flat. The general color is brown. The venter is ivory with conspicuous black markings. At the base of the abdomen the ivory color extends upward, so that when observed from above, the insect appears to bear an oblique ivory blotch on either side of the abdomen. The face, genital plates, and legs are approximately mandarin orange. In newly transformed adults the veins of the forewings are bright red and spots of red occur toward the tips of the wings. Within a few days these areas darken until the dorsal aspect presents a homogeneous brown appearance to the naked eye.

The nymphs (fig. 1, *I*) are olive gray. In the first two instars the eyes are reddish; in the later instars they are darker. The average measurements, in millimeters, of the nymphal stages are as follows:

| | 1st instar | 2d instar | 3d instar | 4th instar | 5th instar |
|---|---|---|---|---|---|
| Length of nymph | 2.0 | 2.5 | 4.0 | 5.0 | 7.5–8.0 |
| Width of head, including eyes | 1.0 | 1.2 | 1.8 | 2.0 | 3.0 |

The adults of *undata* (fig. 1, *D*) are large, robust leafhoppers, measuring from 11 to 13 mm. in length. The head is broad with a rounded anterior margin and a sloping crown. The forewings and pronotum are greenish blue to blue with irregular dark spots and dots. The crown, anterior margin of the pronotum, and the scutellum are orange with characteristic black markings. Ventrally the insect is orange and black. The legs are orange with sparse black blotches.

The nymphs are darker colored than those of *coagulata*. The early stages have a bluish cast, and the later stages are slightly lighter. The fifth-instar nymphs (fig. 1, *C*) bear dark markings on the head, prothorax, and wing pads similar to those on the adults, and some of the adult blue coloring appears on the prothorax and wing pads. The coloring and markings of fifth-instar nymphs of *undata* simulate adult characters much more closely than those of *coagulata*. The

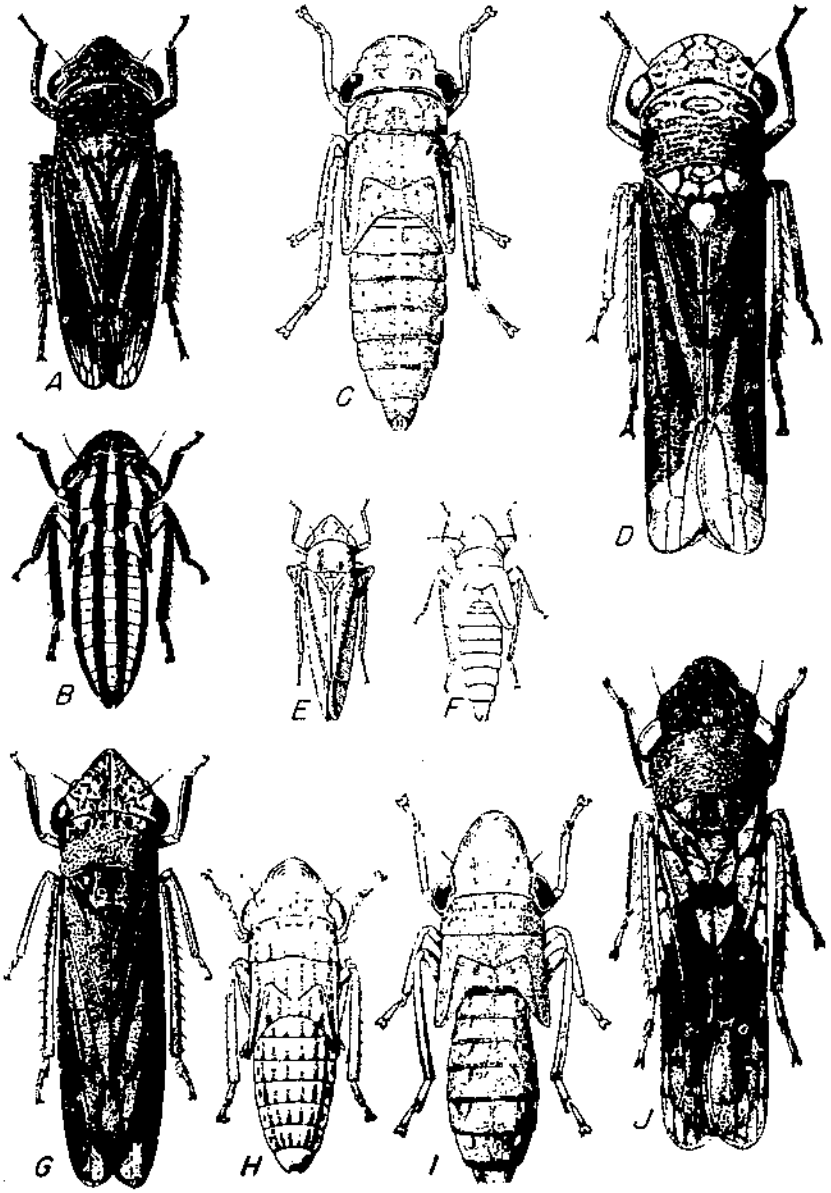


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FIGURE 1.—*Cuerna costalis* adult (*A*) and fifth-instar nymph (*B*), *Oncometopia undata* adult (*D*) and fifth-instar nymph (*C*), *Graphocephala versuta* adult (*E*) and fifth-instar nymph (*F*), *Homalodisca insolita* adult (*G*) and fifth-instar nymph (*H*), *Homalodisca coagulata* adult (*J*) and fifth-instar nymph (*I*). X 6½.

average measurements, in millimeters, of the nymphal stages are as follows:

| | 1st instar | 2d instar | 3d instar | 4th instar | 5th instar |
|---|---|---|---|---|---|
| Length of nymph | 2.0 | 2.8 | 3.5 | 5.0 | 8.5–9.0 |
| Width of head, including eyes | 1.0 | 1.1 | 1.5 | 2.0 | 3.0 |

The overall width of the heads of *undata* nymphs is no greater than that of *coagulata* nymphs. However, the broadly rounded anterior margin and curving crown make the heads of the former species appear appreciably larger than those of the latter.

The adults of *versuta* (fig. 1, *E*) are elongate leafhoppers, but this species is much smaller than any of the Proconiini, measuring approximately 5 mm. in length. The head is bluntly angled anteriorly and the crown is flat. The adults are green with orange or red stripes. During hot weather these stripes are very light colored, and at a casual glance the insect appears to be yellowish green. With the advent of cool weather in the fall the color deepens until the red markings are obtrusive. In the late fall and winter close examination is needed to distinguish this species from small specimens of the generally higher colored *Graphocephala coccinea* (Förster). The head of *versuta* bears a characteristic design of black lines, quite different from the markings on *coccinea*.

The nymphs (fig. 1, *F*) are yellowish white with large, angled heads and a flattened crown. The average measurements, in millimeters, of the nymphal stages are as follows:

| | 1st instar | 2d instar | 3d instar | 4th instar | 5th instar |
|---|---|---|---|---|---|
| Length of nymph | 1.5 | 1.7 | 2.0 | 2.8 | 4.0 |
| Width of head, including eyes | .5 | .6 | .8 | 1.0 | 1.3 |

The adults of *costalis* (fig. 1, *A*) are rather large, robust leafhoppers, though definitely shorter than the *coagulata* or *undata* adults. They average from 7 to 9 mm. in length. Anteriorly the head is rounded and the crown is nearly flat. At a casual glance the insects appear to be dull red. Actually the forewings bear alternate, narrow stripes of red and black. The crown, pronotum, and scutellum are blackish with ivory markings. A conspicuous ivory stripe along each side commences in front of the eyes and continues along the entire length of the body. The venter is black with ivory dots. The legs are black and red.

The nymphs (fig. 1, *B*) are strikingly colored. The dorsal surface bears 4 fuscous and 3 ivory or cream-colored stripes commencing at the middle of the crown and extending to the tip of the abdomen. Other coloring and markings are similar to those of the adults, except that the venter is red instead of black. The average measurements, in millimeters, of the nymphal stages are as follows:

| | 1st instar | 2d instar | 3d instar | 4th instar | 5th instar |
|---|---|---|---|---|---|
| Length of nymph | 1.3 | 2.2 | 2.6 | 4.5 | 5.5–6.0 |
| Width of head, including eyes | .7 | .9 | 1.2 | 1.7 | 2.0 |

The adults of *insolita* (fig. 1, *G*) are rather large, slender leafhoppers but distinctly smaller than the *coagulata* adults. The females average 10 to 11 mm. in length. The males are slightly shorter

and more slender than the females. The general color of the females is dark brown, whereas the males are nearly black. Both bear a conspicuous longitudinal ivory stripe along each side of the body, extending from the eyes to the tip of the abdomen. The legs of recently transformed adults are bright red, but with age this color changes to dull orange or even to orange yellow.

The nymphs (fig. 1, *H*) range from olive gray to greenish gray, the later stages being marked with progressively prominent dark stripes on the abdomen. There is also a characteristic pattern of spots and stripes on the crown, pronotum, and sides of the abdomen. The average measurements, in millimeters, of the nymphal stages are as follows:

| | 1st instar | 2d instar | 3d instar | 4th instar | 5th instar |
|---|---|---|---|---|---|
| Length of nymph | 2.0 | 3.3 | 4.4 | 5.5 | 8.0 |
| Width of head, including eyes | .7 | 1.0 | 1.2 | 1.8 | 2.0 |

## DISTRIBUTION

These five leafhoppers are primarily southern species and *coagulata* is strictly so. It is abundant in the Coastal Plain from the general latitude of Leesburg, Fla., to that of Augusta, Ga. South of Leesburg and north of Augusta the population decreases very rapidly. Specimens have been taken as far south as Homestead, Fla., but in Georgia we have failed to collect *coagulata* north of a line running from Carrollton to Madison. In South Carolina no specimens have been taken in the Spartanburg area. In North Carolina occasional individuals have been collected in the Coastal Plain as far north as Fayetteville, but the species is moderately abundant only near Lumberton. At this latitude we have never found it so abundant near the coast as we have farther inland.

In the Mississippi basin *coagulata* has been reported as far north as St. Louis. This occurrence must have resulted from an accidental movement or from a temporary, northward surge caused by some unusual climatic conditions. During 19 years of surveying we have never taken *coagulata* in the Mississippi Delta north of Marianna, Ark., and Greenwood, Miss., and only rarely at these points. Oddly enough the species is not at all uncommon in the hill country of eastern Mississippi as far north as Pontotoc and is abundant in the Highlands area at Nashville in southwestern Arkansas. In Texas *coagulata* is common throughout the eastern part of the State. Our surveys show it is rather abundant as far west as Brown and Kerr Counties, and specimens have been taken in Val Verde and Edwards Counties.

*O. undata* has a much wider distribution than *H. coagulata*. The former is found in appreciable numbers from the southern tip of Florida at Homestead to northern Maryland near the coast and to northeastern West Virginia farther inland. Occasional specimens have been taken in Pennsylvania, and a specimen has been recorded from Oswego, N. Y. (*4, p. 160*).

Farther west we have taken considerable numbers of *undata* as far north as Vincennes, Ind., and Centralia, Ill. The species is common throughout the Mississippi Delta at least as far north as Lake County, Tenn. It has been collected in the delta counties of southeastern Mis-

souri and throughout the southeastern half of Arkansas from the Missouri line to the Highlands area at Nashville. In Texas the species has been collected near Tyler and North Zulch. It has been reported from Arizona, but westwardly it appears to become scarcer. At Brownwood, Tex., we failed to find it on hosts that are particularly favored farther east and that were supporting considerable populations of *coagulata*. In areas offering optimum conditions for *coagulata* that species is far more common than *undata*, outnumbering it by ratios ranging from 8 to 1 to as much as 60 to 1, the proportions varying greatly from year to year (table 1).

TABLE 1.—*Comparative catches of* Homalodisca coagulata *and* Oncometopia undata *adults by seasons, 1947–52*

| Season and date | Host | *Homalodisca coagulata* | *Oncometopia undata* |
|---|---|---|---|
| | | *Number* | *Number* |
| Winter (hibernation area): | | | |
| Feb. 14–Mar. 20, 1947 | Shrubs in woods | 130 | [1] 6 |
| Early spring: | | | |
| Mar. 29–30, 1948 | Peach | 6 | 203 |
| Midspring: | | | |
| Apr. 18–May 5, 1949 | Ash in nursery | 52 | 225 |
| May 18–20, 1949 | Sunflower | 13 | 35 |
| Late spring and summer: | | | |
| June 15, 1949 | do | 104 | 13 |
| June 22–July 13, 1950 | do | 182 | 26 |
| July 12–18, 1950 | Peach (phony stumps) | 76 | 15 |
| July 21, 1949 | Okra | 174 | 27 |
| Aug. 10–24, 1949 | "Sick" peach and phony stumps. | 90 | 10 |
| Late summer and fall: | | | |
| Sept. 5, 1952 | Phony stumps | 52 | 1 |
| Oct. 6–9, 1952 | Peach | 77 | 1 |
| Oct. 18, 1949 | do | 42 | 1 |

[1] This figure is probably unduly low, since there is considerable evidence that this species hibernates partly in the last nymphal stage.

Until very recently the southward distribution of *undata* was difficult to understand. Although its northern range far exceeded that of *coagulata* and although *undata* is far less abundant than *coagulata* in central and southern Georgia, yet in Florida *undata* is the predominant species from the approximate latitude of Ocala southward. It outranks *coagulata* by as much as 10 to 1 near Lakeland and Bartow and is common as far south as Homestead. Indeed *undata* is much more abundant in Florida than it is in central and south Georgia. Studies made by D. A. Young in 1956 may solve this anomaly. Dr. Young found that the aedeagus of some specimens of *undata* near Jacksonville, Fla., varies distinctly from the aedeagus of males from more northern latitudes. Subsequent collections indicate that the forms in peninsular Florida are all the southern type and that typical *undata* and the Florida form overlap in a narrow zone in extreme southern Georgia. In this zone many of the males have the aedeagus intermediate between the two extremes. At present it is uncertain whether these two forms represent distinct species

or merely varieties or geographical races. Specimens of *undata* from Florida cannot be distinguished from Georgia specimens by any recognized external characters.

*G. versuta* appears to be more restricted in its northern range than *O. undata*. We have taken *versuta* in Virginia and Maryland, but failed to take it in Pennsylvania. It is not recorded as being present in New York. Farther west we found it occasionally at Vincennes, Ind., Anna, Ill., in southeastern Missouri, throughout Arkansas, and as far west as Brownwood, Tex. Our southernmost record is Homestead, Fla.

Osborn (*6, p. 99*) has stated that *costalis* (*lateralis*) "is a northern species," and he has listed several collections from various localities in Maine. Also he (*7, p. 223*) stated that the species "occurs throughout the northern United States from Maine to the Rocky Mountains and also to the south including Tennessee and the Carolinas," although at the same time he has remarked on the paucity of recorded collections from Ohio, except along the Ohio River. Leonard (*4, p. 160*) has recorded specimens from six localities in New York, including the Adirondacks. Medler (*5, p. 32*) has examined 104 specimens from Minnesota and has reported that *costalis* is present "throughout the State."

Although *costalis* obviously has a wide range in the Eastern United States, our surveys indicate that even this species may be classed as fundamentally southern. It is common and appears in large populations throughout the Coastal Plain from North Carolina to east Texas. We have taken *costalis* as far south as Pasco County, Fla.

*H. insolita* invaded the Southeast so recently that its distribution is still indeterminate. At present it occupies much the same area as *coagulata*. Specimens have been taken as far south as Ocala, Fla. To the north it has been collected at Rockingham, N. C., and Guild, Tenn., slightly north of where *coagulata* is found. Surveys suggest that the northward spread of *insolita* is very slow and the species may have about reached its limit in that direction.

## HABITS AND BEHAVIOR

Although the Tettigellinae vary widely in their habits and behavior, they have one characteristic in common—they feed from the xylem of their plant hosts. Several of them seem to obtain all their food from this source, a feature that appears to be critical in natural transmission of phony peach, because the virus itself is confined to the woody cylinder of its hosts. The five leafhopper species described in this bulletin have some habits in common, although they vary notably in others. It appears best to present our data in a general manner, indicating the similarities and dissimilarities among the different species with regard to their seasonal behavior and feeding habits.

### Seasonal Progression

**Hibernation.**—All five species normally overwinter as adults. However, nearly grown nymphs of *coagulata*, *undata*, and *costalis* may begin hibernation as nymphs and transform to adults during warm

periods early in the winter. Once fifth-instar nymphs of *undata* were collected while feeding on laurelcherry on March 31.

In middle Georgia *coagulata*, *undata*, *versuta*, and *insolita* move to wooded areas with the advent of cold weather and spend the entire winter there. They may overwinter in hedgerows or in and around farm buildings, but no direct evidence of such a habit has been obtained. In contrast to the other sharpshooters, *costalis* spends its winters in open fields, orchards, or along the margins of woods, seeking shelter under such matted grasses as Bermuda grass and crabgrass.

Hibernation is incomplete for all five species. The insects are quiescent during cold periods, but warm, daytime temperatures induce appreciable activity, including feeding and, for those species sojourning in woods, considerable flying. At times during the winter specimens have been observed on deciduous trees feeding on the twigs, which may be 15 or 20 feet aboveground. All attempts to carry individuals of *coagulata* over the winter at continuous low temperatures have resulted in death of the insects within less than 2 weeks. Probably feeding at intervals throughout the winter is obligatory for some species.

**Spring.**—When the weather commences to warm up in late winter or early spring, which is from mid-February to early March in central Georgia, insect activity becomes more and more general. *O. undata* leaves the woods rather early. By early April considerable numbers may be found feeding on twigs of peach trees and on many other trees and shrubs growing in open fields and around homesteads. *H. coagulata* appears to be more reluctant to leave the woods, and except for an occasional individual its spring migration lags behind that of *O. undata* by as much as 3 or 4 weeks. So for a limited time *undata* appears to be more abundant than *coagulata*, although actually the latter species was always much more numerous in the area investigated. This early-spring behavior is also anomalous, in that all members of the dilatory species finally leave the woods, whereas an appreciable percentage of the more precocious species remains in the woods throughout the year.

After considerable populations of these two species appear rather suddenly in the field during late March and April, the numbers of adults gradually decline as overwintering insects die off, so that adult populations are at a low ebb in May and individuals are difficult to find. When first-generation adults appear early in June, the numbers rapidly increase, and the adult populations reach their peak during the latter half of June or early in July.

*H. insolita* and *G. versuta* both leave their hibernation quarters by early March, the former moving immediately to grasses and the latter settling on shrubs and perennials, such as wild, or chickasaw, plum, privet, and blackberry.

No marked spring migration of *costalis* occurs. These insects feed on rejuvenated perennial grasses or on low-growing biennials, such as evening-primrose, in the immediate localities where they overwintered, or they move only short distances to find satisfactory food plants.

*H. coagulata* and *O. undata* mostly confine their feeding to twigs of woody plants until such time as stout-stemmed annuals (e. g., sun-

flower, hollyhock) reach a satisfactory stage of growth—an indefinite period from mid-May to early June. *G. versuta* always prefers perennial plants. Though occasional specimens may be found feeding on tender new growth of shrubs and trees, most of these insects spend the entire spring on such hosts as blackberry and ragweed or young cultivated plants, such as sunflower or cotton.

*C. costalis* largely feeds on grasses, but it also feeds in early spring on low-growing broad-leaved weeds. Later in the season some individuals transfer to the stems of taller annuals, such as cotton, sunflower, or ragweed, and even to seedlings of such woody plants as peach.

*H. insolita* is more strictly a grass feeder, seldom being found on any other host.

**Summer.**—During the summer *coagulata* and *undata* feed largely on weeds and certain field crops. However, occasional individuals continue to feed on peach and other tree hosts throughout the summer. If peach trees decline from any cause, such as winter injury or severe scale damage that induces "sour sap," *coagulata* in particular swarms to such trees in great numbers.

*C. costalis* and *H. insolita* attack grasses almost entirely, although the former may still be taken occasionally on crop plants or on broad-leaved weeds. *G. versuta* continues to be a rather diffuse feeder, exhibiting no striking host preferences among the various broad-leaved annuals and perennials. Individual insects may be taken on wild plum and other shrubs or on young trees in hedgerows and thickets.

**Late Summer and Fall.**—In late summer as their favored weeds and field crops begin to mature and dry up, *coagulata* and *undata* transfer more rapidly to woody plants. This movement may begin in late August. By mid-September it is in full swing, and by early October practically all feeding is confined to trees and shrubs. It is at this time that individuals are found on peach trees in greatest numbers.

*G. versuta*, with more cosmopolitan tastes as to herbaceous food, continues to feed on many of the late-blooming Compositae throughout the fall, and no marked trend on the part of this species to seek woody plants at this time of year has been observed. As might be anticipated, during the fall *costalis* feeds more and more on grasses and *insolita* feeds exclusively on this host.

With the maturing of the second generations, *coagulata* and *insolita* increase appreciably in numbers during late September and early October. This particular phenomenon has not been observed for the other three species. In fact *undata* appears to be at its lowest ebb at this time. Since these observations are partly based on data obtained with sticky-board traps, it is quite possible that they do not present an entirely true picture. During the specified period *coagulata* is moving from herbaceous to woody hosts, and *insolita* appears to be very active, perhaps preliminary to migration into winter quarters. On the other hand, *versuta* does not appear to experience any seasonal restlessness at this time, and *costalis*, with no change of host and no fall migration in prospect, is notably quiescent. No explanation of the comparative scarcity of *undata* is forthcoming.

Those species that winter in the woods begin gradually moving from the fields as early as mid-October in some years. The migration is long and drawn out, its rate depending on the occurrence or absence of cold spells of limited duration rather than on general mean temperatures. Usually most of the insects are in the woods by the first of December, but during the abnormally warm autumn of 1947 considerable numbers of *coagulata* were still in peach orchards as late as December 15. In 1948 the fall was again unusually warm, and large numbers of *coagulata* that were feeding in oak trees in the open on December 28 were killed as the result of a sudden freeze.

### Mating and Oviposition

The adults of *costalis*, wintering under matted grass, have been observed in copula as early as January 19, and several mating pairs have been seen during January and February. Such early sexual activity does not appear to result in very early reproductive activity. The earliest date on which we have found egg clusters is March 8. Undoubtedly other clusters have been overlooked, and oviposition may commence sooner than the first of March. However, we have never found any hatched eggs prior to April 12. Mating pairs have been observed during every month from January to August, except July, indicating a pronounced overlapping of generations during each year.

Because of the manner in which *coagulata* and *undata* hibernate and start their yearly activities in early spring, it has not been feasible to observe their foremost matings. Our earliest records for these species were made in April. Actually copulation must occur rather commonly at least in March, because egg masses of *coagulata* have been found in April and once in 1952 as early as April 4. Similarly, egg masses of *undata* have been noted as early as April 5 in 1951 and April 9 in 1952. Mating pairs of *coagulata* have been taken monthly from April through September. Similar captures of paired *undata* have been made monthly from April through August. Although the data are only generally indicative, the greatest numbers of paired *coagulata* and *undata* were taken in June and July and in April and May, respectively, and the next largest numbers in April and in June and July, respectively.

Very few mating pairs of *insolita* have been observed, largely because of the rather obscure location in which they live and because almost all collections of this species have been made by rigorous sweeping. However, one pair was collected as early as March 17 and other mating couples have been observed in June, July, and August.

Data concerning early-season sexual activities of *versuta* are only fragmentary. Actually our earliest observation of copulation was in May. However, the insects are abundant in the field by March 15, and mating and oviposition by the overwintered generation must occur as early as or earlier than for *coagulata* and *undata*. Later observations on mating pairs have been made monthly from June through September.

The four members of the Proconiini—*coagulata*, *undata*, *costalis*, and *insolita*—lay their eggs in clusters. The eggs are inserted just

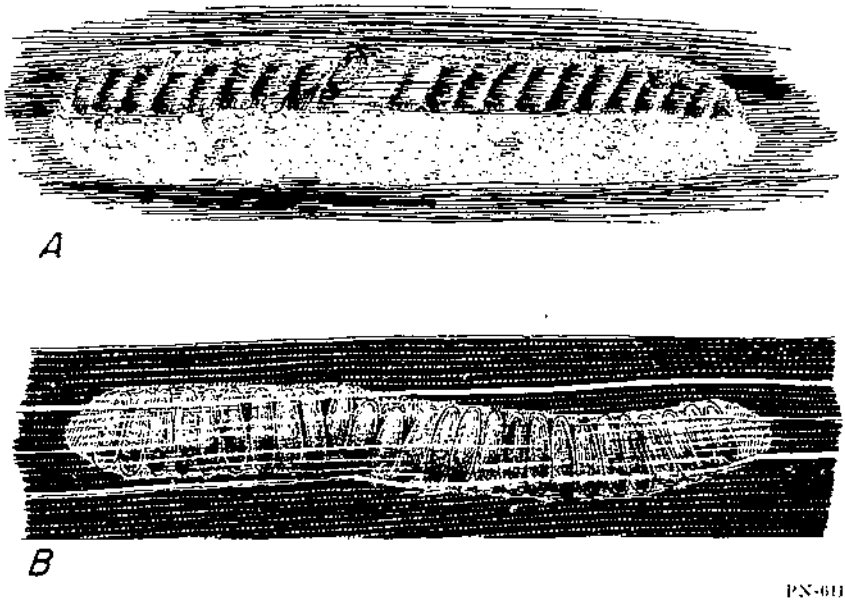


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FIGURE 2.—Egg mass of *Oncometopia undata* in stem of pokeweed (*A*) and of *Cuerna costalis* in blade of Johnson grass (*B*). X 6½.

under the epidermis of a leaf or of a tender plant stem. A clutch consists of 3 or 4 to 28 eggs, the former the result of some interference with the ovipositing female. The eggs lie closely side by side in a single layer. Each egg is inserted independently of the others, but the female deposits them so neatly that the individual oviposition punctures are alined almost straight or in a very slight, even arc. The eggs are inserted deeply enough so that they are fully covered by the epidermis of the supporting leaf or stem, but the covering is so thin that the outline of each egg may be discerned without magnification. As the eggs mature, a change of color may be detected, and when the red eye spots develop shortly before hatching, these spots are strikingly evident. (Fig. 2, *A* and *B*.)

After the completion of a single clutch, the *undata* female covers the entire area with a heavy chalk coating secreted from the anal region. *H. coagulata* and *insolita* also secrete the chalky material, but they coat their egg batches much more lightly. Sometimes the coating is hardly noticeable after a day or two. An interesting habit has been observed in connection with this chalky secretion. The gravid females occasionally stroke the tips of their bodies with their hind tibiae, transferring some of the chalk to their legs. Then bringing the tibiae forward, they transfer the material to their elytra by rubbing them with a circular motion. The action leaves rather large, round spots of chalk on the elytra. These dry quickly and usually remain in place during the rest of the insect's life.

*C. costalis* does not produce the chalky material and of course does not cover its egg clusters as do the other three species.

In the choice of oviposition sites these four species exhibit some very interesting differences in behavior, which in no way conform to taxonomic relationships. In confinement all the species will lay eggs on peach and wild plum, although this procedure appears to be very abnormal under natural conditions. When caged on these hosts, three species oviposit in leaves, showing little if any choice between upper and lower surfaces, whereas *insolita* lays only in twigs.

The observed host plants of the five leafhopper species are recorded in table 2. Under natural conditions *coagulata* oviposits mostly in the leaves of herbaceous plants, both annuals and perennials, although occasional egg packets have been found in the leaves of woody plants. All the observed egg packets were inserted in the lower surface of the leaves, with one exception. One batch was found in the upper surface of a redbud leaf.

TABLE 2.—*Hosts of phony peach insect vectors, based on field oviposition records, 1949–55*

| Host | *Homalodisca coagulata* | *Oncometopia undata* | *Cuerna costalis* | *Homalodisca insolita* | *Graphocephala versuta* |
|---|---|---|---|---|---|
| WOODY PLANTS | | | | | |
| Ash | X | X | | | |
| Crapemyrtle | X | | | | |
| Elderberry | X | | | | |
| Honeysuckle | | X | | | |
| Peach | | | X | | |
| Plum, chickasaw | | X | | | |
| Privet | X | | | | |
| Redbud | X | X | | | |
| Silktree | | X | | | |
| HERBACEOUS PLANTS | | | | | |
| Blackberry | | X | | | |
| Coffeeweed | X | X | | | |
| Cowpea | | | X | | |
| Dahlia | | X | | | |
| Dock | | X | | | |
| Grasses: | | | | | |
| Bermuda | | | X | | |
| Crabgrass | | | X | X | |
| Johnson | X | X | X | | |
| Texas millet | | | X | X | |
| Greenbrier | | X | | | |
| Hibiscus | | X | | | |
| Hollyhock | X | X | | | |
| Lambsquarters | X | X | | | |
| Okra | X | X | | | X |
| Pokeweed | | X | | | |
| Ragweed | | X | | | X |
| Sunflower | X | X | | | X |

*O. undata* is less consistent in its choice of sites for oviposition. It too mostly prefers herbaceous to woody plants, but it lays its eggs rather indifferently in both leaves and stems. Like *coagulata*, it prefers the lower surface when ovipositing in leaves, the only exception in our observations again being the redbud. Our records of *undata* are much more numerous than those of *coagulata*—undoubtedly because the heavily whitened egg packets of the former are so much more conspicuous than those of *coagulata*.

*C. costalis* and *H. insolita* oviposit in grasses, the former in the lower surface of the blades, the latter in the leaf sheaths. The eggs of *insolita* have been found only in Johnson grass and Texas millet, except for a single cluster observed in crabgrass. Those of *costalis* have been observed in Johnson and Bermuda grass, as well as in Texas millet and crabgrass. One batch of eggs of this species was found in the lower surface of a cowpea leaf and another in the upper surface of a low-hanging peach leaf. This last site was undoubtedly abnormal.

In contrast to the other four species, *versuta* lays its eggs singly. These are deposited just under the epidermis of leaves and are apparent as very small wet spots, an effect probably due to the separation of the epidermis from the leaf parenchyma during oviposition. As with the other vectors, *versuta* will lay eggs in peach leaves when confined on them. However, we have never observed the eggs on peach in the open, nor have we ever found nymphs on this host. In the field, eggs have been found in the leaves of ragweed, sunflower, and okra. Eggs can be detected only as the result of tedious searching, and it seems certain that the species must oviposit in many other annuals and perennials, since small nymphs have been observed, sometimes in abundance, on such plants. This is particularly true of blackberry. Under natural conditions all eggs we have found have been laid in the upper side of the leaves.

## Food Plants

Since all five species of leafhoppers are about equally effective in the experimental transmission of phony peach, a knowledge of their natural feeding habits, particularly their definite association or lack of association with peach, is of paramount importance as a guide to weighing their probable role as natural vectors of the disease.

Most of these sharpshooters are found on a great variety of plants. *H. insolita* appears to confine its choice to a limited number of grasses, but the other four species accept a very wide range of food plants, apparently without reluctance. As an example, *coagulata* has been observed feeding naturally on over 100 species of plants belonging to 31 families, from Pinaceae to Compositae (table 3). Its actual food range is even wider, since new hosts are being recorded yearly. The list of observed hosts of *undata* is slightly smaller, undoubtedly because this species is much less abundant than *coagulata* in central Georgia and consequently has been less frequently observed in the field. All available data suggest that *undata* will feed naturally on any plant that *coagulata* will feed on and vice versa.

TABLE 3.—*Food plants of phony peach insect vectors*

| Host | *Homalodisca coagulata* | *Oncometopia undata* | *Cuerna costalis* | *Homalodisca insolita* | *Graphocephala versuta* |
|---|---|---|---|---|---|
| **WOODY PLANTS** | | | | | |
| Anacardiaceae: | | | | | |
| Mango (*Mangifera indica*) | | X | | | |
| Sumac (*Rhus* sp.) | X | X | | | |
| Aquifoliaceae: | | | | | |
| Hollies (*Ilex* spp.) | X | X | | | |
| Yaupon (*Ilex vomitoria*) | X | | | | |
| Bignoniaceae: | | | | | |
| Catalpa (*Catalpa bignonioides*) | X | | | | |
| Trumpetcreeper (*Campsis radicans*) | X | X | X | | |
| Caprifoliaceae: | | | | | |
| Elderberry (*Sambucus canadensis*) | X | | | | |
| Honeysuckle (*Lonicera japonica*) | | | | | X |
| Elaeagnaceae: | | | | | |
| Elaeagnus (*Elaeagnus* sp.) | X | X | | | |
| Euphorbiaceae: | | | | | |
| Tung (*Aleurites fordii*) | X | X | | | |
| Fagaceae: | | | | | |
| Oaks (*Quercus* spp.) | X | X | | | X |
| Ginkgoaceae: | | | | | |
| Maidenhair-tree (*Ginkgo biloba*) | X | | | | |
| Hamamelidaceae: | | | | | |
| Sweetgum (*Liquidambar styraciflua*) | X | X | | | |
| Juglandaceae: | | | | | |
| Pecan (*Carya illinoensis*) | | X | | | |
| Walnut, black (*Juglans nigra*) | | X | | | |
| Lauraceae: | | | | | |
| Sassafras (*Sassafras albidum*) | X | | | | |
| Leguminosae: | | | | | |
| Redbud (*Cercis* sp.) | X | X | X | | |
| Silktree (*Albizzia julibrissin*) | X | X | X | | |
| Wisteria (*Wisteria* sp.) | X | | | | |
| Liliaceae: | | | | | |
| Yucca (*Yucca aloifolia*) | X | X | | | |
| Lythraceae: | | | | | |
| Crapemyrtle (*Lagerstroemia indica*) | X | X | X | | |
| Magnoliaceae: | | | | | |
| Sweetbay (*Magnolia virginiana*) | X | | | | |
| Meliaceae: | | | | | |
| Chinaberry (*Melia azedarach*) | X | | | | |
| Moraceae: | | | | | |
| Fig (*Ficus*) | X | | | | |
| Nyssaceae: | | | | | |
| Blackgum (*Nyssa sylvatica*) | X | | | | |
| Oleaceae: | | | | | |
| Ash (*Fraxinus* sp.) | X | X | | | X |
| Jasmine (*Jasminum primulinum*) | X | | | | |
| Privet (*Ligustrum* sp.) | X | X | X | | X |
| Pinaceae: | | | | | |
| Arborvitae (*Thuja* sp.) | X | | | | |
| Pine (*Pinus palustris*) | ? | | | | X |
| Pittosporaceae: | | | | | |
| Pittosporum (*Pittosporum* sp.) | X | | | | |
| Rosaceae: | | | | | |
| Apple (*Malus sylvestris*) | X | X | | | |
| Cherry, black (*Prunus serotina*) | | | | | X |
| Cotoneaster (*Cotoneaster* sp.) | X | X | | | |
| Firethorn (*Pyracantha coccinea*) | X | X | | | |

TABLE 3.—*Food plants of phony peach insect vectors*—Continued

| Host | *Homalodisca coagulata* | *Oncometopia undata* | *Cuerna costalis* | *Homalodisca insolita* | *Graphocephala versuta* |
|---|---|---|---|---|---|
| **WOODY PLANTS—continued** | | | | | |
| Rosaceae—Continued | | | | | |
| Laurelcherry (*Prunus carolliniana*) | X | X | | | X |
| Peach (*Prunus persica*) | X | X | X | X | X |
| Pear (*Pyrus communis*) | X | | | | X |
| Plum, chickasaw (*Prunus angustifolia*) | X | X | X | | X |
| Plum, cultivated (*Prunus* spp.) | X | X | | | |
| Salicaceae: | | | | | |
| Willow (*Salix nigra*) | | X | | | |
| Theaceae: | | | | | |
| Camellia (*Camellia japonica*) | X | X | | | |
| Ulmaceae: | | | | | |
| Elm (*Ulmus americana*) | | | | | X |
| Vitaceae: | | | | | |
| Grapes (*Vitis* spp.) | X | X | X | | X |
| **HERBACEOUS PLANTS** | | | | | |
| Amaranthaceae: | | | | | |
| Pigweed: | | | | | |
| (*Amaranthus hybridus*) | X | X | | | |
| (*Amaranthus spinosus*) | X | X | | | |
| Asclepiadaceae: | | | | | |
| Milkweed (*Asclepias* sp.) | X | | | | |
| Chenopodiaceae: | | | | | |
| Lambsquarters (*Chenopodium album*) | X | X | | | X |
| Compositae: | | | | | |
| Bitterweed (*Helenium tenuifolium*) | | | | | X |
| Boneset (*Eupatorium perfoliatum*) | X | | | | |
| Chrysanthemum (*Chrysanthemum* sp.) | | | | | X |
| Cocklebur (*Xanthium* sp.) | X | X | | | X |
| Dahlia (*Dahlia* sp.) | | X | X | | |
| Dogfennel (*Eupatorium capillifolium*) | X | | | | |
| Goldenglow (*Rudbeckia laciniata* var. *hortensia*) | X | | | | |
| Goldenrod (*Solidago* sp.) | X | X | | | X |
| Horseweed (*Erigeron canadensis*) | X | | | | |
| Lettuce, wild (*Lactuca canadensis*) | X | X | | | |
| Ragweed (*Ambrosia artemisiifolia*) | X | X | X | | X |
| Sunflower (*Helianthus* spp.) | X | X | X | | X |
| Cruciferae: | | | | | |
| Turnip (*Brassica rapa*) | | | X | | X |
| Geraniaceae: | | | | | |
| Geranium, wild (*Geranium* sp.) | | | | | X |
| Gramineae: | | | | | |
| Bermuda grass (*Cynodon dactylon*) | | | X | | |
| Corn (*Zea mays*) | X | X | | | |
| Crabgrass (*Digitaria sanguinalis*) | | | X | X | X |
| Johnson grass (*Sorghum halepense*) | X | X | X | X | X |
| Rye (*Secale cereale*) | | | | | X |
| Ryegrass (*Lolium multiflorum*) | | | X | | |
| Texas millet (*Panicum texanum*) | | | X | X | |
| Wheat (*Triticum aestivum*) | | | X | | |
| Iridaceae: | | | | | |
| Gladiolus (*Gladiolus* sp.) | X | | | | |

TABLE 3.—*Food plants of phony peach insect vectors*—Continued

| Host | *Homalodisca coagulata* | *Oncometopia undata* | *Cuerna costalis* | *Homalodisca insolita* | *Graphocephala versuta* |
|---|---|---|---|---|---|
| HERBACEOUS PLANTS—continued | | | | | |
| Labiatae: | | | | | |
| Wild bergamot (*Monarda fistulosa*) | X | | | | |
| Leguminosae: | | | | | |
| Coffeeweed: | | | | | |
| (*Cassia occidentalis*) | X | X | X | | |
| (*Cassia tora*) | X | X | X | | |
| Cowpea (*Vigna sinensis*) | X | X | X | | X |
| Lupine, blue (*Lupinus angustifolius*) | | | X | | |
| Peas, Austrian (*Pisum sativum* var.) | | | X | | |
| Peas, garden (*Pisum sativum*) | | | X | | |
| Liliaceae: | | | | | |
| Asparagus (*Asparagus officinalis*) | X | | | | |
| Malvaceae: | | | | | |
| Cotton (*Gossypium herbaceum*) | X | X | X | | X |
| Hibiscus (*Hibiscus* sp.) | | X | | | |
| Hollyhock (*Althaea rosea*) | X | X | X | | X |
| Okra (*Hibiscus esculentus*) | X | X | X | | X |
| Onagraceae: | | | | | |
| Evening-primrose: | | | | | |
| (*Oenothera biennis*) | | | X | | X |
| (*Oenothera laciniata*) | X | X | | | |
| Phytolaccaceae: | | | | | |
| Pokeweed (*Phytolacca americana*) | X | X | X | | |
| Polygonaceae: | | | | | |
| Dock (*Rumex* sp.) | | | X | | |
| Rosaceae: | | | | | |
| Blackberry (*Rubus* spp.) | | X | | | X |

Even so, these two species do exhibit a certain amount of food preference. In central Georgia, sunflower, hollyhock, okra, and lambsquarters are favored herbaceous hosts, together with such field crops as cotton, corn, and cowpeas. Our observations have not been sufficiently exhaustive to designate the outstanding favorites among woody plants. However, oak, ash, silktree, and crapemyrtle are near the top of the list and peach is undoubtedly a favorite.

The selection of a woody host at any one time appears to depend considerably on the temporarily satisfactory condition of that plant and equally on the unsatisfactory condition of alternate food plants. During 3 consecutive years large numbers of *coagulata* and *undata* were attracted in early spring to ash trees growing in a nursery. They were not found on this host until new growth started, and they left as soon as the new leaves were fully opened. In 1948 and 1949 *coagulata* fed very freely on crapemyrtle bushes of varying size near Fort Valley. Since then no specimens have been found on these particular plants. In 1948 and 1949 large numbers were taken on crapemyrtle growing in a nursery near Fort Valley. Subsequently, very few were found on crapemyrtle in this nursery until 1952, when they were again abundant. Many other variables and unconformities might be recorded with regard to the feeding habits of *coagulata*

and *undata*. However, two features of these phony peach vectors are outstanding: (1) Their wide choice of food plants, with the subsequent effect on efforts to control the species with insecticides; and (2) their pronounced attraction to peach as a favored host, particularly during the spring and fall.

The older nymphs of these two species have been collected on almost all hosts that have been recorded for the adults. However, nymphs in the first two instars are generally unable to survive on woody plants. Many times when gravid females confined in tight cloth cages have laid eggs in the leaves of peach or plum, all resulting nymphs died without reaching the second instar. All attempts failed to rear the younger stages on peach twigs in an insectary. Some newly hatched individuals did develop very slowly and molted once, but all died during the second instar.

Although *versuta* feeds indifferently on woody and herbaceous hosts, no seasonal migration from one type to the other has been observed, nor has evidence been obtained that indicates any pronounced attraction to woody hosts at any time. Scattered specimens are commonly found on wild plum throughout most of the growing season. Individual insects are occasionally taken on peach, but any association between this leafhopper and peach appears to be casual.

*C. costalis* feeds for the most part on a wide variety of grasses, low-growing herbs, such as evening-primrose, and seedlings of both herbaceous and woody plants, particularly when they are growing in grassy areas. Sudden clean cultivation of infested grass plots is particularly effective in driving this leafhopper to other host plants. At times *costalis* is found feeding on tall-stemmed plants as much as 4 or 5 feet aboveground. However, this species generally likes to stay close to the soil.

*H. insolita* limits its choice even more to a small group of grasses. Thus far we have found it commonly only on Johnson grass and Texas millet, except in one locality in northwestern Florida, where it was feeding freely on another *Panicum* (?) too immature for identification. However, the adults have been observed twice on peach, once on a twig about 6 feet aboveground and once on low-hanging twigs of a dehorned tree.

Although *costalis* frequently feeds on young peach seedlings and individuals have been taken occasionally from older trees, there is no evidence of any regular association of either *costalis* or *insolita* with peach orchard trees.

## Feeding Habits

The adults and older nymphs of *coagulata* and *undata* feed on stems of their hosts or occasionally on stout leaf petioles of such plants as sunflower, okra, and cotton. The nymphs in the first two instars usually feed on the larger veins of the leaves and mostly on the undersurface. On stems or twigs the insects assume a position parallel to the axis, with the head downward. This last trait is very pronounced. With few exceptions they adopt a head-up position only immediately after or preparatory to flight. On trees these insects seldom feed on horizontal twigs, but select shoots that are growing upward—a char-

acteristic that further emphasizes the importance of the head-down position. However, on grapes they feed rather freely on horizontal canes when acceptable upright shoots are not available, and no orientation toward or away from the main trunk is observable.

The adults rarely walk forward on twigs. If disturbed, they dart very rapidly sideways around the twig, placing it between themselves and the cause of the disturbance. The exact nature of their vision is not known. Although they can distinguish between colors as demonstrated by their reaction to different-colored sticky boards, they probably register movement more than form.

When someone approaches an infested plant, nearly all the insects will dart around to the back of the stem or twig on which they are resting. This action takes place when the person is still several feet from the plant. On the other hand, if someone stands within a foot or two of an occupied twig and moves any object behind and close to the twig, the insects on the back side will move around to the side facing the observer and frequently will remain there unless again disturbed by a quick movement on the part of the observer. It is this habit of hiding, particularly marked in *coagulata* and *undata*, that led to the original designation of sharpshooters for these particular insects, a term that has been extended to include all members of the subfamily, even some species in which the trait is not strongly developed.

During much of the year both *coagulata* and *undata* tend to be solitary feeders, particularly when a favored host is locally abundant, as commercial plantings of okra or cotton. Then only an occasional plant is infested. Seldom are more than one or two insects found on a single plant. On the other hand, small plantings of okra, such as in home gardens, or small patches of sunflower may be heavily infested with as many as 15 to 20 sharpshooters on one individual host. Gregariousness is also exhibited on weak trees or even on single limbs if they are dying from severe scale injury or are prematurely defoliated from some other natural cause. Artificial defoliation of peach limbs in early fall does not noticeably attract the insects. Extreme examples of gregariousness have been noted. Over 120 *coagulata* leafhoppers were collected from one very weak peach tree, and many others were seen. In late December over 500 individuals were observed on the ground under a large willow oak on the morning after a severe freeze. Very few could be found under five other oaks growing in the same yard.

On herbaceous plants *coagulata* tends to feed well up on the stems, frequently as high as 8 or 10 feet on tall sunflowers. Also, this species appears to have a particular aversion to heavy shade. Although *undata* may be found feeding in the immediate vicinity of *coagulata*, generally it tends to locate nearer the ground.

The young of both these species from the third to the fifth instars have feeding habits generally similar to those of the adults. The nymphs are notably solitary in habit by the time they become large enough to feed on stems, even though the eggs from which they have hatched are laid in packets. Seldom are more than two nymphs observed on one host plant, and generally they feed singly. This phenomenon may result from a high mortality among young nymphs. On the other hand, these nymphs are powerful jumpers and their range

is rather wide. Thus the young from one batch of eggs may disperse over a considerable area by the time they are half grown.

Sharpshooters do not appear to be attracted to stout-stemmed herbaceous plants until the stems have become rather woody. When feeding on peach, they decidedly prefer year-old twigs as compared with growth of the current year. On the other hand, new growth of ash, crapemyrtle, silktree, and grape appears to be more attractive than older wood.

The other two members of the Proconiini—*costalis* and *insolita*—exhibit the traits and habits of sharpshooters, modified by the nature of their host plants and microenvironment. When feeding on tall-stemmed plants *costalis* behaves just like *coagulata* and *undata*, except that it is apt to locate even lower on a stalk than *undata*. Both *costalis* and *insolita* feed head down on the stems of their principal hosts, the grasses, or occasionally on the midribs of the blades. Because grasses grow so densely, numerous adults and nymphs are commonly found living within a limited area, simulating gregariousness, but one grass stem is usually occupied by only one insect. Large local populations appear to result from failure to disperse, owing partly to the lack of any need to seek acceptable food rather than to any tendency to congregate.

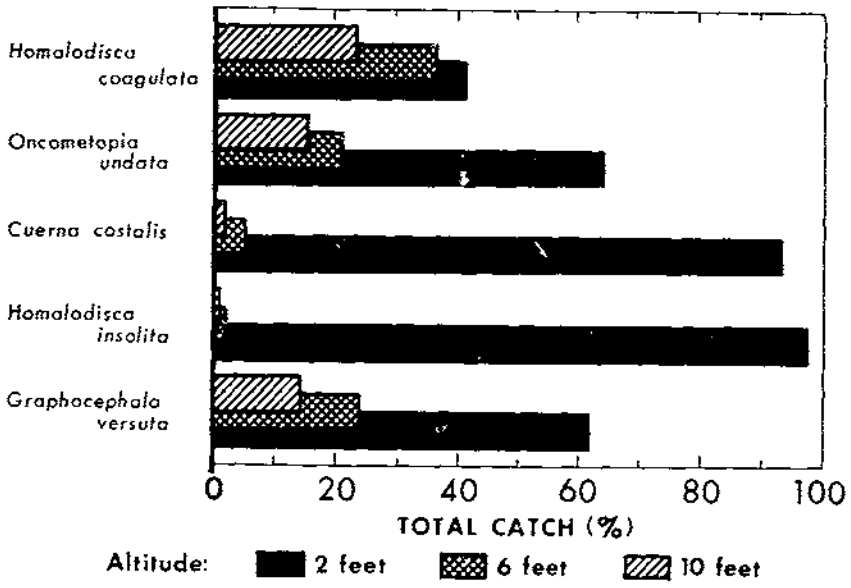
Unlike the members of the Proconiini, *versuta* uses stems as only one of its feeding sites. Many adults will be found on leaves, frequently on the upper surface. *G. versuta*, which lays eggs singly, tends much more toward gregariousness, especially in the nymphal stages, than the species that lay their eggs in clusters. However, *versuta* is more generally and evenly distributed than the other species, possibly because of its greater abundance and its comparative lack of selectivity in picking its host plants.

### Flight Characteristics

In an attempt to obtain information concerning altitude of flight and seasonal movements to and from wooded areas, 6 special assemblages of sticky-board traps were set up around a small woodland of deciduous trees at the United States Horticultural Field Laboratory near Fort Valley, Ga. A single assemblage comprised 12 boards attached to a pole. The boards were arranged in 3 groups of 4 boards each, located at distances of 2, 6, and 10 feet aboveground when measured to the bottom of the boards. The poles were so oriented that the 4 boards of each group faced the 4 cardinal points of the compass.

Insofar as developing information on direction of flight, the experiment failed. It quickly became evident that an insect flying from north to south was as apt to veer and light on the east- or west-facing board as it was to fly directly to the board that faced due north. On the other hand, the installation did furnish very satisfactory data concerning the general altitude at which the different species of sharpshooters fly.

The assemblages of traps were installed in 1950 and have been maintained continuously since that time. The data obtained each year from 1950 through 1954 conformed notably, except once or twice when the total catch of a species was too small to furnish reliable figures.




BN-6161

FIGURE 3.—Comparative flight altitudes of five insect vectors of phony peach, showing percentage of total catch at indicated heights, 1950–55.

Figures for the 5-year period are presented graphically in figure 3.

Because of certain weaknesses in the attraction of sticky-board traps, our records probably deal only with the local activities of the insects involved. No exact data have been obtained on distances commonly flown or on the altitude of flight during movements of any appreciable magnitude. It is true that many of the trapped insects were migrating to or from the woods. Although some members of the four species that hibernate in woods travel considerable distances each spring and fall, probably these migrations are broken up into several short movements.

Throughout the Southeastern States Johnson grass, crabgrass, and Bermuda grass are very common weeds. Hence, it is easily conceivable that *costalis* is a rather sedentary species. It might be anticipated that *insolita* would also move about very little, at least during the growing season. Survey data furnished strongly presumptive evidence that this species extended its range some 1,000 or 1,500 miles in a period of about 10 years, during which it thoroughly invaded the area into which it moved. However, once the species has attained a state of equilibrium in the newly invaded territory, it appears doubtful that most of its members will move far from where they are hatched.

Because of their more diverse feeding habits, the range of *coagulata* and *undata* might be greater than that of *costalis*. This is partly true, but when obliged to change hosts even *coagulata* and *undata* commonly seek the nearest acceptable food plants rather than make long flights. These species sometimes concentrate on summer herbaceous hosts outside, but closely adjacent to, peach orchards. After these

summer hosts mature, numbers of sharpshooters are commonly found concentrated on peach trees in the first 4 or 5 rows of the orchards. Similarly phony peach spreads within a young orchard immediately adjacent to an older infected orchard.

Exceptions do occur. Individual trees sometimes overwhelmingly attract insects over very appreciable distances. For example, *coagulata* may be lured all the way across a large block of trees. The situation is demonstrated rarely when the first case or cases of phony peach in a new planting occur on the opposite side of the planting from the nearest source of inoculum.

Although most individuals of the five leafhopper species appear to be rather circumscribed in their movements, occasionally insects move farther during the growing season. These moves may be deliberate, but probably most of them are accidental. In collections of single specimens of *coagulata* and *undata* at altitudes of 3,000 feet (*2, p. 65*), the insects must have been caught by wind currents and blown about involuntarily, and presumably the more numerous specimens collected at 300 feet were not there voluntarily.

### Fluctuating Populations

During the late forties *coagulata*, *undata*, *versuta*, and *costalis* were abundant in central Georgia, and the annual incidence of new cases of phony peach reached a high level. In late November 1950 a severe freeze occurred, with minimum temperatures as low as 8° F. Not only was this freeze unusually low for the Southeast but it was most unseasonal. As a result, large numbers of unprotected sharpshooters still feeding in orchards and open fields were killed.

The following year *coagulata* and *undata* were notably scarce and the number of *versuta* decreased obviously. Even *costalis* was affected to some extent, though less than the other species. During the next 2 or 3 years the rate of spread of phony disease declined even though populations of all four species built up to some extent, but not to the prefreeze level.

A prolonged drought and excessively high temperatures during the entire summer prevailed in 1954. Populations of all species, including *insolita*, were normal during the spring but progressively decreased as the summer advanced. In the fall of 1954 collections with sticky-board traps were the lowest in 5 years, and records obtained from traps hung in wooded areas indicated that very few sharpshooters were moving into hibernation quarters. In 1955 populations of all five species were the smallest that we had observed during 10 years of study. Again the rate of spread of the phony virus declined.

General use of the new organic insecticides in peach orchards during the spring and again in late summer and early fall, together with widespread use of these materials on cotton and other field crops throughout the growing season, may have contributed to the present recession in vector populations, but such possible effects are not measurable or even demonstrable. On the other hand, circumstantial evidence of the effect of severe climatic phenomena is too strong to question.

### Rearings

As has been reported by other workers (*1*), it is difficult to rear any member of the Tettigellinae in confinement. Of the five species, only the grass feeders *costalis* and *insolita* have been maintained through direct lineage from early spring to late fall. *O. undata* has been carried through two full generations and the first four instars of a third. *H. coagulata* has been reared lineally through the fourth instar of the second generation. In addition, this species has been reared to the adult stage from field-collected eggs that were laid well after second-generation adults of *coagulata* had appeared in our lineal rearings. Data from field observations on seasonal abundance of adults and various nymphal stages, percentage of mating insects, and egg-laying activities furnish strongly presumptive evidence that these last insects represent a partial third generation.

*G. versuta* has been reared directly through three generations. In addition, two full generations were reared, starting with field-captured nymphs contemporaneous with reared nymphs of the third generation. This incomplete evidence that *versuta* has four full generations a year is supported by the evidence (table 4) that the nymphal periods of *versuta* are appreciably shorter than those of the other species.

Most of the life-history studies were conducted in an insectary. It was a frame roofed building with wide eaves. The lower side walls were boarded: the upper 4 feet from the top of the benches to the eaves was covered with 16-mesh screen. Conditions were not entirely satisfactory, since the host plants never received direct sunlight. Such plants soon lost their effectiveness as food sources, and the hosts had to be replaced more frequently than would otherwise have been necessary. Sometimes nymphs that lingered in one instar for a considerable time transformed to the next instar very quickly when moved to fresh plants. Also data obtained as a result of a few rearings in out-of-door cages indicated that the developmental period for the insects reared in the insectary was somewhat longer than that occurring under more natural conditions.

A number of different plants were tested as possible hosts. It was found that Johnson grass was best for *costalis* and *insolita*, although the former species also developed successfully on Bermuda grass. *H. coagulata* and *O. undata* were more difficult to satisfy. In the early studies sunflower, okra, and cotton were the principal hosts. Cowpeas eventually proved to be the best overall plant under insectary conditions. Cowpeas were also a satisfactory host for *versuta*.

Difficulty in rearing these leafhoppers was partly due to (1) the use of too roomy cages and (2) the accumulation of excessive amounts of honeydew in small cages. Early experience showed that *coagulata* and *undata*, particularly, are very restive under confinement. In wire-screen cages of 2 feet or more, the adults flew against the sides with such force that they killed themselves in a very short time. On the other hand, if several nymphs were confined in smaller cages, many of them became entangled in honeydew, with resultant high mortalities.

Our most successful rearings were accomplished with single nymphs caged in lamp chimneys on plants grown in 6-inch flowerpots. Broad-leaved plants did not survive so well in such cages as they did under screen, but glass sides greatly facilitated observations on development and obviated frequently removing the cages. For mass rearings of *costalis* and *insolita*, wire cylinders over Johnson grass grown in 10-inch pots were quite satisfactory.

**Matings.**—Apparently the females of all five species mate only once. At least secondary matings have not been observed and singly mated females have produced large numbers of eggs that were laid over a considerable period of time.

Under experimental conditions females of all the species have manifested considerable diversity in the length of the preoviposition period, the time varying from approximately 1 day to as much as 9 days with members of the Proconiini. Females of *versuta* have shown even greater variation, the observed extremes being 6 and 20 days.

**Oviposition.**—Although complete oviposition records have been obtained for only one species, *insolita*, incomplete records indicate that all the Proconiini are prolific reproducers. One female *insolita* laid 65 clusters, totaling 1,170 viable eggs during an oviposition period of 87 days. Several others produced between 600 and 800 eggs apiece.

**Egg Stage.**—Few data have been obtained on the duration of the egg stage. Available figures indicate a marked seasonal variation, presumably due to the effect of temperature. Eggs of *costalis* laid between March 26 and April 2 hatched in from 23 to 32 days. Eggs of *coagulata* and *undata* laid on April 20 hatched in 12 days. In August the total period from mating to hatching for one lot of eggs laid by *costalis* was only 10 days. Eggs of *versuta* laid on April 29 hatched in 16 days. Three lots of eggs laid in August hatched in 8 to 11 days.

**Nymphal Stage.**—Data on the duration of each of the five nymphal stages by generations and by species are presented in table 4. Lacunae in direct lineage records are indicated by the blanks in fifth-instar columns for the second generation of *coagulata* and for the third generation of *undata*.

**Generations.**—Definite evidence has been obtained that *costalis* and *insolita* have two full generations and a partial third one annually. Circumstantial evidence indicates that this is also true for *coagulata* and *undata*. However, there is such marked overlapping of generations by the end of the season that positive proof of the occurrence of a third generation can only be adduced from uninterrupted lineal rearings.

The inevitability of such profound overlapping is manifest when average developmental and oviposition periods are compared. Thus, *insolita* develops from egg to adult in about 44 days during the summer, whereas oviposition periods of as much as 87 days have been recorded. As a result, many first-generation females are still actively ovipositing up to the time when the insects begin to move into winter quarters.

TABLE 4.—*Length of nymphal and adult stages of phony peach insect vectors, Fort Valley, Ga.*[1]

| Stage | 1st generation | | | 2d generation | | | 3d generation | | | 4th generation | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Number reared | Duration of stage | | Number reared | Duration of stage | | Number reared | Duration of stage | | Number reared | Duration of stage | |
| | | Range (Days) | Average (Days) | | Range (Days) | Average (Days) | | Range (Days) | Average (Days) | | Range (Days) | Average (Days) |
| **HOMALODISCA COAGULATA** | | | | | | | | | | | | |
| Nymphal: | | | | | | | | | | | | |
| 1st | 53 | 8–19 | 11. 9 | 22 | 7–15 | 9. 2 | 27 | 6–25 | 8. 4 | | | |
| 2d | 47 | 4–19 | 7. 3 | 18 | 4–8 | 5. 9 | 14 | 5–10 | 7. 4 | | | |
| 3d | 38 | 5–24 | 11. 1 | 13 | 4–11 | 6. 2 | 8 | 7–24 | 11. 8 | | | |
| 4th | 27 | 5–28 | 11. 4 | 11 | 7–24 | 12. 2 | 5 | 8–28 | 16. 6 | | | |
| 5th | 15 | 12–30 | 17. 8 | 0 | | | 2 | 23–33 | 28. 0 | | | |
| Adult | 15 | 5–85 | 64. 1 | 0 | | | 2 | 50–70 | 60. 0 | | | |
| **ONCOMETOPIA UNDATA** | | | | | | | | | | | | |
| Nymphal: | | | | | | | | | | | | |
| 1st | 47 | 8–18 | 10. 7 | 25 | 6–14 | 8. 2 | 27 | 6–15 | 7. 6 | | | |
| 2d | 41 | 5–17 | 9. 0 | 19 | 4–19 | 7. 8 | 12 | 5–12 | 7. 5 | | | |
| 3d | 29 | 4–28 | 10. 9 | 17 | 5–16 | 8. 9 | 6 | 7–12 | 10. 0 | | | |
| 4th | 25 | 5–21 | 11. 4 | 10 | 5–37 | 15. 9 | 3 | 9–21 | 14. 3 | | | |
| 5th | 18 | 8–29 | 15. 1 | 2 | 14–25 | 19. 5 | 0 | | | | | |
| Adult | 18 | 38–70 | 56. 1 | 2 | 61–76 | 68. 5 | 0 | | | | | |

CUERNA COSTALIS

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nymphal: | | | | | | | | | | | | |
| 1st | 82 | 7–35 | 14. 2 | 21 | 7–14 | 7. 2 | 47 | 5–15 | 6. 8 | | | |
| 2d | 75 | 4–35 | 10. 7 | 17 | 5–15 | 7. 8 | 24 | 4–35 | 9. 3 | | | |
| 3d | 71 | 5–19 | 9. 4 | 14 | 4–13 | 7. 1 | 11 | 4–26 | 13. 3 | | | |
| 4th | 63 | 6–33 | 11. 6 | 12 | 5–17 | 9. 7 | 7 | 9–40 | 21. 4 | | | |
| 5th | 44 | 7–35 | 14. 0 | 8 | 12–53 | 25. 9 | 4 | 23–36 | 31. 5 | | | |
| Adult | 44 | 43–97 | 59. 9 | 8 | 35–84 | 59. 9 | 4 | 71–87 | 80. 0 | | | |

HOMALODISCA INSOLITA

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nymphal: | | | | | | | | | | | | |
| 1st | 129 | 5–9 | 7. 7 | 121 | 4–8 | 4. 4 | 153 | 4–10 | 5. 5 | | | |
| 2d | 124 | 5–9 | 5. 6 | 114 | 4–9 | 4. 6 | 137 | 4–9 | 6. 6 | | | |
| 3d | 120 | 5–8 | 5. 5 | 88 | 4–17 | 5. 9 | 107 | 4–14 | 7. 0 | | | |
| 4th | 116 | 5–25 | 6. 9 | 57 | 4–15 | 8. 1 | 87 | 5–14 | 8. 8 | | | |
| 5th | 96 | 5–29 | 12. 1 | 43 | 6–18 | 10. 9 | 72 | 8–42 | 19. 0 | | | |
| Adult | 96 | 30–54 | 37. 8 | 43 | 27–46 | 34. 0 | 72 | 28–77 | 46. 9 | | | |

GRAPHOCEPHALA VERSUTA

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nymphal: | | | | | | | | | | | | |
| 1st | 17 | 6–8 | 6. 2 | 16 | 4–10 | 6. 3 | 11 | 7–11 | 8. 6 | 2 | 5–5 | 5. 0 |
| 2d | 14 | 4–12 | 7. 1 | 15 | 4–15 | 5. 9 | 9 | 3–8 | 6. 0 | 2 | 6–8 | 7. 0 |
| 3d | 11 | 4–8 | 5. 9 | 14 | 4–15 | 6. 7 | 6 | 3–10 | 7. 0 | 2 | 6–6 | 6. 0 |
| 4th | 8 | 5–19 | 8. 4 | 13 | 4–14 | 6. 5 | 4 | 3–10 | 7. 5 | 2 | 7–12 | 9. 5 |
| 5th | 8 | 5–14 | 8. 6 | 12 | 7–17 | 10. 3 | 4 | 9–21 | 13. 0 | 2 | 14–14 | 14. 0 |
| Adult | 8 | 25–41 | 36. 1 | 12 | 26–59 | 35. 7 | 4 | 37–59 | 44. 3 | 2 | 38–45 | 41. 5 |

[1] All species were reared in 1951 except *insolita*, which was reared in 1953.

*G. versuta* has three full generations a year, with strong presumptive evidence for a partial fourth generation.

**Cessation of Mating.**—In our cages no third-generation adults appeared prior to September 1, none laid eggs, nor were any observed in copula. With few exceptions adults of the second generation that matured after September 1 also failed to mate or oviposit. However, females that started oviposition prior to early September continued to lay eggs well into the fall, sometimes as late as November 1. In the field only two mating pairs of *coagulata* were observed during the first half of September and none after the middle of the month. Cessation of mating, then, appears to be seasonal, fully effective in third-generation adults but not completely so for late-developing members of the second generation. The basic factor or factors are unknown. Certainly temperature is not a primary factor, since hot weather frequently prevails in the Fort Valley area well into and often throughout September. Perhaps one basic cause stems from nutritional changes in the maturation of the host plants.

## PARASITES

Hymenopterous parasites were reared from field-collected eggs of all five species of leafhoppers. Data obtained from these rearings are presented in table 5. All the material with two exceptions was collected in the vicinity of Fort Valley. *Lymaenon* sp. was reared from one cluster of *coagulata* eggs collected near Meridian, Miss., and from one cluster of *undata* eggs collected near Plant City, Fla. All the reared egg parasites were identified by A. B. Gahan or B. D. Burks, Entomology Research Division, Agricultural Research Service.

TABLE 5.—*Egg parasites reared from phony peach insect vectors, Fort Valley, Ga., 1949–55*

| Parasite | *Homalodisca coagulata* | *Oncometopia undata* | *Cuerna costalis* | *Homalodisca insolita* | *Graphocephala versuta* |
|---|---|---|---|---|---|
| **MYMARIDAE** | | | | | |
| *Anagrus giraulti* Cwfd | X | | | | |
| *Cosmocomoidea morrilli* How | X | | | | |
| *Lymaenon ashmeadi* (Grlt.) | X | X | X | | |
| *Lymaenon fasciatus* (Grlt.) | X | | | | |
| *Lymaenon novifasciatus* (Grlt.) | | | | | X |
| *Lymaenon* sp. | X | X | | X | |
| **TRICHOGRAMMATIDAE** | | | | | |
| *Abbella acuminata* (Ashm.) | | | X | X | |
| *Oligosita americana* Grlt | | | | X | |
| *Ufens niger* (Ashm.) | | | X | | |
| *Ufens spiritus americanus* Grlt | X | | | | |
| *Ufens spiritus spiritus* Grlt | X | X | | | |

Two species of Strepsiptera were reared from leafhopper adults—*Halictophagus omani* R. Bohart from *costalis* and *H. oncometopiae* (Pierce) from *undata*. The Strepsiptera were identified by Richard M. Bohart, University of California.

None of the parasites appear to be effecting any appreciable amount of economic control. Although considerable numbers of parasitized eggs of both *costalis* and *insolita* may be found in limited areas, the overall percentage of parasitism is very low. This is even more true with *coagulata* and *undata*. It is interesting to note that the three species of Trichogrammatidae—*Abbella acuminata* (Ashm.), *Oligosita americana* Grlt., and *Ufens niger* (Ashm.)—which were reared in greater numbers than all the other species of egg parasites combined, confine their attacks to eggs laid in grasses close to the surface of the ground.

The exact amount of control exercised by the Strepsiptera is not known. Leafhoppers parasitized by these insects are definitely discommoded in walking and hopping, and flight is probably seriously curtailed. On the other hand, the parasites do not appear to prevent completely the normal biological processes of their hosts. At least parasitized females of *costalis* laid viable eggs, although there was some indication that they laid fewer than normal females.

## DISEASES

An unidentified fungus attacks both adults and nymphs of *coagulata* during some years. Diseased specimens have been taken on peach, okra, sunflower, dogfennel, sweetbay, and sassafras. In 1949, when the disease appeared to be more prevalent than in subsequent years, about 50 affected adults were seen on peach twigs in a low area near a swamp. In this particular orchard no diseased specimens were found on higher ground a short distance away. Other collection data support the hypothesis that low altitudes and moist conditions greatly facilitate the operation of the fungus, although occasional affected adults and nymphs have been observed at higher locations under drier conditions. Dead bodies of affected insects cling for many months to the twigs or stems on which they died.

According to our observations this fungus disease is not of present economic importance. It appears doubtful that adequate insect control could be effected through artificial manipulation of the disease organism.

## SUMMARY

Five leafhoppers of the subfamily Tettigellinae have been incriminated as vectors of phony peach. These are *Homalodisca coagulata* (Say), *Oncometopia undata* (F.), *Graphocephala versuta* (Say), *Cuerna costalis* (F.), and *Homalodisca insolita* (Wlk.). The first two species are primary natural vectors. *G. versuta* is next in importance. Whether the last two species induce natural spread, except rarely, is doubtful.

The species *coagulata*, *undata*, *versuta*, and *insolita* hibernate in the woods; *costalis* overwinters under matted grasses in open fields and in

orchards. The first three species are very general feeders, including many trees and shrubs among their hosts. *G. costalis* feeds principally on grasses and herbaceous plants, whereas *H. insolita* restricts its feeding to a few species of grass. Only *coagulata* and *undata* include peach among their favorite host plants. All five species are stem feeders, a critical factor in the transmission of phony peach, which is a xylem-limited disease.

Populations of all five species fluctuate markedly, largely as the result of favorable or unfavorable weather conditions. Low populations of the vectors, particularly *coagulata* and *undata*, are followed by a decline in the rate of spread of phony peach.

The four members of the Proconiini—*coagulata*, *undata*, *costalis*, and *insolita*—lay their eggs in clusters under the epidermis of a leaf or of a tender plant stem. Most eggs of the first two species are laid in the leaves of herbaceous plants, whereas *costalis* and *insolita* oviposit in the blades or leaf sheaths of grasses. *G. versuta* lays its eggs singly in the leaves of herbaceous plants.

The four members of the Proconiini have two complete and a partial third generation annually, whereas *versuta* has three full generations with presumptive evidence for a partial fourth generation.

Egg parasites have been reared from all five leafhopper species, and two species of Strepsiptera have been reared from *undata* and *costalis* adults. However, there is no evidence that these parasites have any profound effect on the size of insect populations.

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