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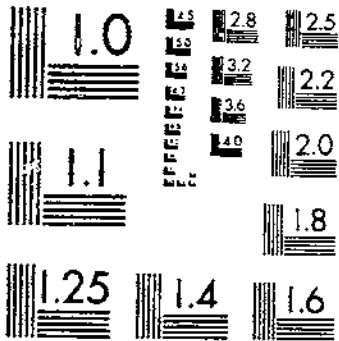
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IMPORTANT BIOLOGICAL AND MORPHOLOGICAL CHARACTERISTICS OF THE FOLIAR-FEEDING

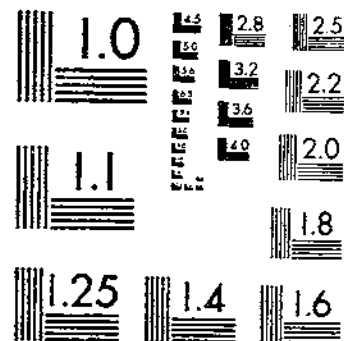
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On January 24, 1978, four USDA agencies—Agricultural Research Service (ARS), Cooperative State Research Service (CSRS), Extension Service (ES), and the National Agricultural Library (NAL)—merged to become a new organization, the Science and Education Administration (SEA), U.S. Department of Agriculture.

This publication was prepared by the Science and Education Administration's Federal Research staff, which was formerly the Agricultural Research Service.

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Drawings of aphids by Judy Duff, scientific illustrator, Macon, Ga.

IMPORTANT BIOLOGICAL AND MORPHOLOGICAL CHARACTERISTICS OF THE FOLIAR-FEEDING APHIDS OF PECAN

By W. L. Tedders¹

ABSTRACT

The foliar-feeding aphids of pecan, *Carya illinoensis* (Wangenh.) K. Koch, were studied at Byron, Ga., to determine species found there, general seasonal abundance, physical development and reproduction, feeding locations, gross physical damage caused by feeding, and natural enemies. Species found are the black pecan aphid, *Tinocallis caryaefoliae* (Davis), the blackmargined aphid, *Monellia caryella* (Fitch), and *Monelliopsis nigropunctata* (Granovsky). *Monellia costalis* (Fitch) is shown to be the melanistic summer form of *M. caryella*. Detailed drawings of the nymphal and adult viviparae and the adult males and oviparae are presented. All three species were found during all periods of the pecan-growing season, feeding only in the vascular system of the leaves and physically damaging the veins at the feeding site. Each species is highly selective in choosing vein size, and each species shows preferences for specific zones of the compound leaves. The damage caused by each species varied with the age of the leaf tissue, the aphid population, and the length of time the aphids had fed. All species can cause defoliation. The most important predators of these aphids are *Olla abdominalis* (Say) and *Hippodamia convergens* (Guérin-Meneville). *Aphelinus perpallidus* Gahan attacks all three species but is of minor importance. Other predators are listed. A previously unreported fungus (*Entomophthora* sp.) was found to parasitize *Monellia caryella* in certain years, causing a significant decrease in the numbers of this aphid. **KEYWORDS:** aphid biology, aphid ecology, aphid habits, aphid morphology, Aphididae of *Carya illinoensis*, *Monellia caryella*, *Monellia costalis*, *Monelliopsis nigropunctata*, pathogenic fungi, predaceous insects, *Tinocallis caryaefoliae*.

INTRODUCTION

The biology and morphology of the foliar-feeding Aphididae² of pecan, *Carya illinoensis* (Wangenh.) K. Koch, have been incompletely studied. Three species of so-called yellow pecan aphids—*Monellia caryella* (Fitch), *Monellia costalis* (Fitch), and *Monelliopsis nigropunctata*

(Granovsky)—and the black pecan aphid, *Tinocallis caryaefoliae* (Davis), have been reported from pecan (12, 13).³

Field populations of pecan aphids sometimes contain all forms of all species simultaneously, and the largest part of any population usually consists of immature forms. A description of the forms that appear during a pecan-growing season is not available. As a result, pecan-aphid researchers have been confused about the iden-

¹ Research entomologist, Southeastern Fruit and Tree Nut Research Laboratory, Science and Education Administration, U.S. Department of Agriculture, Byron, Ga. 31008.

² Hemiptera (Homoptera).

³ Italic numbers in parentheses refer to items in "Literature Cited," page 29.

tity of the yellow species. For example, some researchers have grouped the yellow aphids as *Monellia* spp. or only as yellow aphids (4, 14, 15).

The effects of feeding by the yellow species have not been studied, and their damage was not previously observed. Early workers did not consider the yellow species economically important, but the importance of these aphids has been questioned in recent years.

Feeding by *T. caryaefoliae* kills large areas of leaflets. Heavy damage often results in premature defoliation, which reduces nut quality. Premature defoliation also reduces pistillate and staminate bloom of pecan trees during the following spring, reducing yield (19). The threshold of economic importance, however, has never been measured.

Damage to pecan by all species can result when populations suck large quantities of liquids from the leaves, especially during droughts. These aphids, especially the yellow ones, excrete a sticky honeydew that collects on the upper surfaces of the leaves and supports a superficial growth of sooty mold fungi (Capnodiaceae). Honeydew alone on the leaves may interfere with the functioning of the leaves. The dense black growth of sooty mold on honeydew shades the leaves, reducing photosynthesis (21). Often, sooty mold growth on pecan trees is so abundant that foliage appears black.

Because of a general lack of information about these aphids, a study was undertaken at Byron, Ga., to determine some of the basic biological facts about this insect complex. Studies were made to determine the true identity of the species found feeding on pecan foliage, general seasonal abundance and development, precise feeding niches, gross physical damage to the foliage, and natural enemies. The information developed herein is basic to understanding these aphids as problems on pecans and necessary for establishing economic thresholds for each. This information will be useful to pecan researchers for reducing the number of pesticides applied to pecans for controlling these aphids, resulting in economic and ecological savings.

BIOLOGY

A study was made during 1973, 1974, and 1975, at the Southeastern Fruit and Tree Nut Research Station at Byron, Ga., to learn more

about the biology of the aphid species found on pecan.

Materials and Methods

Aphids were collected periodically from pecan trees and other *Carya* spp. growing in the field from early spring, when the buds began to open, until late fall. These aphids were placed on pecan seedlings in the laboratory to observe their acceptance and their ability to mature and reproduce on it as a host plant. Such acceptance, positive identification, and the frequency with which the aphids were found on pecan in the field were the bases for determining whether or not a species was a pecan pest.

The pecan seedlings were propagated by the method of Tedders et al. (20) and were contained in wooden frame cages measuring about 60 by 120 by 70 centimeters. The cages were covered on four sides with white polyester organdy (41 mesh per centimeter) and on the top with double-strength window glass. Two 40-watt plant-growth lamps were operated on the outside of the glass top for 15 hours each day. The lamps were controlled automatically with a timer. The air temperature inside the cages was the same as ambient room temperature and averaged about 22° C. Stock aphid colonies were maintained on the seedlings by adding new seedlings as the old ones became crowded and by removing most of the old, damaged ones.

To identify the species, living aphids were collected weekly from unsprayed pecan trees on the laboratory grounds and irregularly from pecan and hickory trees as far south as Albany, Ga., and as far north as Clemson, S.C. This area for study was thought to be representative of the pecan-growing industry because the literature contains no mention of the existence of other foliar-feeding species. Some collections were made as early as 1966. Some collected aphids were placed in 70 percent ethanol for subsequent identification, and living aphids were returned to the laboratory on foliage in plastic bags for further study.

For aphid counts during 1973, five compound leaves were randomly taken from each of four unsprayed 'Schley' pecan trees and five leaves from each of four unsprayed 'Stuart' pecan trees. All leaves were collected from branches 5 to 10 feet above the ground. The trees were sampled once weekly. Adults and all nymphal

stages were identified as to species. Similar collections were made during 1974 from 'Stuart' trees and in 1975 from 'Schley' and 'Moore' trees, and five leaves were taken from each of five unsprayed trees on each examination date.

The aphid feeding locations were determined at the time of collection, and the damage inflicted on the pecan foliage was observed and recorded in the laboratory. Aphid damage in the field was often masked by the damage of other insects and mites, as well as by various leaf diseases. Additional confusion was caused by overlapping damage inflicted by mixed populations of the various aphid species. The problem of separating the damage caused by one aphid species from that of mites, diseases, and other insects (including the other aphid species) was overcome by colonization of each species in separate cages in the laboratory.

Aphid development and reproduction studies were attempted in the field and responses were often similar, but differences resulted from climatic conditions. In the spring, cold weather slowed development and reproduction, and warm weather hastened it. The reverse was often true in the summer.

Frequent rainfalls and interference from predators and pathogens rendered most of the field studies incomplete. The aphid development and reproduction studies were therefore conducted in the laboratory on pecan seedlings.

Various insects and fungi were evaluated as predators, parasites, or pathogens of specific aphids colonized on seedlings in the laboratory. The initial identification of the predatory and parasitic insects was made by the staff and collaborators of the Systematic Entomology Laboratory, Agricultural Research Service (ARS), Beltsville, Md. Predation, parasitism, and pathogenicity on the aphids were verified in caged field tests.

All aphid honeydew studies were conducted under laboratory conditions on pecan seedlings. Honeydew samples were collected as droppings on pieces of preweighed aluminum foil.

Results and Discussion

Species found on *Carya*

The only aphids found feeding and reproducing on the foliage of pecan were the black pecan aphid, *Tinocallis caryaefoliae* (Davis); the blackmargined aphid, *Monellia caryella* (=cos-

talis) (Fitch); and *Monelliopsis nigropunctata* (Granovsky).

The fundatrices and several subsequent generations of *M. caryella*, which were collected from the field in April and early May, showed a remarkable absence of black pigmentation in the nymphal and adult forms, except on the antennae. These forms were reared in the laboratory and subsequent generations gradually developed the typical black margins on the wings, head, and body. Full color in the adults and nymphs did not occur for six or seven generations after fundatrix emergence, about the last week in May. These findings were confirmed in field studies.

Monellia caryella (Fitch) and *Monellia costalis* (Fitch) were thus found to be the same aphid, *M. costalis* being only the melanistic summer form. Phillips et al. (13) were incorrect in suggesting that three species of yellow aphid attack pecan. *Monellia caryella* (Fitch) pre-dates *M. costalis* (Fitch) and is therefore the correct name. The common name, blackmargined aphid, is descriptive of the melanistic summer form (*M. costalis*) but should be retained as the common name for *M. caryella*.

M. nigropunctata and *T. caryaefoliae* were collected many times from *Carya tomentosa* Nutt., *C. glabra* (Mill.) Sweet, *C. aquatica* (Michx. f.) Nutt., and *C. illinoensis* (Wangenh.) K. Koch. These specimens were transferred easily to pecan seedlings in the laboratory and were found to mature and reproduce normally. *M. caryella* was collected frequently from *C. aquatica* but never from other *Carya* spp., except *C. illinoensis*. These aphids also were found to mature and reproduce normally on pecan seedlings.

Three additional Aphididae were collected from *Carya* spp. other than *C. illinoensis*. All three eventually matured on laboratory pecan seedlings and reproduced, but each with much difficulty. Maturation took up to 2 weeks, the alate females would not stay on the seedlings, and only three or four nymphs were produced by each species after numerous attempts to colonize them. These species were identified as *Monellia hispida* Quednau from *C. tomentosa* and *C. glabra* in Houston County, Ga., *Monellia microsetosa* Richards from *Carya ovata* in Rabun County, Ga., and *Protopterocallis canadensis* Richards from *C. tomentosa* in Houston County, Ga.

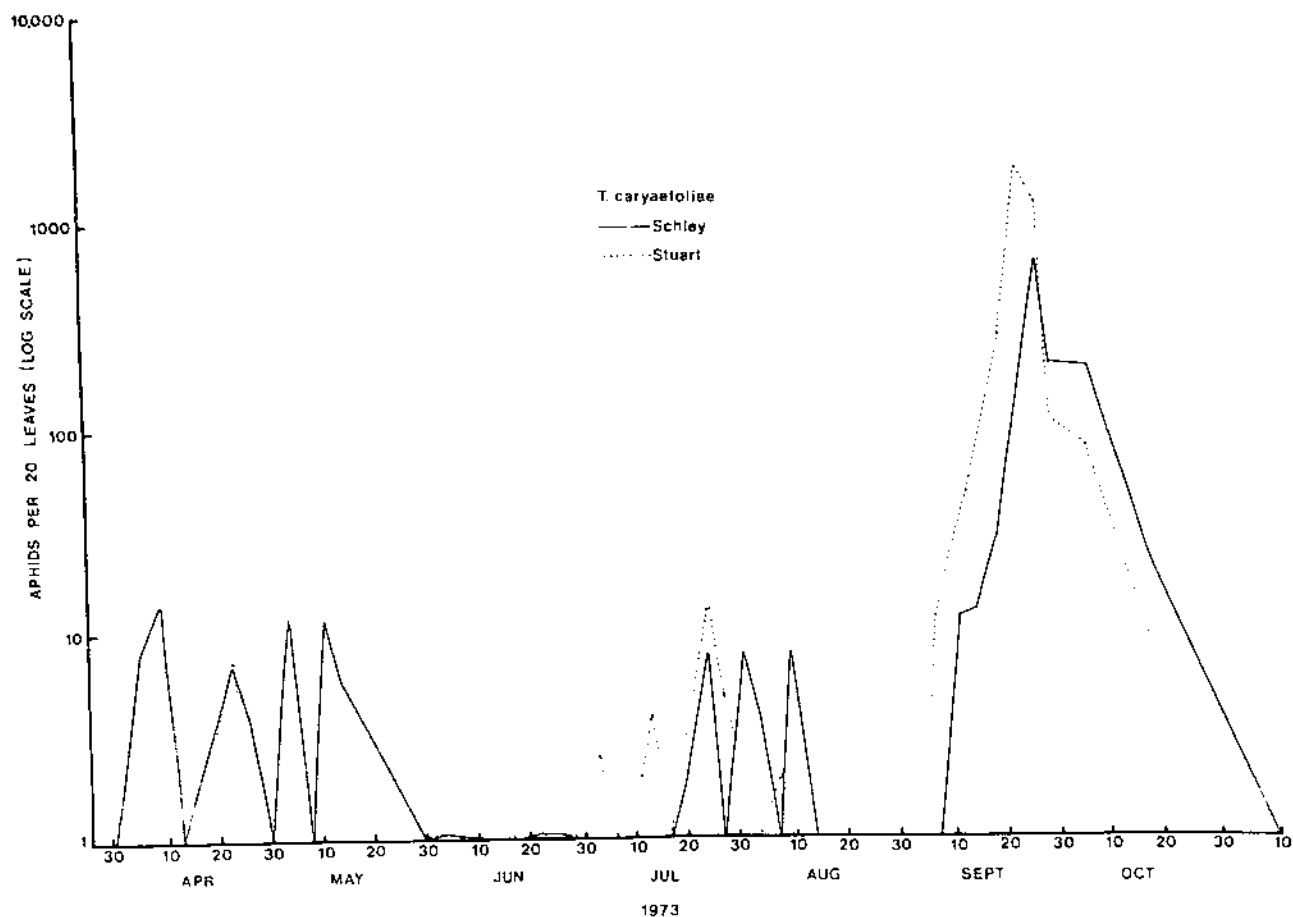
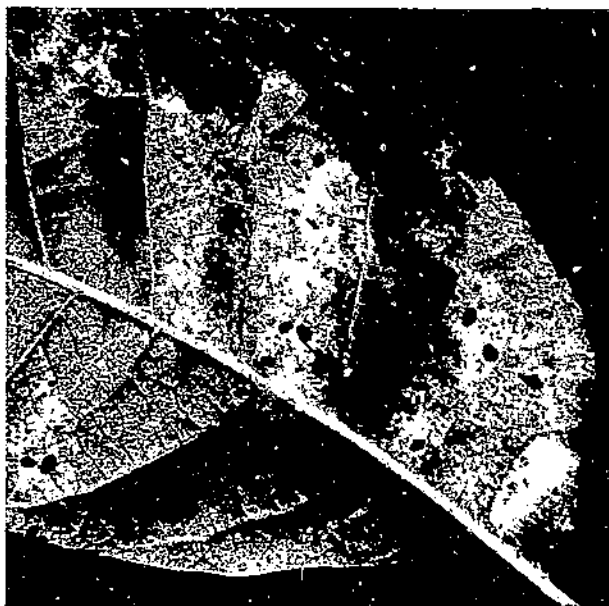


FIGURE 1.—Number and seasonal distribution of *T. caryaefoliae* collected from 'Schley' and 'Stuart' pecan leaves.

TABLE 1.—Frequency of aphid feeding on parts of the vascular system of a compound pecan leaf

Aphid	Frequency of observation on— ¹					
	Rachis	Petiole	Primary vein	Secondary vein	Tertiary vein	Quaternary vein
<i>T. caryaefoliae</i>	0	0	0	0	2	4
<i>M. caryella</i>	2	3	4	3	2	1
<i>M. nigropunctata</i>	0	0	0	1	4	3

¹ Not observed=0, rarely observed=1, occasionally observed=2, frequently observed=3, most often observed=4. Aphid departure from feeding on the preferred vein was related to aphid size. Large aphids departed to large veins and small aphids departed to smaller veins.



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FIGURE 2.—*T. caryaefoliae* feeding on quaternary veins of the lower surface of a pecan leaflet.

The giant bark aphid, *Longistigma caryae* (Harris), was often collected from pecan, but this aphid feeds on the stems and was never found feeding on the foliage. The green peach aphid, *Myzus persicae* (Sulzer), was occasionally found feeding and reproducing on greenhouse pecan seedlings but never on *Carya* spp. in the field. However, it is a well-known omnivorous greenhouse pest. Alates of the strawberry aphid, *Chaetosiphon fragaefolii* (Cockerell), were found on pecan in the field on two occasions, but these were not reproducing and were considered to be vagrants.

Seasonal abundance, feeding niche, damage

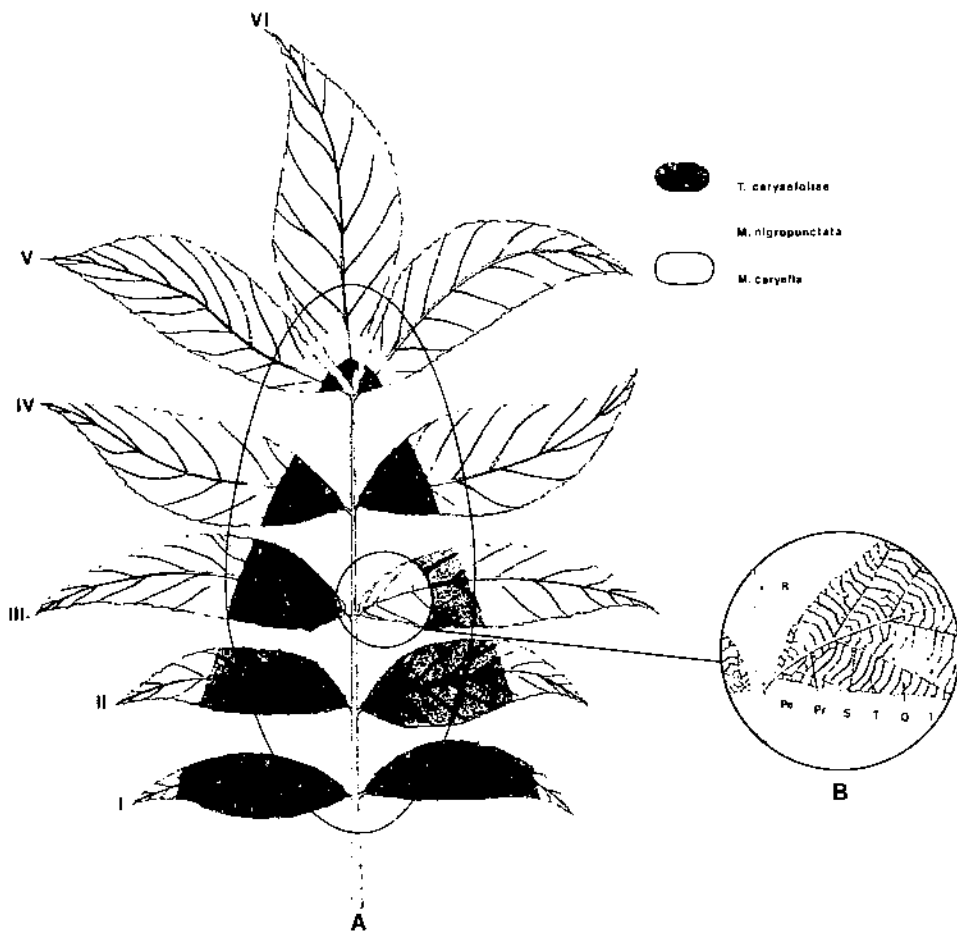
Tinocallis caryaefoliae.—First instars were randomly distributed on the elongating and unfolding buds of pecan in the spring as early as March 30, 1973, April 2, 1974, and March 26, 1975. They were usually found somewhat earlier on 'Schley' trees than on 'Stuart' trees (fig. 1). (Spring development of 'Schley' usually precedes 'Stuart'.) As the buds elongated, this species was found randomly scattered over the buds, and the appearance of these aphids on any seedling or cultivar coincided with the growth of the buds. As leaves formed, the aphids were randomly distributed over the lower surface of the developing leaves and occasionally on the

upper surface. This is the opposite of what Davis (3) found. In the spring, this species was not abundant and was not a problem, although these aphids were often the first to appear. The earliest damage to immature foliage was observed on May 4, 1973, May 6, 1975, and May 4, 1976. Damage to immature foliage at that time was incipient and limited to tiny spots, about 1 millimeter square, on the veins and surrounding tissue.

Larger populations were observed later in the year, and minor damage was observed as early as late May. The aphids became more selective in choosing feeding sites and preferred the quaternary (figs. 2, 3B) and smallest veins of the leaflets (table 1), which supply the photosynthetic units (vein islets). Occasionally, adults and fourth-instar nymphs fed on the next larger tertiary veins. Damage first appeared as a small black dot on the vein at the feeding puncture, with chlorosis (yellowing) of the surrounding vein islets. Additional feeding on adjacent quaternary veins increased chlorosis of vein islets and broadened chlorotic areas. The chlorotic areas tended to be quadrilateral or rectangular (1) because of the arrangement of larger veins that delineated the chlorosis of the vein islets. The intensity of the yellowing was proportional to the age of the leaf, the length of time that an aphid fed at the site, and the size of the individual aphid. Yellowing on younger tissue was less noticeable. Newly born aphids fed for 2 days before chlorosis was detected and 3 days before chlorosis was decidedly noticeable. Pecan cultivars in the spring showed different degrees of chlorosis, with 'Stuart' showing somewhat less than 'Schley'. A few seedlings were highly resistant to damage by this aphid.

Defoliation before July was rare. Most often, damage inflicted during June appeared "arrested" after a population disappeared, and the damaged area did not dry out and die but remained as slightly discolored areas throughout the remainder of the season.

In addition to showing preference for the quaternary veins during this period, *T. caryaefoliae* showed a zonal preference for the basal half of the leaflets, especially the basal leaflets of a compound leaf (fig. 3A). Counts of aphids on the leaflets of one side of the leaf and the apical leaflet showed that about 32 percent were on the basal (I) leaflet and 1 percent were on the apical (VI) leaflet (table 2). There was no



PN-5948

FIGURE 3.—Lower surface of compound pecan leaf. A, Zones of feeding preference by each species and leaflet designation; B, enlargement of leaf structure.

TABLE 2.—Aphids found on leaflets during the period of zonal preference

Aphid	Percentage on leaflet ¹					
	I	II	III	IV	V	VI
<i>T. caryaefoliae</i>	32	28	24	12	4	1
<i>M. caryella</i>	17	21	22	18	14	8
<i>M. nigropunctata</i>	1	6	7	14	38	34

¹ Leaflet I is basal; leaflet VI is apical (see fig. 3).

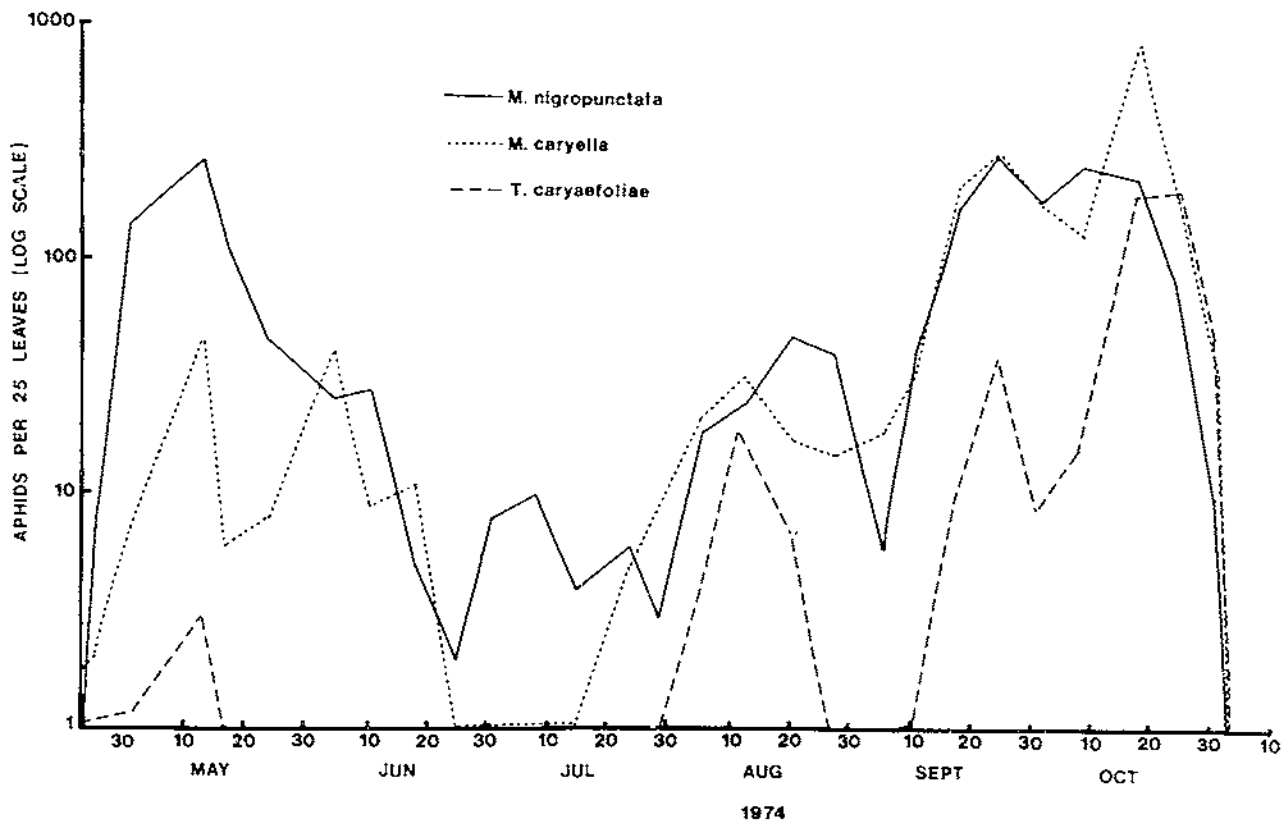


FIGURE 4.—Comparison of number and seasonal distribution of *M. nigropunctata*, *M. caryella*, and *T. caryaefoliae* collected from 'Stuart' pecan leaves.

difference in numbers found on opposing leaflets of a leaf. Populations were noticeably small during June. Damaging populations occurred by mid-July 1973 (fig. 1) and mid-August 1974 (fig. 4). Heavy, damaging populations were almost always present from mid-September until frost. Damage to foliage during the late summer and early fall was similar, but yellowing was intensified and easily recognized. The chlorotic areas of leaflets became bright yellow, then rapidly dried out and turned brown as they died (fig. 5). An aphid that developed from birth to adulthood and grew to average size was capable of causing a chlorotic area averaging about 1 square centimeter. Bissell (1) found damage to be 0.5 square centimeter. Shedding of basal (I) and progressively distal leaflets because of damage during this period was common, and heavy damage on all leaflets sometimes caused the entire leaf to abscise.

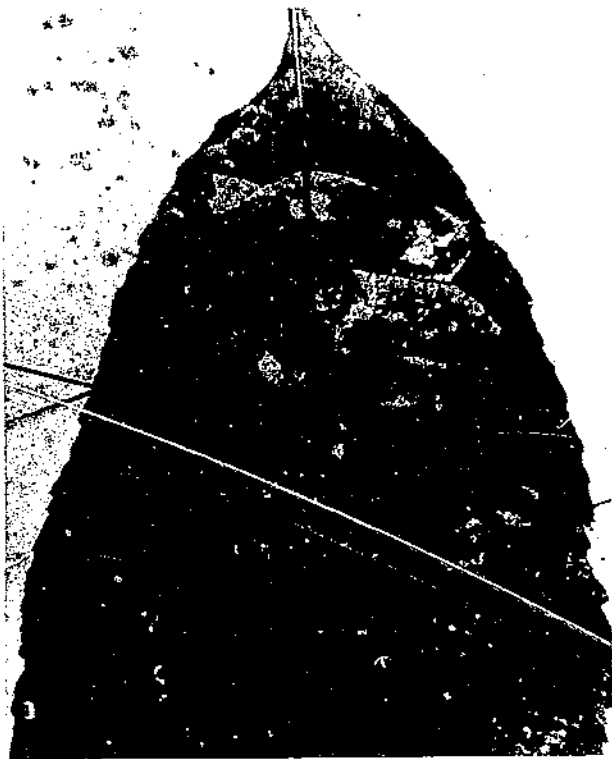
T. caryaefoliae usually passed through all stages of its development near the birth site, especially if the population was small. Crowded populations produced small aphids that caused

small chlorotic spots. Crowded aphids were prone to jump when disturbed, thus effecting migration.

During the later summer and fall, about 74 percent of the aphids were found on the lower surface and the remainder on the upper surface. Orientation by this species with relation to the leaflet midrib appeared to be random.

After the alate fundatrices appeared in the spring, alate viviparae were found throughout the growing season until November 10, 1973. Apterous oviparae were found from October 10 through November 30, and these were most abundant from October 22 to 25. Males were found only from October 21 to 25. In Mississippi, Kislanko (7) found oviparae on October 22 and November 24 and males on October 22. Eggs of this species are pale, then darken to shiny black, and were observed on October 22. Eggs were beneath loose bark on the tree trunk in scattered groups of few to many.

Monellia caryella.—First instars were collected on April 5, 1973, April 30, 1974, and April 8, 1975. This species was usually found 7



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FIGURE 5.—Late-season damage by the black pecan aphid.

to 10 days later than *T. caryaefoliae*. Again, aphids were found on 'Schley' before 'Stuart' (fig. 6). These specimens were randomly distributed over the lower surfaces of immature leaves and sometimes found on upper surfaces. They were not abundant during the spring, and damage was not observed on immature foliage. Similar to *T. caryaefoliae*, populations of *M. caryella* generally became larger as the season progressed. Proportionally more of this species than of *T. caryaefoliae* or *M. nigropunctata* were found during middle and late summer.

In 1973, the largest populations were observed during late June and early July on 'Stuart' and during September and October on 'Schley'. *M. caryella* became highly selective in choosing feeding sites and fed on the primary and secondary veins (fig. 3B) of leaflets (table 1). The zonal preference of *M. caryella* was the basal half of the leaflets (fig. 3A), and a preference was noted for the leaflets nearest the center of the leaves (table 2). Adults and fourth-instar nymphs preferred the large primary vein (fig. 7), and smaller nymphs often preferred the secondary vein. Usually, *M. caryella* oriented itself to be nearly parallel with the vein on which it was feeding and faced toward the direction of leaflet attachment (fig.

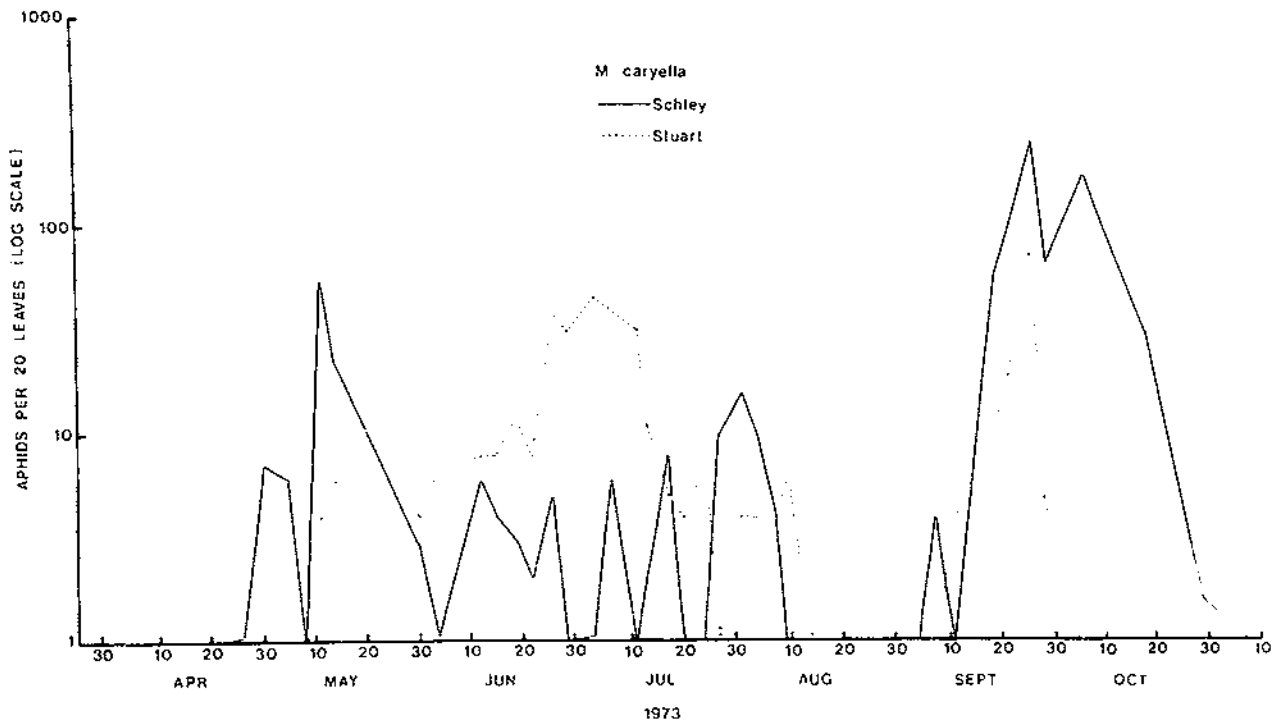


FIGURE 6.—Number and seasonal distribution of *M. caryella* collected from 'Schley' and 'Stuart' pecan leaves.

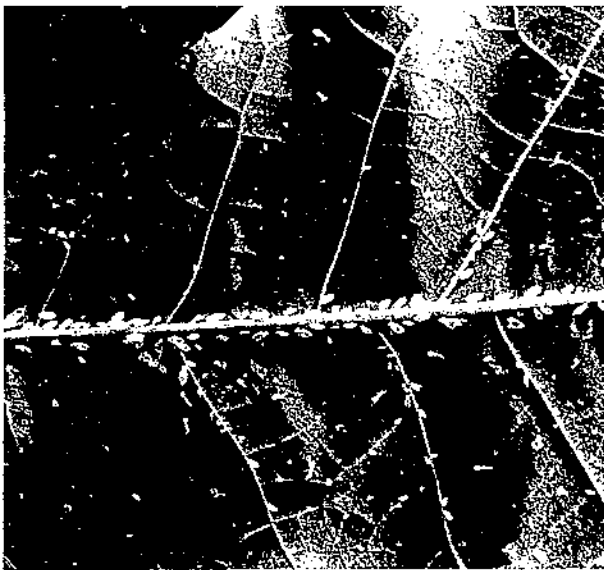
7). More than 80 percent of all stages were found on the lower surfaces, and those found on the upper surfaces were usually fourth instars.

Damage to leaflet veins by *M. caryella* was observed first in late July or early August and usually was confined to the basal half of the leaflets (fig. 8) where the feeding occurred. Damage to veins first appeared as discoloration beneath the epidermis of the vein. Discolored spots then became somewhat sunken and were brownish to black. Numerous feeding spots coalesced after the aphid population had decreased, resulting in easily detectable dead sections from 5 to 10 millimeters long on the veins. All damage to veins was on leaf lower surfaces. Chlorosis resulting from heavy damage was highly variable, but generally the appearance of heavily attacked leaves was somewhat less than vigorous and the color of the leaves took on a grayish-brownish cast.

As with *T. caryaefoliae*, the degree of damage was proportional to the age of the leaf and the amount of aphid feeding. Damage varied with cultivars, 'Stuart' being more susceptible than 'Schley'. Many seedling trees were often severely damaged. Leaflet shedding was observed in August on 'Stuart' and was usually limited to the basal leaflets and occasionally the next distal leaflets. Heavily damaged leaflets in the laboratory and field were always associated with previously large populations of *M. caryella*.

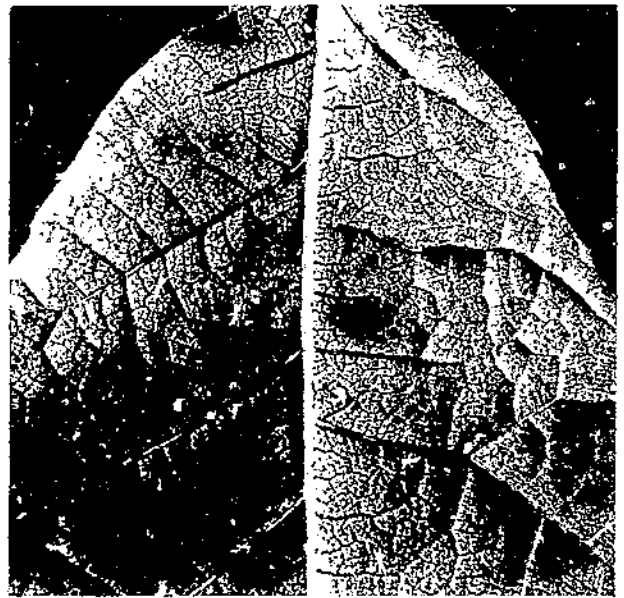
A large population of 600 or more *M. caryella* could not be maintained on laboratory seedlings that were previously damaged from the feeding by this species. This condition suggests a residual repellent effect or stimulus to migrate caused by the feeding damage. This phenomenon was repeated many times in the laboratory and large colonies of *M. caryella* never developed on damaged leaves or leaves that had previously supported a large *M. caryella* population. The condition was manifest in the field by the collapse of the population in August 1973 and June-July 1974 (figs. 4, 6). Acceptance of leaves, survival, and fecundity in the laboratory were greatest on older seedlings with hardened mature leaves that had not been previously damaged. This, as well as normal population buildup by reproduction, may account for population increases as the season progresses and the occurrence of the greatest abundance of this species in late summer and early fall.

After the alate fundatrices appeared in the spring, alate viviparae were found for the rest of the growing season until November 5, 1973. Apterous oviparae were found from October 10 until December 1, and these were more or less evenly distributed through that period. Similarly, males were found from October 10 until November 17 and were most abundant about



PN-5950

FIGURE 7.—*M. caryella* feeding on the primary and secondary veins of the lower surface of pecan leaflet.



PN-5951

FIGURE 8.—Late-season damage by *M. caryella* to secondary veins of a pecan leaflet.

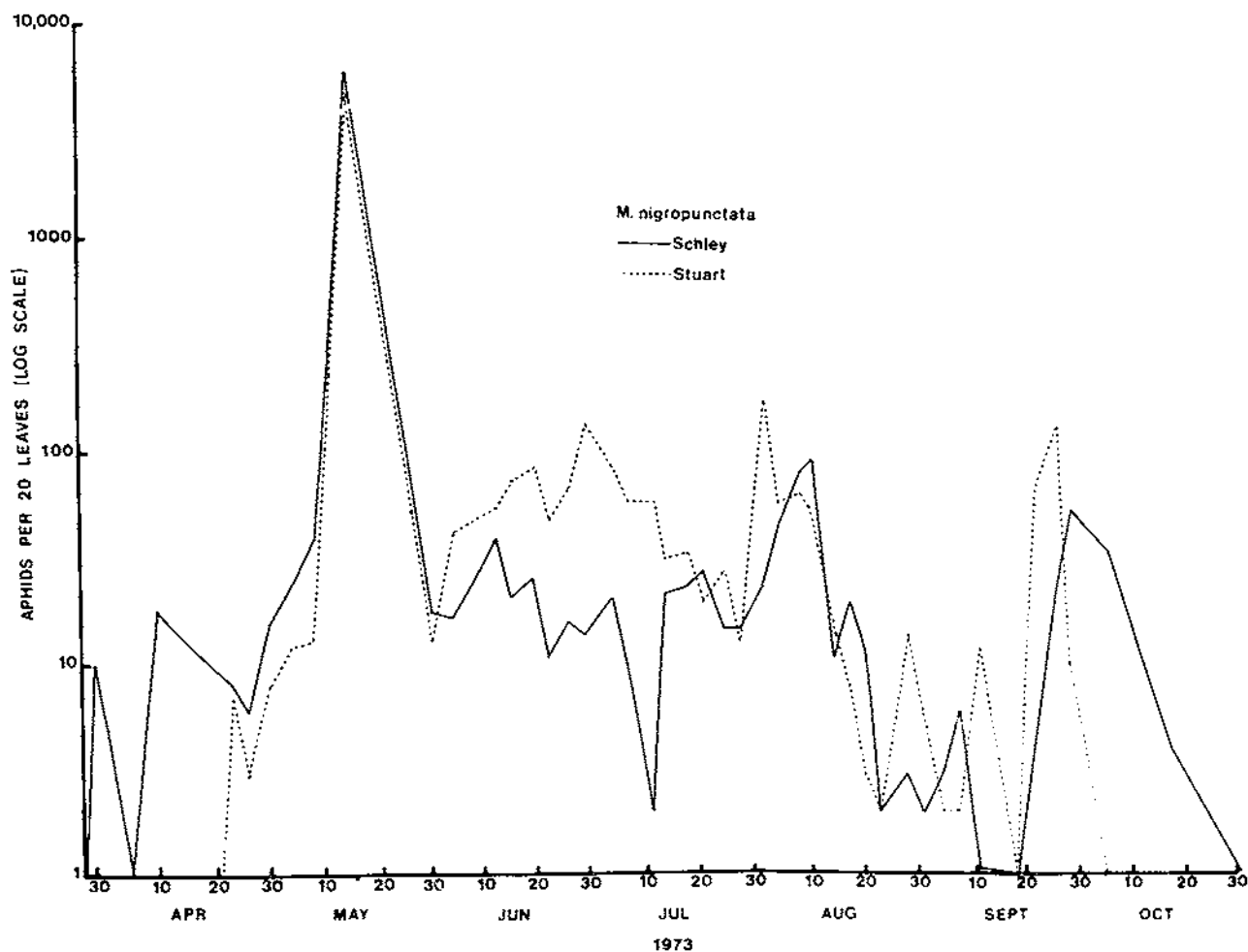


FIGURE 9.—Number and seasonal distribution of *M. nigropunctata* collected from 'Schley' and 'Stuart' pecan leaves.

November 5. Eggs of this species were yellow to orange and soon turned dark to black. They were larger than those of *M. nigropunctata* and were first found on October 19. Eggs were also in widely scattered small groups beneath the loose bark on the tree trunk and large scaffold limbs.

Monelliopsis nigropunctata. — First instars were seen feeding randomly on and within the folds of developing buds and on the lower surfaces of developing leaflets in the spring. This species was found on March 28, 1973, April 2, 1974, and March 26, 1975. During May, extremely large populations occurred (fig. 9), and the species exhibited a zonal preference for the less developed tender apical leaflets (fig. 10), with progressively less preference for basal leaflets (fig. 3A). A preference for the apical ends of leaflets was also evident. Counts of aphids on leaflets on one side of the leaf and the

apical leaflet revealed that about 34 percent were on the apical (VI) leaflet and about 1 percent were on the basal (I) leaflet (table 2). There were no differences in numbers on opposing leaflets. The apical leaflets were the least developed and tenderest leaflets of a compound leaf in May.

This species normally fed on the tertiary vein (fig. 3B) at the point where this small vein joins the next larger (secondary or primary) vein (fig. 10). First- and second-instar nymphs frequently fed on quaternary veins (table 1). The only effect observed by the feeding of this species on expanding leaflets in the field was a slight downward curling. This effect was overcome with the disappearance of large aphid populations and with maturity of the leaflet.

As the leaves became harder, the species lost its zonal preference and became randomly distributed over the lower surfaces of all leaflets.



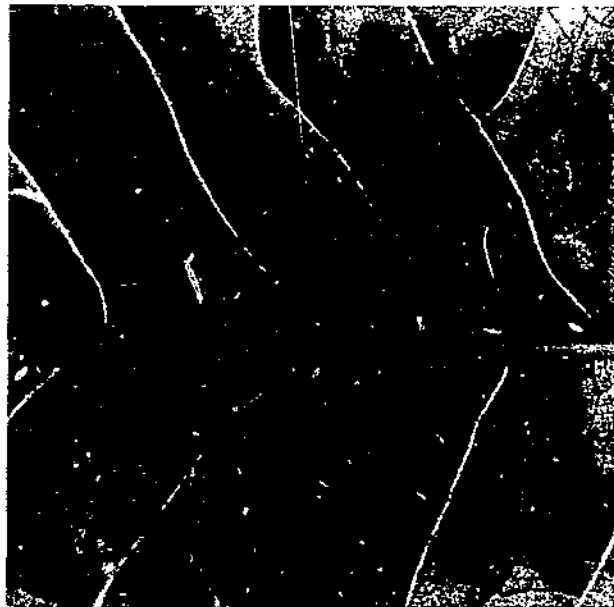
PN-5952

FIGURE 10.—*M. nigropunctata* feeding on tertiary veins of the lower surfaces of pecan leaflets.

However, the preference for tertiary veins was retained.

As with *M. caryella*, this species oriented itself nearly parallel to the primary and secondary veins (although feeding on tertiary veins) and faced in the direction of leaf attachment. More than 97 percent of all stages of this species were found on the lower surfaces of the leaves.

Damage to leaflet veins by *M. nigropunctata* was first observed in July, generally over leaf lower surfaces at the feeding sites (fig. 11). Significant damage to leaflets was hardly noticeable, since damage to veins was only 1 or 2 millimeters long and appeared to be the result of prolonged feeding by individual aphids. Heavy populations often damaged almost all tertiary veins on a leaflet. General chlorosis of the leaflet was not distinguishably different from that caused by *M. caryella*, and leaf color was similar. As with the other two species, damage to the leaflet veins was proportional to the age of the leaf and the amount of previous feeding. Damage to cultivars was variable, but 'Stuart' seemed more susceptible than 'Schley'. A repellent effect after the feeding by large populations was not noticeable in the laboratory with this species, and the field population never completely disappeared (figs. 4, 9).



PN-5953

FIGURE 11.—Late-season damage by *M. nigropunctata* to tertiary veins of a pecan leaflet.

Acceptance of leaves, survival, and fecundity in the laboratory were greatest on young seedling leaves, and this may account for the greatest abundance of this species in the spring before the leaves reached maturity and full size. Large populations feeding on laboratory seedlings with leaves not fully expanded arrested foliage growth at 68 percent of its potential size, compared to seedlings without aphids. (These data, by analysis of variance, were significantly different at the 95-percent level of confidence.) This effect did not occur in similar tests of *T. caryaefoliae* or *M. caryella*, and the effect was not substantiated for *M. nigropunctata* in the field.

After the alate fundatrices appeared in the spring, alate viviparae were found until November 23, 1975. The apterous oviparae were found from October 17 until November 26. Males were found from October 14 through November 22 and were never abundant. The dark-orange eggs of this species are smaller than those of *M. caryella* and were first found on November 18. They were laid in cracks and crevices and under the bark of large and small limbs. Many eggs were found in unprotected areas on the terminal growth of the current years growth near the buds. The eggs were almost black before hatching.

M. nigropunctata was the easiest of the three

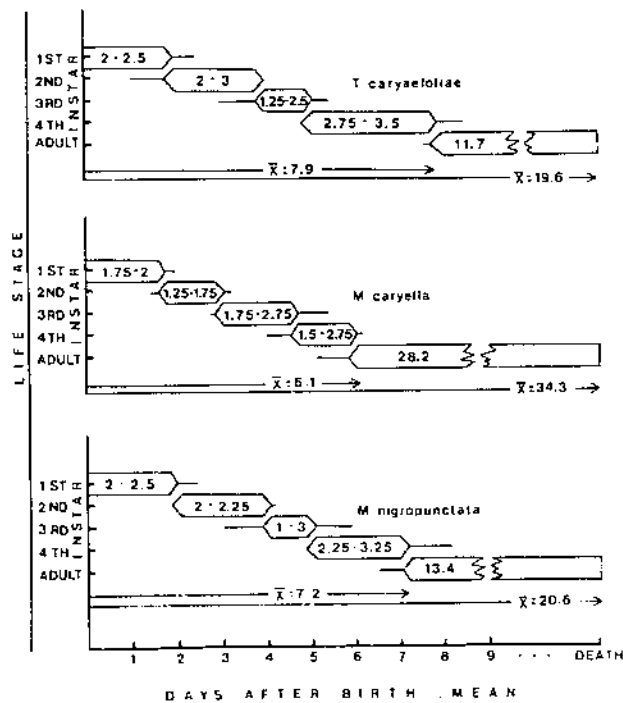


FIGURE 12.—Time of development of nymphal stages of the three aphid species from birth to maturity and length of adult life.

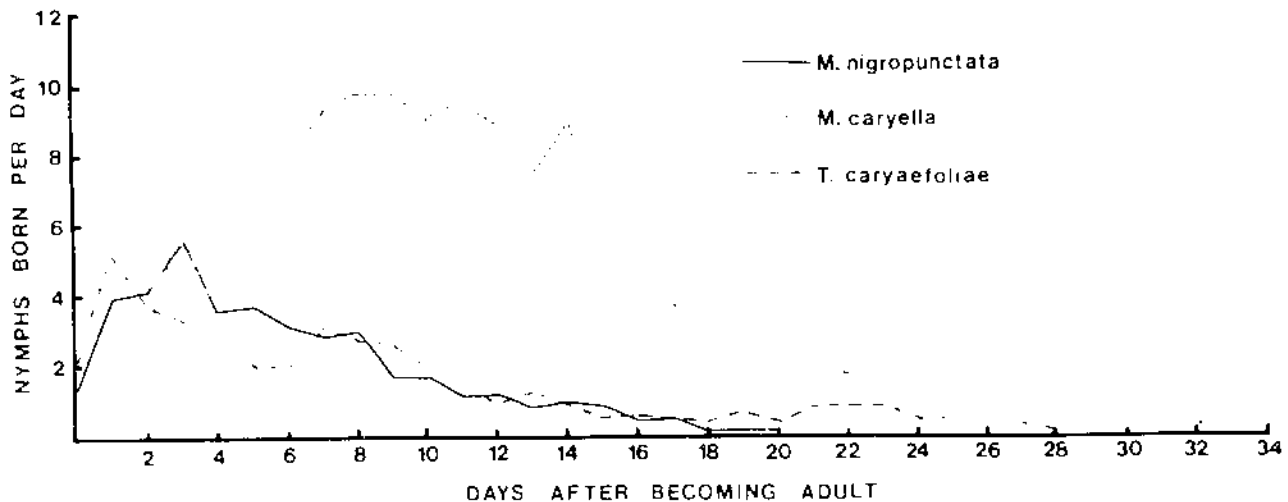


FIGURE 13.—Mean reproduction by alate viviparae of *T. caryaefoliae*, *M. caryella*, and *M. nigropunctata*.

species to observe on pecan foliage because of its bright pale-yellow color, its lack of pigmentation, which acts as camouflage (as was the case with *M. caryella*), and the openness of the feeding site. Even first-instar nymphs were easily detected.

Development and reproduction

Tinocallis caryaefoliae.—Alate viviparae required 7.9 days to develop from birth to adulthood (fig. 12). Of the four instars, the third was the shortest and the fourth was the longest. The viviparae were mature and began reproducing on the day they became adults. Maximum daily reproduction occurred 1 day after maturity and reproduction continued for an average of 10.4 days, or 89 percent of the adult life (table 3). Individuals gave birth to an average of 35 young. Numerous individuals were capable of reproducing for 28 days (fig. 13).

T. caryaefoliae was normally found from the last of March until frost. With an egg hatch on March 26 and continuous regeneration until November 15, a total of 234 days, a maximum of 30 generations was calculated. Moznette et al.

(9) suggested about 20 generations. Based on a life cycle beginning on the day of maximum reproduction by an adult and ending on the day of maximum reproduction by the F_1 generation, this species would produce 26 generations annually.

Monellia caryella.—Alate viviparae required 6.1 days to develop from birth to adulthood (fig. 12). The stadia of the four instars were about equal in duration. Adults were mature and began reproducing 1 day after becoming adults. Maximum daily reproduction occurred on the 8th day, and 8 to 10 aphids were born daily from the 5th to the 14th day after emergence into adulthood. Reproduction lasted an average of 18 days, or 64 percent of the adult life (table 3). Adults produced an average of 125 nymphs each. Numerous adults were capable of reproducing for 33 days and produced over 200 nymphs (fig. 13).

M. caryella was normally found from April 5 until frost (224 days). Continuous reproduction was calculated to produce 32 generations. This figure is not in agreement with 21 generations as found by Turner (22). However, based on a life cycle from maximum reproduction to maximum reproduction of the F_1 generation, the species would have about 16 generations annually.

Monelliopsis nigropunctata.—Alate viviparae required 7.2 days to develop from birth to adulthood (fig. 12). Of the four instars, the third usually was the shortest. Adults were sexually mature and began reproducing on the first day. Maximum reproduction was usually on the third day after maturity (fig. 13). Adults reproduced for an average of 10.7 days, or 80 percent of the adult life (table 3). Many adults reproduced for 19 days, and individuals reproduced an average of 38 young.

Eggs of this species usually hatched about April 1, and there were 228 days until the average first frost. The species was calculated to

have 32 generations annually. Based on a life cycle from maximum reproduction to maximum reproduction of the F_1 generation, there would be 22 generations annually.

Natural enemies

The foliar-feeding aphids of pecan are attacked by numerous parasites and predators and one or more diseases.

Coccinellidae.—The Coccinellidae probably devour more aphids than any other predator. At least 10 species of lady beetles were collected from pecan trees during the aphid studies. The most effective control agent was *Olla abdominalis* (Say), an arboreal species that feeds readily on all three aphid species from mid-April until the first frost in November. It was found in all stages of development on the limbs and foliage of the trees, and large numbers of hibernating adults were found beneath the loose bark of the large limbs and tree trunk in November.

The second most important lady beetle on pecan is *Hippodamia convergens* (Guérin-Meneville). This species is not a permanent inhabitant of pecan trees but is attracted to the trees in large numbers when large aphid populations occur there. It, too, feeds readily on all three aphid species. *Hippodamia convergens* was often found reproducing on the trees in the spring and late summer.

Other predators.—Two reduviid nymphs, *Zelus exsanguis* (Stål) and *Sinea spinipes* (Herich-Schaeffer), feed heavily on the three aphid species. *Zelus exsanguis* was easily found from July 1 into November, becoming especially abundant in September and October. *Sinea spinipes* was found on the foliage of pecans from April into November. It, too, is more abundant in September and October. Both species appear to be permanent residents of pecan trees.

TABLE 3.—*Reproduction and longevity statistics for the alate viviparae of T. caryaefoliae, M. caryella, and M. nigropunctata*

Aphid	Adults studied	Progeny			Adult life (days)		Reproducing (mean)
		Total	Mean	Range	Total Mean	Reproducing Range	
<i>T. caryaefoliae</i>	21	732	34.9	4-86	11.7	4-30	10.4
<i>M. caryella</i>	10	1,245	124.5	80-215	28.2	2-45	18.0
<i>M. nigropunctata</i>	14	530	37.9	5-83	13.4	4-38	10.7

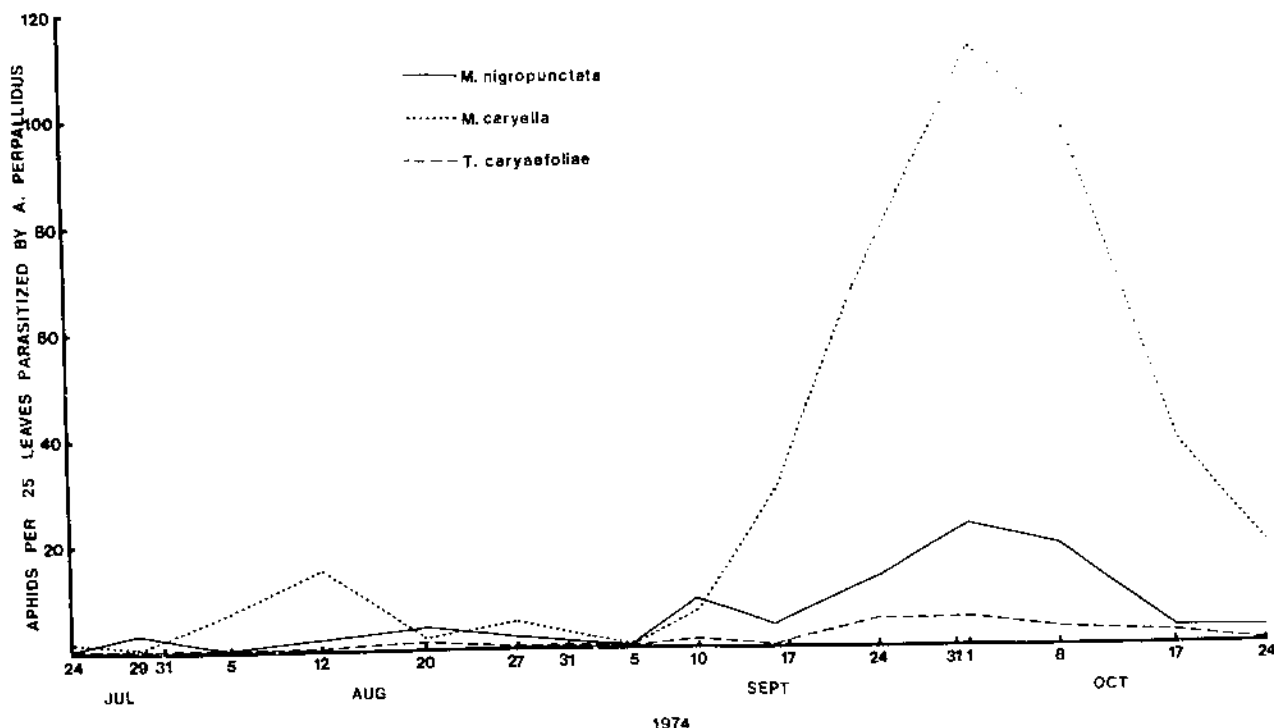


FIGURE 14.—Seasonal occurrence of *A. perpallidus* mummies of *T. caryaefoliae*, *M. caryella*, and *M. nigropunctata*.

TABLE 4.—Frequency of the life stages of *T. caryaefoliae*, *M. caryella*, and *M. nigropunctata* killed by *A. perpallidus* (1974–75)

Aphid	Specimens examined	Life stage (percent)		
		Instar		
		3d	4th	Adult
<i>T. caryaefoliae</i>	36	69.4	30.6	0
<i>M. caryella</i>	361	26.9	44.1	29.1
<i>M. nigropunctata</i>	120	51.7	45.8	2.5

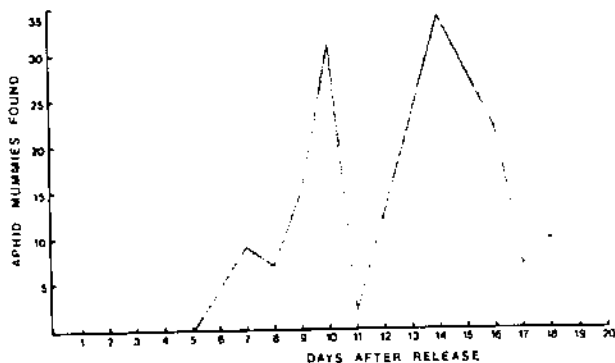


FIGURE 15.—Development of two generations of *A. perpallidus* to the mummy stage on the host *M. caryella* in the laboratory.

A pentatomid, *Podisus maculiventris* (Say), was found on pecan foliage from April into November and was extremely abundant during the last of September. This species is also a permanent resident of pecan trees. *Micromus posticus* (Walk.) and *Hemerobius humulinus* L. were the most frequent collected of the hemerobiids and were abundant during August and September. Nine species of chrysopids were collected from pecan trees. *Chrysopa rufilabris* Burm., the most important species, was collected from May through October. *Allochrysa virginica* (Fitch), the second most important, became abundant in August and September. Five species of Syrphidae were frequently found on pecans during September and October. *Allograpta obliqua* (Say) appears to be the most common.

Parasitoids.—The aphelinid, *Aphelinus perpallidus* Gahan, and a previously unreported and unidentified braconid, *Trioxys* sp., were the only aphid parasitoids found. Three specimens of the *Trioxys* sp. were collected on August 12, 1975, and the host was *M. nigropunctata*.

A. perpallidus, a tiny yellow wasp, was found in low numbers as adults in early April and as aphid mummies from May 1 until the end of

July. The population increased thereafter through October, and into November in some years. The greatest numbers were usually found in October (fig. 14). The species parasitized all three kinds of aphids, and attacks appeared to be directly proportional to host abundance.

In laboratory tests, *A. perpallidus* required 7 to 10 days to complete a life cycle, with 7 days being the usual (fig. 15). All aphid mummies were swollen and shiny black and were stuck to the leaf surface. *T. caryaefoliae* mummies were always third or fourth instars and never adults. *M. caryella* and *M. nigropunctata* were frequently killed as adults but most frequently as fourth and third instars, respectively (table 4). All three species were usually attacked as first instars and occasionally as second instars. Moznette et al. (9) found that *A. perpallidus* and the other natural enemies that he listed "cut down the numbers of aphids enormously."

Diseases.—During and following a period of humid weather in late September 1974, a large population of *M. caryella* collapsed because of infection by an unidentified fungus. Aphids killed by the fungus were swollen, often deformed, and attached by rhizoids of the fungus to the leaf surface. Killed aphids were first a pinkish-ivory color and gradually became smokey gray as the conidiophores issued from the aphids. The fungus was identified as an *Entomophthora* sp. The conidia were of the typical bell shape, as described by Gustafsson (5), and the species appears to be near *Entomophthora planchoniana* Cornu. Unfortunately, cultivation of this fungus on artificial media containing Sabourauds' agar was not successful.

Moznette et al. (9) found *Cladosporium* on black pecan aphids, but it was not observed in this study.

Overview

The spring appearance of *T. caryaefoliae* and *M. nigropunctata* nymphs was correlated well with the beginning development of the tree. These two species appeared on growing buds at about the same time, and newly hatched nymphs were never found before bud break. Most probably, growing buds and leaves serve as an attractant to the newly hatched nymphs.

All three species of aphids were similarly abundant during the spring, summer, and fall of 1974 on 'Stuart' trees (fig. 4). All three spe-

cies were least abundant during June and July, but the factors responsible for the small populations are not completely understood. Parasites and predators were not the limiting factors, because they too were at an extremely low level, and the nuclei for aphid populations were always present. High temperature and rainfall were not responsible, because large populations were developed in sleeve cages on the foliage of trees in the field at that time. Heavy rains often washed aphids from the foliage but at best provided only temporary reductions in numbers. During 1974, populations of all three species were greatest during September and October. *M. nigropunctata* was the most abundant aphid that year, and *T. caryaefoliae* was the least abundant. Parasites and predators likewise were most abundant during that period.

All three species overwinter as eggs under loose bark, in crevices, and occasionally on the unprotected outer surfaces of bark of the small limbs, main branches, and trunks of the trees. Turner (22) found this true of *M. costalis*, and Moznette et al. (9) found the same for the black pecan aphid.

There is considerable overlapping by the asexual and sexual forms within each species from the last of September until the end of the season. Clear-cut changes from asexual to sexual forms were never observed. These findings do not agree with the statement of Osburn et al. (11) that "all except the last generation produce living young." Also, the alate males of the species were observed to mate only with apterous oviparae and never with alate sexuparae, as indicated by Lieby (8).

Crowded colonies of long duration are not a general characteristic of the three species. Crowded colonies of *M. nigropunctata* (fig. 10) in the spring and of *M. caryella* in the spring and summer (fig. 7) do occur, but they usually last for 1 or 2 weeks. Colonies of *T. caryaefoliae* crowded to the extent of the other two species were never observed.

Much orchard-to-orchard variation in the susceptibility of a given cultivar to aphid attack was observed for all three species. This variation seems to be a function of numerous limiting factors such as parasites, predators, diseases, climate, tree condition, and cultural practices. Within an orchard of maximum cultivars, the susceptibility of trees of one cultivar may vary but usually for only a few days. This difference

can often be attributed to distances between trees. However, the time of attack in a mixed orchard often varies by 2 weeks to a month from cultivar to cultivar. Resistance to attack by 'Curtis', 'Moore', and 'Moneymaker' pecans (10) is not permanent, probably a function of changes in tree physiology. Most cultivars change rapidly in their susceptibility to attack between August 15 and frost. Season-long aphid resistance was observed in only a few cases.

Laboratory colonization showed that the yellow species can severely damage the leaf. Field observations confirmed this. All three species feed only in the vascular system of the leaves, damaging the veins at the feeding site. Each species is highly selective in choosing vein size. The three species occasionally probe the leaf for a suitable feeding site, but having quickly located a suitable site, they settle down for long periods of feeding. Probing does not damage the leaf. Frequently, new feeding sites are selected either just before or just after ecdysis. This is especially true of *M. nigropunctata*.

Tissue damage at the point of stylet insertion by the three species is somewhat similar at the start and usually was noticeable when a large population attacked hardened, mature leaves late in the season. The feeding site turns dark brown to black with apparent death of surrounding cells. Damage could have been caused by mechanical disruption of cell walls, digestion of the cell wall by aphid secretions, invasion of leaf tissue by a pathogen, or a plant reaction to the feeding activities. Damage increases in severity with leaf age. Leaf age and aphid population seem to be the most important factors in producing damage.

Vascular damage by all three species is often severe in the late summer and causes defoliation. Aborted leaflets with typical damage were observed as early as late July and early August of 1973 and 1974. All three species prefer to feed on the lower surface of the leaflets. A comparison of the species to determine the order of their preference for the lower surface showed that *M. nigropunctata* is greater than *M. caryella* is greater than *T. caryaefoliae*.

The three species not only compete with the tree for water and photosynthesized food, but they also cause a more subtle damage by depositing honeydew onto the upper surfaces of the leaves below them. Honeydew supports the growth of sooty molds (Capnodiceae), which

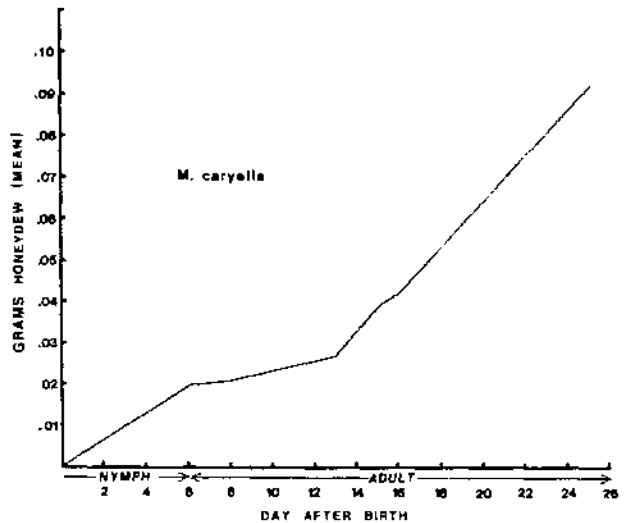


FIGURE 16.—Total honeydew produced during the life-span of *M. caryella*.

shade the leaves and probably interfere with photosynthesis. *M. caryella* was the heaviest producer of honeydew. The individuals produced an average of 0.92 gram per aphid during the first 25 days of life (fig. 16). The honeydew produced during days 6 to 13 (first week of adulthood) appeared somewhat reduced, but production was otherwise fairly constant. In tests beginning with equal numbers of each aphid species on seedlings in the laboratory, *M. caryella* produced 154 percent more honeydew per colony than *M. nigropunctata*, and 390 percent more than *T. caryaefoliae* after 56 days of continuous reproduction. Water removed from the honeydew after oven-drying at 50° C for 6 days for *T. caryaefoliae*, *M. caryella*, and *M. nigropunctata* was 14.8, 9.5, and 12.7 percent, respectively.

Sexual forms of all three species were produced in the laboratory on seedlings by changing the 15-hour-light, 9-hour-dark photoperiod to 12 hours of light and 12 hours of dark. Sex differences usually began to appear after 2 or 3 generations with this photoperiod. The availability of old, hardened seedlings for food appeared to hasten this process.

Alate viviparae of all three species were maintained on seedlings in the laboratory for 12 months under a light-dark photoperiod of 15 hours to 9 hours. The *M. nigropunctata* colony began to dwindle in January of each year, and the colony was lost in 2 out of 3 years before they became available in the field the following

April. Population decline resulted from death of first-instar nymphs soon after birth. A similar phenomenon was observed with *T. caryaefoliae*, but dwindle usually began about mid-February, and the colony was not lost. No such phenomenon occurred with the *M. caryella* colony.

Alates and nymphs of the species that were collected in 1973 and 1974 were placed in alcohol and examined to determine the numbers of each stadium and adults. All observed aphids were removed from the foliage for counts. The percentages of each stage between collections from different orchards, cultivars, and years at Byron were not significantly different. With *M. nigropunctata*, the first instars always exceeded 50 percent of the collection, and the adults were about 3 percent or less. The distribution of stages of *T. caryaefoliae* was more like *M. nigropunctata* than *M. caryella*, but first instars represented about 32 percent of those collected and adults about 6 percent. Distribution of *M. caryella* stages was more even. First instars represented about 24 percent and adults 11 percent (table 5). The large number of third-instar *M. caryella* indicates a high mortality of the first and second instars and low mortality of the third instar. Table 5 shows the average of each stage found for each species and the total number of specimens examined. Presumably, this information can be used to compute total field populations for a species by counting the individuals of one stage.

The biology and life history of *M. nigropunctata* and *T. caryaefoliae* are similar. *M. caryella* was different in most facets of this study.

MORPHOLOGY

A complete redescription of the three aphid species is not necessary. Bissell (2), Davis (3), Hottes and Frison (6), and Richards (17, 18) have published accurate descriptions of alate viviparae. However, for pecan researchers the alates usually constitute the least part of a field population of aphids. The following drawings and descriptions add information about the fourth-instar alate nymph and alate viviparous female and present new information about the first- through third-instar nymphs, the male, and the apterous oviparous female of each species. The drawings are of intact (less legs and the wings on one side) living aphids or of specimens freshly killed in alcohol.

TABLE 5.—Life stages of the alates of *T. caryaefoliae*, *M. caryella*, and *M. nigropunctata* found on field-collected samples of pecan foliage (1973-74)

Aphid stage	[Percent]		
	<i>T. caryaefoliae</i> ¹	<i>M. caryella</i> ²	<i>M. nigropunctata</i> ³
1st instar	32.3	23.6	52.6
2d instar	31.2	19.7	31.7
3d instar	18.6	27.5	8.1
4th instar	11.7	18.7	4.5
Adult	5.9	10.2	2.7

¹ 4,941 specimens.

² 1,548 specimens.

³ 15,873 specimens.

All three species are similar in their morphology in that the first instars normally have four antennal segments, second instars have five antennal segments, and third instars, fourth instars, and all adults always have six antennal segments. Fourth instars always have wing pads, and thus are easily separated from third instars. Between the wings alate adults have a frenum composed of a pair of upturned hooks on the anterior edge of the hindwing, which engages a short downward fold in the posterior edge of the forewing. This attachment holds the wings together during flight.

Tinocallis caryaefoliae (Davis)

In early April, the fundatrices and probably one or more subsequent generation of alates were predominately yellow during the first through fourth stadia and had little dark pigment except for the cornicles, legs, and antennae, which appeared dusky. These forms were easily confused with *M. nigropunctata* because of their color and pincushion appearance, especially the first and second instars. However, dusky legs, antennae, and truncate cornicles provided good characteristics to aid in the identification of the species. By the last week of April, all forms were well pigmented and dark. Adults were never yellow.

Figure 17, A-E, illustrates the most frequently observed nymphal forms and alate viviparae.

First-instar summer forms were pale yellowish green to nearly clear immediately after birth but after feeding became olive green to greenish

(Continued on page 20.)

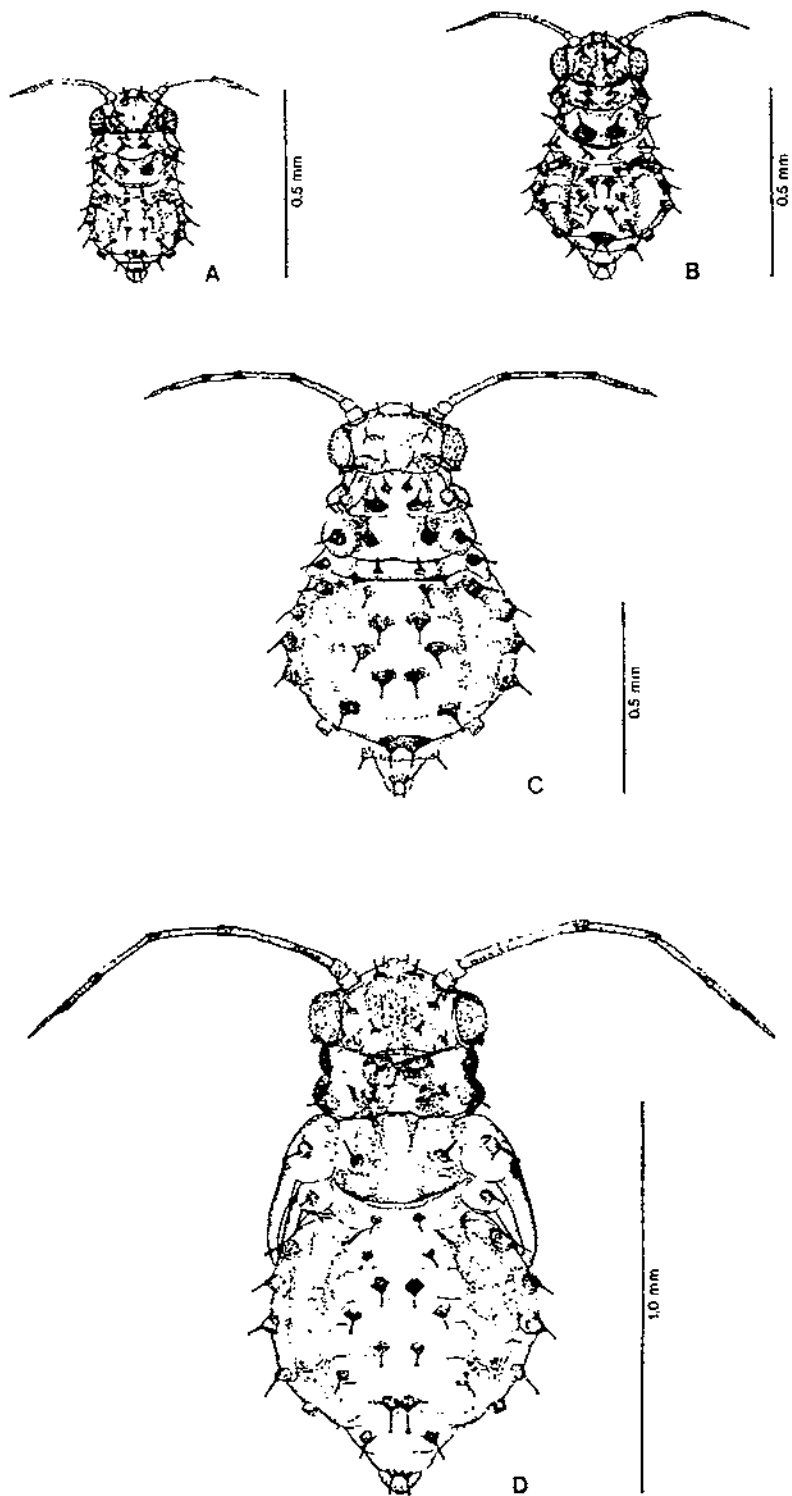


FIGURE 17.—*T. caryeifoliae* summer forms. A, First instar; B, second instar; C, third instar; D, fourth instar.

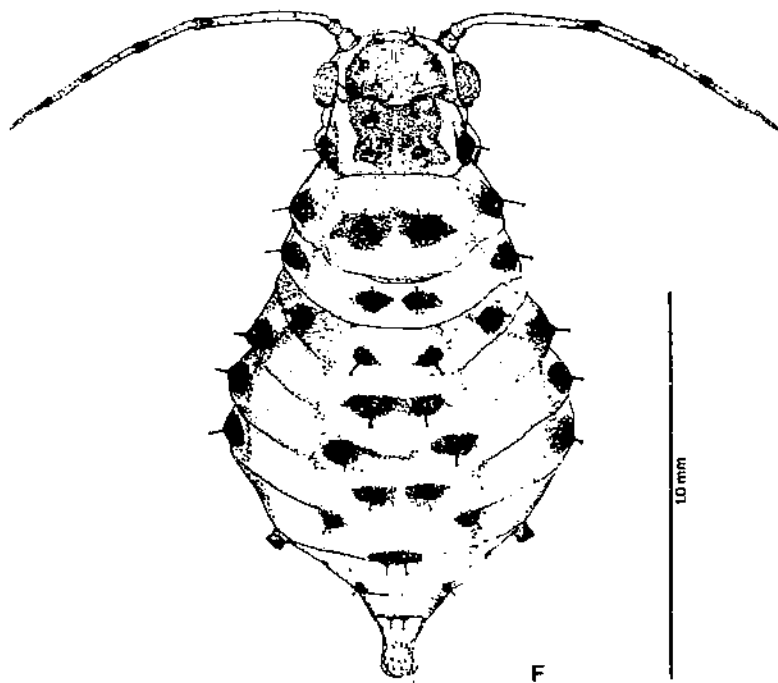
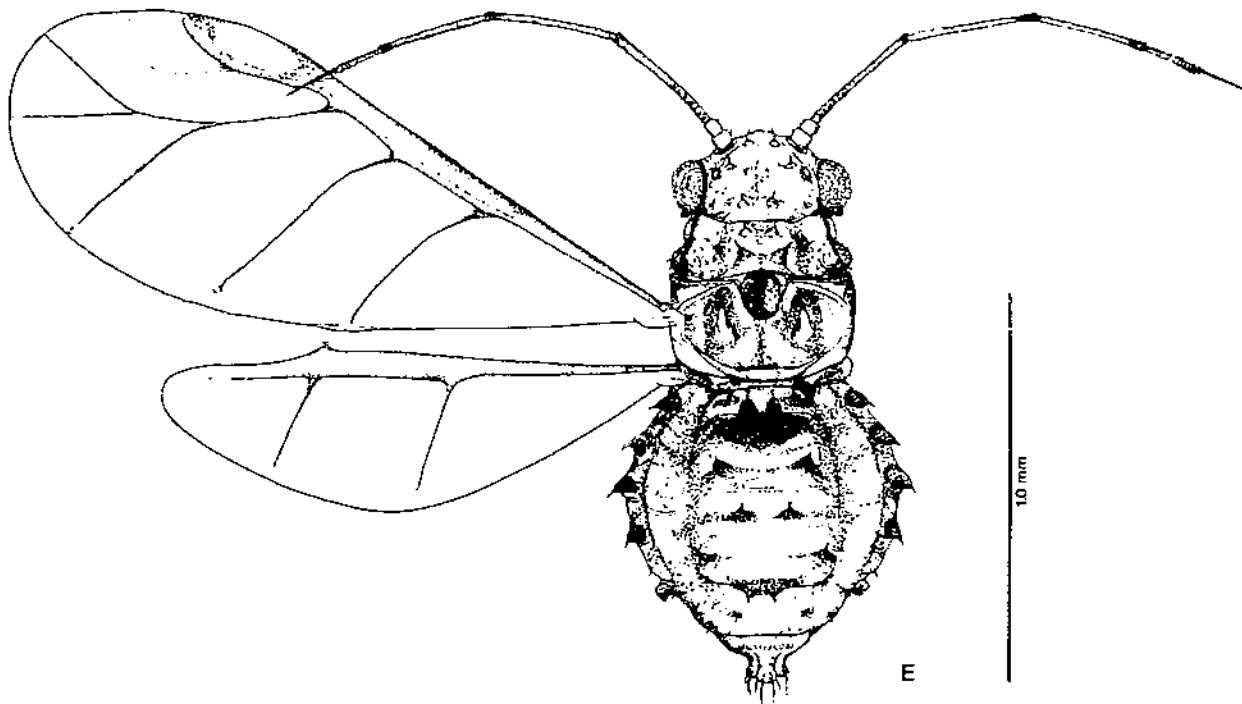


FIGURE 17.—*T. caryaefoliae* summer forms—Continued. E, Alate vivipara; F, apterous ovipara.

black. The nymphal stadia thereafter were about the same color or slightly darker. Just before moulting, the abdominal tubercles of nymphs were less prominent because of internal expansion of the aphid. Aphids in this state were basically olive green to black but usually had a reddish to brownish cast, especially the fourth instar.

Body length, abdominal width, and antennal length for first instars (fig. 17A) averaged 0.47, 0.28, and 0.27 millimeter, respectively; for second instars (fig. 17B), 0.64, 0.39, and 0.38 millimeter, respectively; for the third instars (fig. 17C), 1.02, 0.62, and 0.58 millimeters, respectively; and for fourth instars (fig. 17D), 1.36, 0.75, and 0.93 millimeters, respectively (table 6).

Average measurements of alate viviparae (fig. 17E) were: body length, 1.4 millimeters; abdominal width, 0.78 millimeter; antennal length, 1.45 millimeters; forewing length, 1.99 millimeters; and hindwing length, 1.38 millimeters. Measurements of the body length of the alate viviparae compared well with Davis' fig-

ures, and the body width was exactly the same as measured by Davis (3). In this study, abdominal width varied greatly, and the extremes were caused by the presence or absence of internal embryos, a condition related to the age of the aphid. Antennal segments III-VI were somewhat longer, and an average of 11 sensoria were found on antennal segment III, as opposed to 13 found by Davis (3). Bissell (2) found a range of 4 to 20 secondary sensoria, and the greater numbers occurred in the spring. Total sensoria on the antenna averaged 13 (table 7). Measurements of the antennal segments of the fourth instar averaged about 16 percent longer than measurements by Richards (17), but figures were comparable for the alate viviparae. Richards' (17) failure to mention the white waxy spots on the thorax and abdomen was probably a result of the chemical preparation of his specimens. Davis (3) did observe them.

Body length, abdominal width, and antennal length for apterous oviparae (fig. 17F) averaged 1.68, 0.95, and 1.1 millimeters, respectively. Apterous oviparae were considerably longer

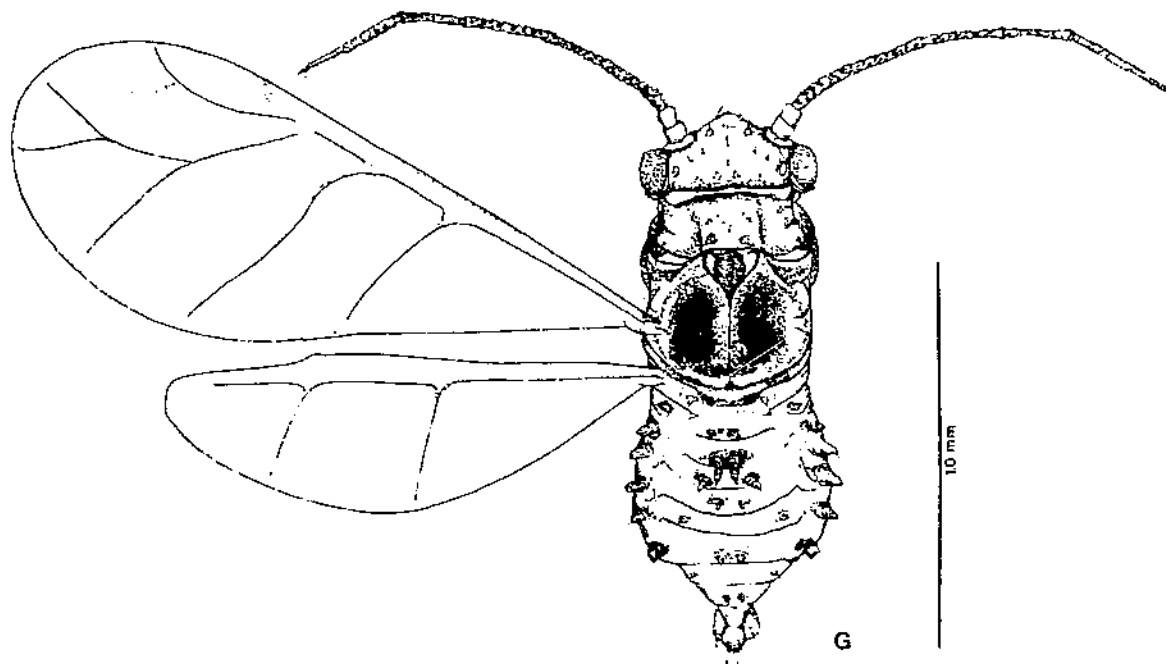


FIGURE 17.—*T. caryae foliae* summer forms—Continued. G, Male.

TABLE 6.—Measurements of living and freshly killed in alcohol, first through fourth instars, alate males and females, and apterous females of *T. caryaefoliae*, *M. caryella*, and *M. nigropunctata*

[Millimeters]

Aphid form	Aphids examined	Body length		Abdominal width		Antennal length ¹		Antennal segment length (mean)				Wing length (mean)	
		Mean	Range	Mean	Range	Mean	Range	III	IV	V	VI ²	Fore	Hind
<i>T. caryaefoliae</i>													
1st instar	5	0.47	0.46-48	0.28	0.27-30	0.27	0.23-27	0.10	0.09
2d instar	5	.64	.61-.65	.39	.35-.41	.38	.35-.41	.12	.07	0.12
3d instar	5	1.02	.96-1.09	.62	.61-.63	.58	.54-.61	.16	.09	.10	0.15
4th instar	5	1.36	1.36	.75	.75-.78	.93	.91-.95	.30	.14	.16	.21
Alate female	5	1.40	1.10-1.67	.78	.54-.80	1.45	1.20-1.53	.45	.31	.27	.27	1.99	1.38
Male	12	1.40	1.27-1.45	.60	.44-.69	1.20	.91-1.45	.36	.22	.18	.28	1.99	1.30
Apterous female	5	1.68	1.64-1.71	.95	.91-.98	1.10	.98-1.10	.36	.18	.16	.23
<i>M. caryella</i>													
1st instar	5	0.70	0.68-71	0.28	0.27-31	0.42	0.41-44	0.15	0.15
2d instar	5	.97	.95-.99	.36	.34-.39	.56	.54-.58	.15	.10	0.20
3d instar	4	1.16	1.08-1.36	.49	.41-.57	.75	.75	.12	.12	.14	0.26
4th instar	5	1.55	1.49-1.70	.72	.68-.78	1.14	1.10-1.20	.27	.20	.22	.31
Alate female	5	1.98	1.80-2.10	.86	.79-.95	1.57	1.40-1.80	.42	.26	.27	.40	1.94	1.24
Male	2	1.70	1.60-1.71	.73	.73	1.35	1.35	.38	.27	.26	.36	1.90	1.20
Apterous female	5	1.70	1.60-1.75	.80	.76-.81	1.02	.98-1.20	.29	.18	.18	.26
<i>M. nigropunctata</i>													
1st instar	4	0.56	0.48-.61	0.27	0.22-.28	0.34	0.27-.35	0.14	0.13
2d instar	4	.74	.70-.75	.29	.27-.34	.38	.34-.41	.11	.09	0.13
3d instar	4	.89	.88-.99	.41	.38-.44	.52	.47-.54	.13	.07	.09	0.13
4th instar	4	1.36	1.30-1.40	.54	.51-.54	.65	.65-.72	.18	.10	.12	.17
Alate female	5	1.60	1.50-1.80	.62	.59-.67	.88	.87-.90	.26	.18	.16	.20	1.70	1.20
Male	5	1.27	1.10-1.30	.47	.43-.51	.91	.83-.91	.25	.18	.15	.26	1.31	.84
Apterous female	7	1.60	1.40-1.64	.65	.61-.73	.84	.72-1.00	.22	.18	.15	.18

¹ Length includes segments I and II.

² Antennal segment VI includes unguis.

TABLE 7.—Counts of primary and secondary antennal sensoria of the alates of *T. caryaefoliae*, *M. caryella*, and *M. nigropunctata*

Aphid alate	Specimens examined	Sensoria per segment ¹								Mean total
		III		IV		V ²		VI ²		
		Mean	Range	Mean	Range	Mean	Range	Mean	Range	
<i>T. caryaefoliae</i>										
Male	2	44	42-45	20	19-20	13	12-14	3	3	80
Female	11	11	7-15	0	0	1	1	1	1	13
<i>M. caryella</i>										
Male	6	35	33-38	14	12-15	9	9-10	4	3-5	62
Female	6	4	3-5	0	0	1	1	1	1	6
<i>M. nigropunctata</i>										
Male	6	18	16-31	10	6-15	8	6-11	2	2-3	38
Female	6	7	5-11	0	0	1	1	1	1	9

¹ Sensoria do not occur on the 1st and 2d antennal segments.

² Includes primary sensorium.

and wider than the viviparae (table 6), but the antennae were shorter. Larger body size was caused by the presence of unlaidd eggs because oviparae collected from foliage had rarely oviposited. While the chaetotaxy did not change, the tubercles supporting setae were much less prominent than those of the viviparae.

Average measurements for males (fig. 17G) were: body length, 1.4 millimeters; abdominal width, 0.6 millimeter; antennal length, 1.2 millimeters; forewing length, 1.99 millimeters; and hindwing length, 1.3 millimeters. Males were somewhat smaller than the viviparae, and the range in size of individuals was less. Tubercles were prominent but diminutive, and the pterothorax was enlarged as compared with the viviparae. Males had an average of 80 sensoria on each antenna (table 7).

The number of setae on the head, thorax, and abdomen was constant on all forms except for the cauda and anal plates of the adults. Setae became only slightly longer with each molt, and hence setal length relative to the aphid size changed drastically. The six dorsoabdominal setae located on segments II, III, and IV formed an almost perfect hexagon that was evident on all forms, especially the nymphs, and is a good identifying character.

Monellia caryella (Fitch)

The alate fundatrices, their nymphal forms, and several subsequent generations of alate

viviparae and their nymphs lacked the typical black pigmentation except on the antennae. First-instar nymphs were pale yellow to almost colorless immediately after birth and had little or no detectable black pigment on the fourth antennal segment apex. Subsequent nymphal stadia were pale yellow but less clear, and the amount of black pigmentation on the antennal apexes was still less than typical.

Typical pigmentation patterns on the nymphs and alate viviparae occurred about the last of May, but adults and nymphs did not develop full pigmentation until the first of June. This finding agreed with Quednau (16), who reasoned through observations of *M. caryella* and *M. costalis* collections that *M. costalis* was the melanistic summer form of *M. caryella*.

Figure 18, A-E, illustrates the most frequently encountered nymphal and alate viviparae (summer) forms.

First through third instars were pale yellow (fig. 18, A-C) and maculated with a black spot on the lateral dorsum of the mesothorax and metathorax and abdominal segments I through VII. Spots on abdominals I and V were always wider than those on other abdominal segments. Small and variable amounts of dark pigment occurred at the bases of the spinal setae. The apexes of the antennal segments other than I and II were dark.

Body length, abdominal width, and antennal length for first instars (fig. 18A) averaged 0.70, 0.28, and 0.42 millimeter, respectively; for

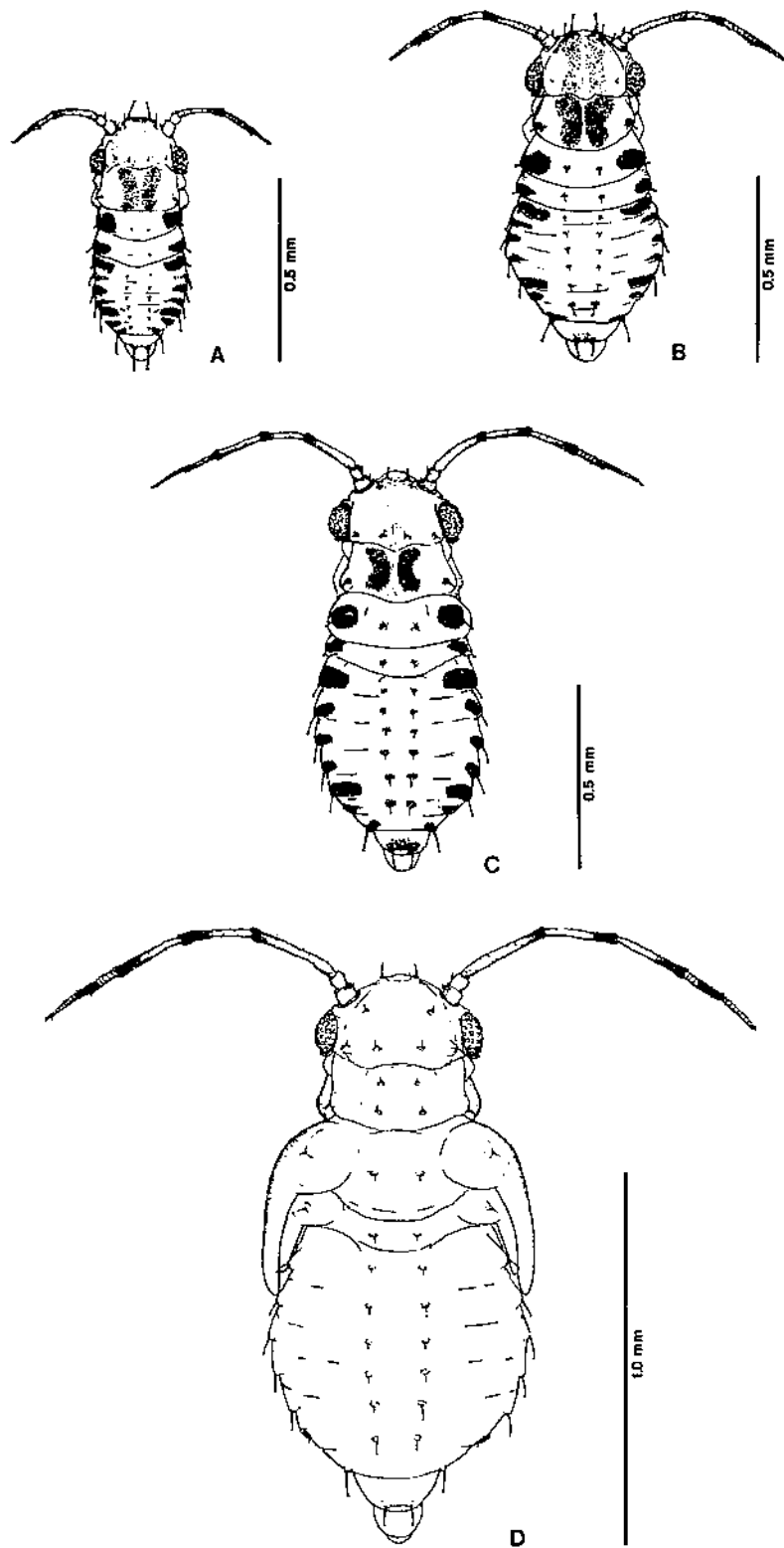


FIGURE 18.—*M. caryella* summer forms. A, First instar; B, second instar; C, third instar; D, fourth instar.

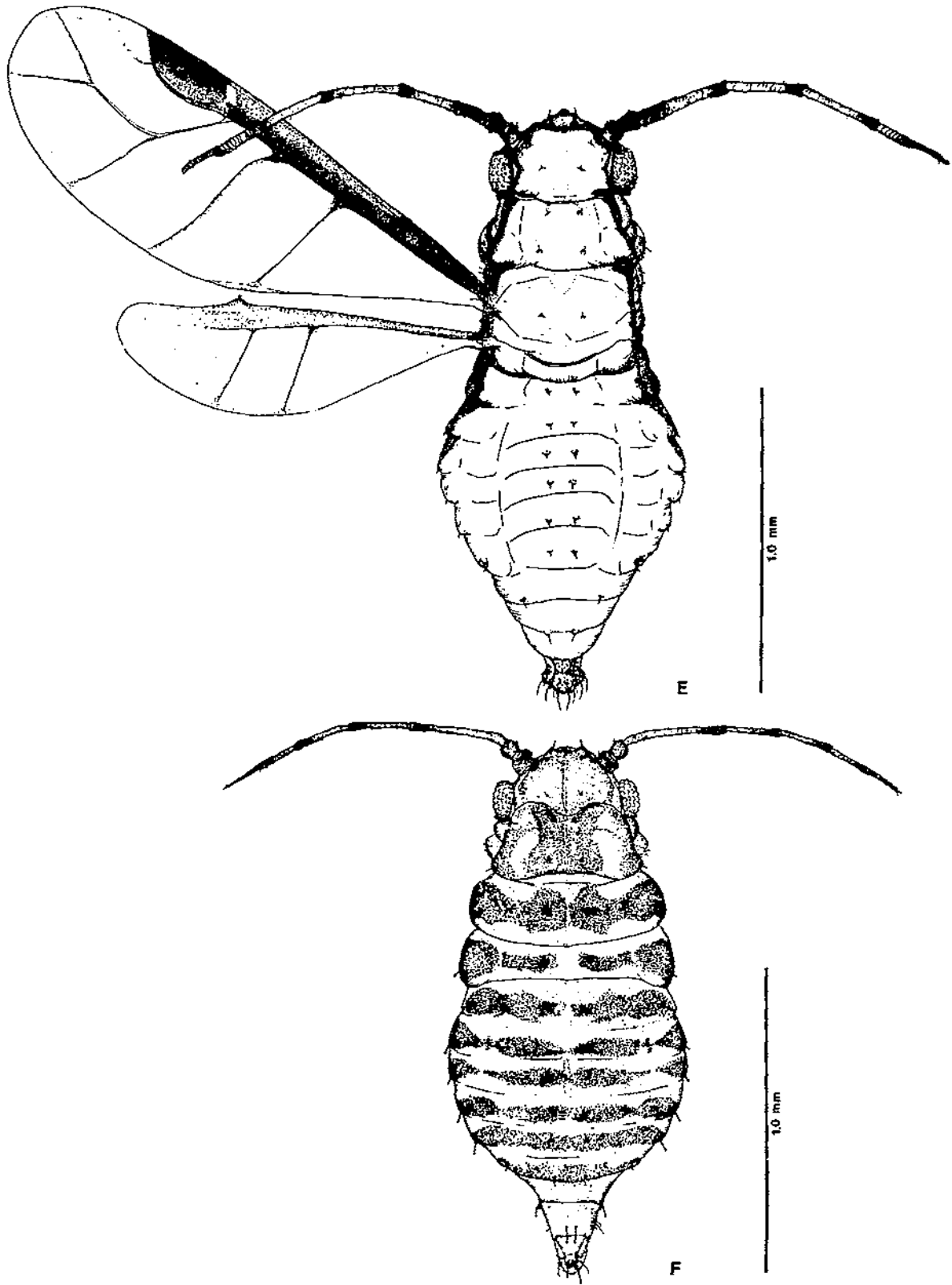


FIGURE 18.—*M. caryella* summer forms—Continued. E, Alate vivipara; F, apterous ovipara.

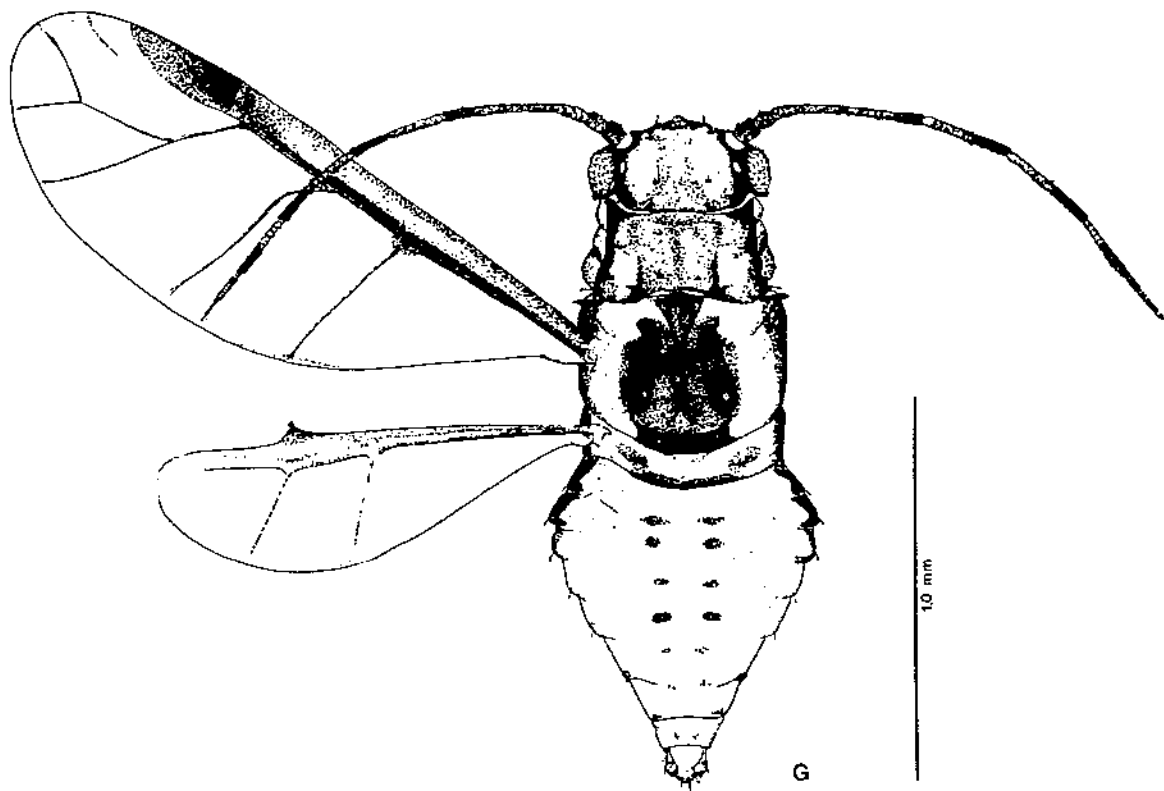


FIGURE 18.—*M. caryella* summer forms—Continued. G, Male.

second instars (fig. 18B), 0.97, 0.36, 0.56 millimeter, respectively; for third instars (fig. 18C), 1.16, 0.49, and 0.75 millimeters, respectively; and for fourth instars (fig. 18D), 1.55, 0.72, and 1.14 millimeters, respectively (table 6). Fourth instars were nearly immaculate except for black on the antennal apices of segments III–VI and small amounts of dark pigment at the bases of the spinal setae and the lateral edges of the thorax and wing pads.

Summer forms of the alate viviparae (fig. 18E) had heavily pigmented black costal veins that were easily observed because the wings were held horizontally over the abdomen when at rest. (Few aphid species hold their wings like this.) Black pigmentation was heaviest in all forms during October and November. Variation in the pigmentation of individuals occurred throughout the season. Average measurements of the summer alate viviparae (table 6) were: body length, 1.98 millimeters; abdominal width, 0.86 millimeter; antennal length, 1.57 millimeters; forewing length, 1.94 millimeters; and hindwing length, 1.24 millimeters. Richards' figures for *M. costalis* (17) compare well with

these measurements. Measurements of the width varied widely for the same reasons as for *T. caryaefoliae*. Antennal lengths varied greatly and antennae averaged 6 sensoria each (table 7).

Oviparous females were a dirty orangish-yellow color and appeared banded (fig. 18F) because of the pattern of dark pigmentation. Bands across the first and fifth abdominal segments were the most prominent. This form was usually smaller than that of the alate female. Body length, abdominal width, and antennal length averaged 1.7, 0.80, and 1.02 millimeters, respectively (table 6).

Males (fig. 18G) were slightly smaller than the alate viviparae. Average measurements were: body length, 1.7 millimeters; abdominal width, 0.73 millimeter; antennal length, 1.35 millimeters; forewing length, 1.90 millimeters; and hindwing length, 1.20 millimeters (table 6). Males were easily recognized by the abundance of black pigment on the pterothorax, the head, and the areas around the spinal setae. The pterothorax was enlarged compared to the viviparae. Males had an average of 62 sensoria on each antenna (table 7). The numbers and ar-

rangement of the setae on the head, thorax, and abdomen were constant on all forms except for the cauda and anal plates of adults.

M. caryella nymphs were dorsally depressed compared to *M. nigropunctata*, and the setae were much shorter, were difficult to see, and formed angles less than 45° with the body.

Monelliopsis nigropunctata (Granovsky)

The first through third instars of the fundatrices and of several subsequent generations of the alate viviparae had no dark pigment on the apexes of the antennal segments, but it was present on the fourth-instar antennal segments. These aphids were clear and light yellow but were not as pale as *M. caryella*. By May, apical ends of antennal segments V and VI of the third instar were slightly pigmented as was segment VI (apical) of the second instar. In June, all nymphal forms were distinctly yellow and had small amounts of pigment at the bases of the dorsal abdominal setae and on the apexes of all antennal segments except I and II. However, this was highly variable for the entire year. The pigmentation around the dorsoabdominal setae of the viviparae was also variable.

Figure 19, A-E, illustrates the most frequently observed summer forms of nymphs and the alate viviparae.

Body length, abdominal width, and antennal length for first instars (fig. 19A) averaged 0.56, 0.27, and 0.34 millimeter, respectively (table 6). First instars usually had only two rows of dorsal setae running lengthwise the thorax and abdomen, but fragments of two additional rows were occasionally observed on the first or second abdominal segments.

Second instars (fig. 19B) averaged 0.74 millimeter in body length, 0.29 millimeter in abdominal width, and 0.38 millimeter in antennal length (table 6). Two additional rows of thoracic and abdominal setae were evident but often poorly developed.

Third instars (fig. 19C) averaged 0.89 millimeter in body length, 0.41 millimeter in abdominal width, and 0.52 millimeter in antennal length (table 6). Four well-defined rows of dorsal thoracic and abdominal setae were evident.

Fourth instars (fig. 19D) averaged 1.36 millimeters in body length, 0.54 millimeter in abdominal width, and 0.65 millimeter in antennal length (table 6). Thoracic and abdominal setae

were the same as that of the third instar, only longer and more clearly defined. Pigmentation around the bases of these setae was often lacking but always present on the apexes of antennal segments III through VI.

Average measurements for alate viviparae (fig. 19E) were: body length, 1.6 millimeters; abdominal width, 0.62 millimeter; antennal length, 0.88 millimeter; forewing length, 1.7 millimeters; and hindwing length, 1.2 millimeters (table 6). Pigment was more evident around the dorsoabdominal setae of the first and second segments than those of other abdominal segments.

Granovsky (6) described well the alate viviparous female of *M. nigropunctata*. His measurements of the antennae, however, were about 22 percent shorter than in this study (table 6). Apparently, he misplaced the decimal point in his measurements of the antennal segments, and the decimals should be moved two places to the left. This form averaged 9 sensoria on each antenna (table 7).

Body length, abdominal width, and antennal length of apterous oviparae averaged 1.6, 0.65, and 0.84 millimeters, respectively (table 6), measurements similar to those for the alate viviparae. The pigmentation of this form was greatest but somewhat variable. They were usually well pigmented (spotted) around the setae bases and on the apexes of antennal segments III through VI (fig. 19F). This form was yellowish orange and appeared spotted or checkered.

Average measurements for males (fig. 19G) were: body length, 1.27 millimeters; abdominal width, 0.47 millimeter; antennal length, 0.91 millimeter; forewing length, 1.31 millimeters; and hindwing length, 0.84 millimeter (table 6). They were heavily pigmented over the central area of the dorsal pterothorax with dark pigment on the prothorax and head. Irregularly shaped black spots surrounded the dorsoabdominal setae. Males were decidedly smaller and darker than the alate viviparae, and thus easily recognized. Males averaged 38 sensoria on each antenna (table 7).

Generally, *M. nigropunctata* nymphs were bullet shaped, and the long setae of the nymphs and oviparae tended to stand out from the body at 45° to nearly 90°, presenting a pincushion appearance. Because of their color and the openness of feeding sites, the nymphs of this species

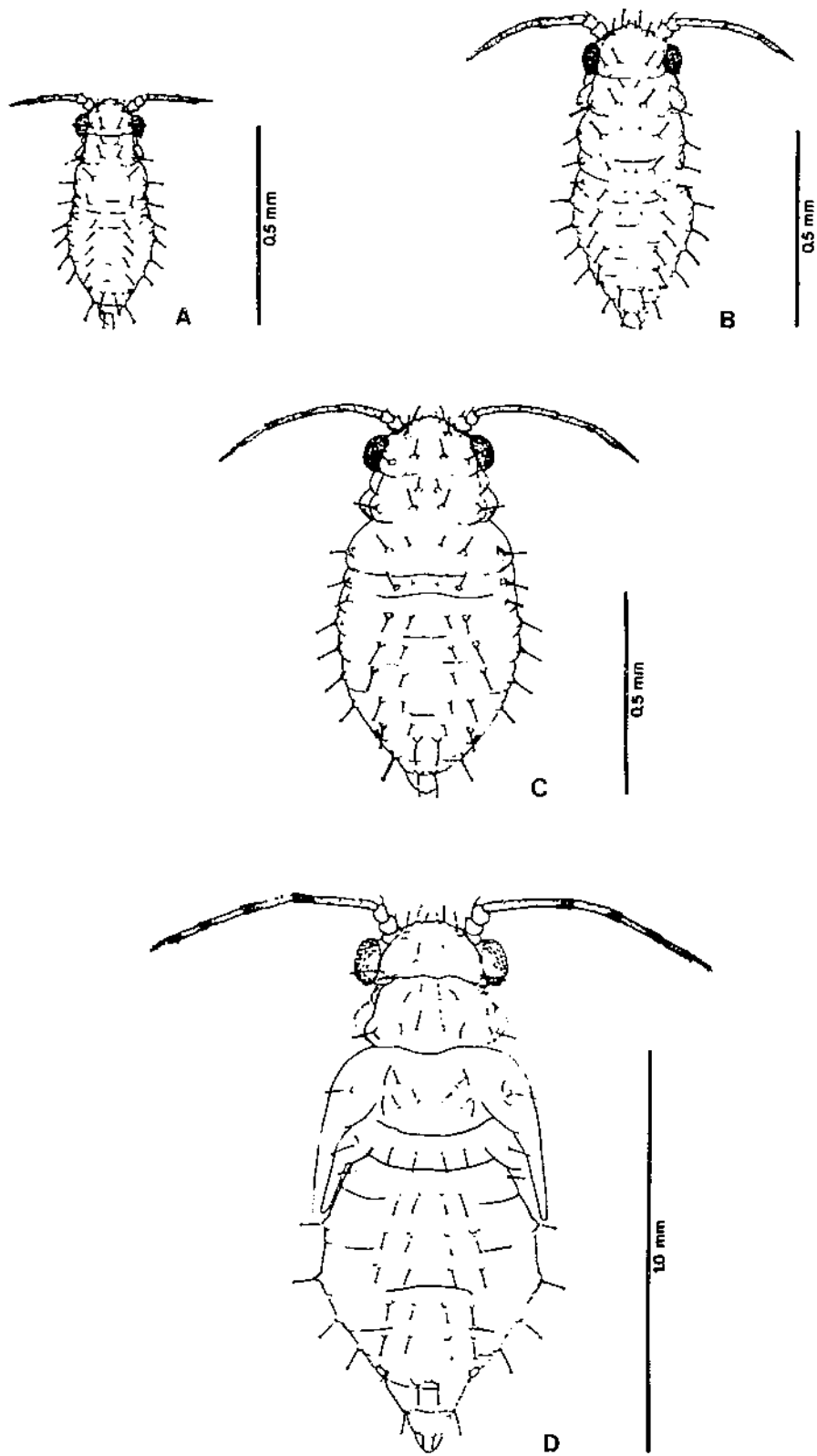


FIGURE 19.—*M. nigropunctata* summer forms. A, First instar; B, second instar; C, third instar; D, fourth instar.

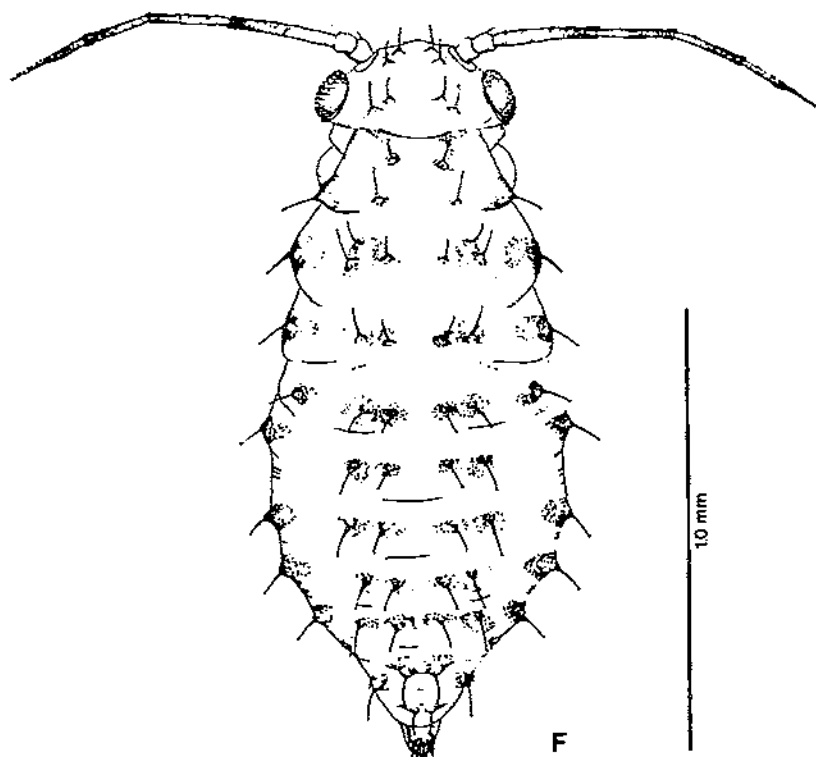
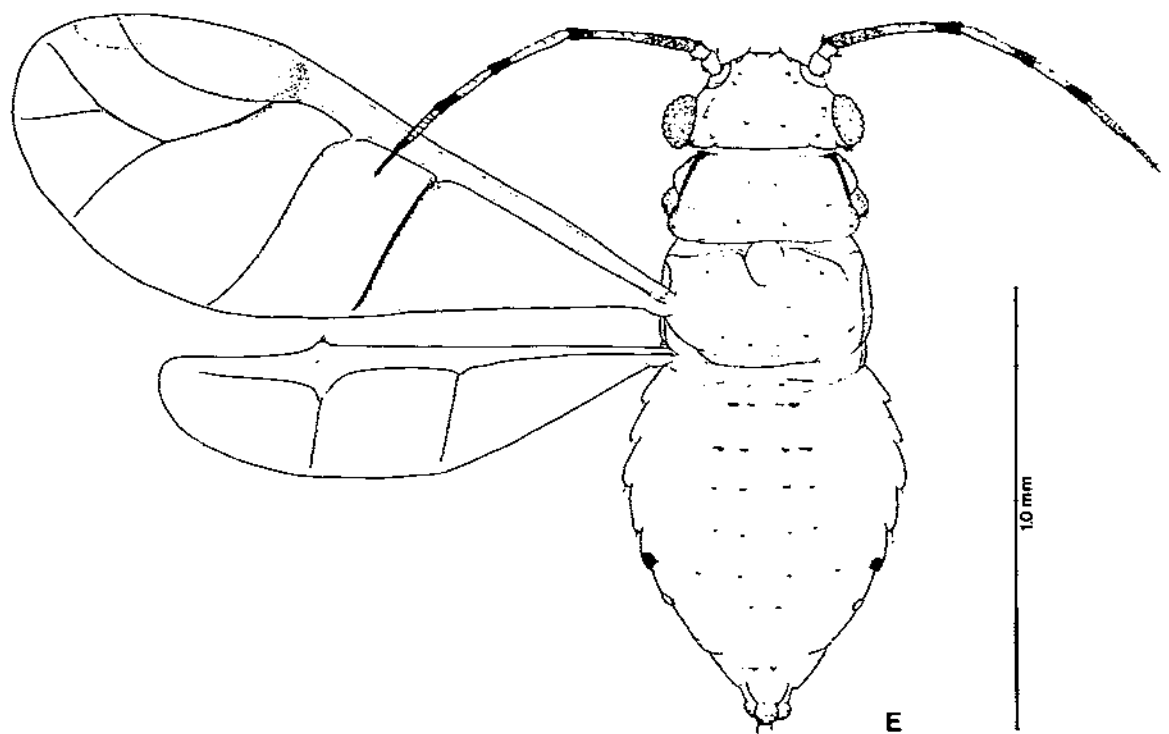


FIGURE 19.—*M. nigropunctata* summer forms—Continued. E, Alate vivipara; F, apterous ovipara.

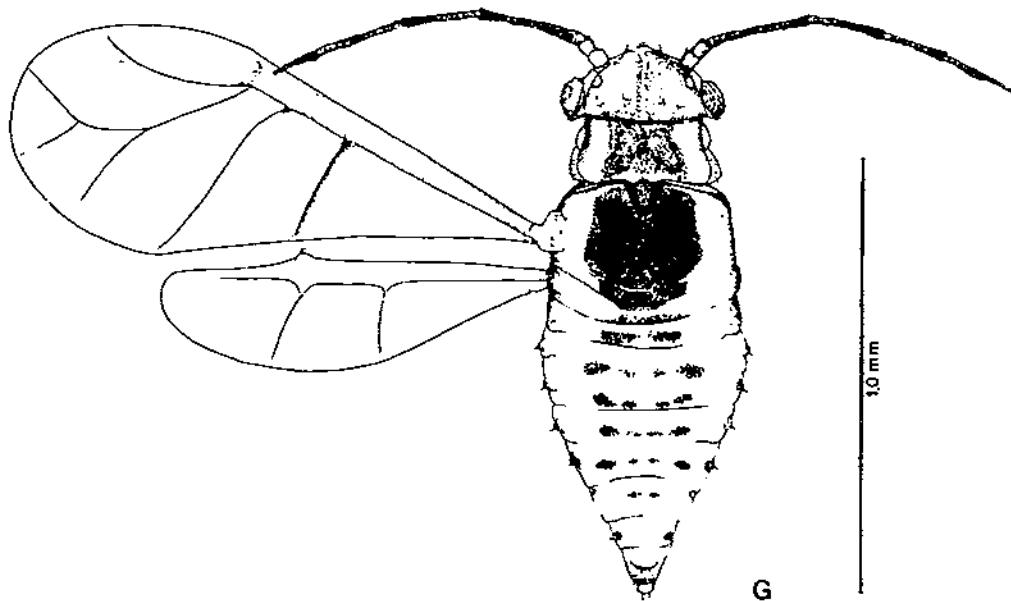


FIGURE 19.—*M. nigropunctata* summer forms—Continued. G, Male.

were easy to detect on pecan foliage, regardless of their smaller size.

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