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Larva of *Calothysanis amaturaria* Walker (Lepidoptera: Geometridae) feeding on bindweed. Photograph by M. Keith Kennedy, Department of Entomology, Michigan State University. Determination by M. C. Nielsen.

Vol. 14, No. 2 of The Great Lakes Entomologist was mailed on 14 July 1981
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SEASONAL FLIGHT PATTERNS OF HEMIPTERA IN A NORTH CAROLINA BLACK WALNUT PLANTATION. 5. LYGAEOIDEA

J. E. McPherson and B. C. Weber

ABSTRACT

The seasonal flight patterns of 31 species of Lygaeoidea collected in window traps in a North Carolina black walnut plantation are described. Flying height distributions and seasonal flight activities of Antillocoris pilosulus (Stål), Crophius disconotus (Say) and Geocoris punctipes (Say) are considered in detail.

This is the fifth in a series of papers on seasonal flight patterns of Hemiptera in a black walnut (Juglans nigra L.) plantation near Asheville, North Carolina, and deals with the superfamily Lygaeoidea; earlier papers dealt with the Pentatomoidea (1980), Coreoidea (1981a), Reduvioidae (1981b), and Cimicoidea (1981c). The study was conducted from 24 March to 14 October in 1977, and from 24 March to 13 October in 1978. Specimens were collected weekly by window trapping; traps were suspended at 1, 2, 3, 4, 5, 6 and 7 m. The study site and trap construction were discussed in detail by McPherson and Weber (1980). All hemipteran specimens collected during this study are deposited in the Entomology Collection, Zoology Research Museum, Southern Illinois University, Carbondale.

RESULTS AND DISCUSSION

Thirty one lygaeid species were collected during the two years of this study with the lygaeids being best represented; numbers of specimens collected for all taxa ranged from one to 311 (Table I).

Most of the species were collected in numbers too low to permit conclusions about seasonal flight patterns. However, Antillocoris pilosulus (Stål), Crophius disconotus (Say) and Geocoris punctipes (Say) were collected in sufficient numbers (Table I) to allow a more detailed discussion of flying height distributions and seasonal flight activities.

A. pilosulus has been swept from grasses in a dry cranberry bog in New York (Torre-Bueno 1912); found in a grass clump and at lights in Missouri (Froeschner 1944); in the pitcher plant Sarracenia purpurea L. in North Carolina (Wray and Brimley 1943); in the litter of the shrub Rhododendron catawbiense Michaux and in leaf litter along a mesophytic woodland edge, both sites in North Carolina (Sweet 1964); apparently in the thick litter beneath the bayberry, Myrica pensylvanica Loiseleur-Deslongchamps, in Connecticut (Sweet 1964); and beneath stones on the slopes of hillside pastures in Indiana (Blatchley 1926). It apparently is univoltine and overwinters as adults (Sweet 1963).

In the present study. A. pilosulus adults were found from late March to mid-October (Table I). They were collected at all seven flying heights with almost 40% captured at 4–5 m (Fig. 1).

This species overwintered as adults but the number of generations per year is unclear from the data available (Fig. 4). If, as Sweet (1963) suggested, this species is univoltine, then the
Table 1. Seasonal flight activity of Lygaeoidea during 1977–78 in a North Carolina black walnut plantation.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>No. Collected</th>
<th>Collection Height (m)</th>
<th>Range of Collection Dates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lygaeidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Antillocorus pilosulus</em> (Stål)</td>
<td>311</td>
<td>4.26±0.10 1–7</td>
<td>31 March–13 Oct.</td>
</tr>
<tr>
<td><em>Belonochilus numenius</em> (Say)</td>
<td>38</td>
<td>5.71±0.25 2–7</td>
<td>1 April–6 Oct.</td>
</tr>
<tr>
<td><em>Blissus leucopterus</em> (Say)</td>
<td>1</td>
<td>6.00</td>
<td>—</td>
</tr>
<tr>
<td><em>Crophius disconotus</em> (Say)</td>
<td>79</td>
<td>3.09±0.20 1–7</td>
<td>19 May–13 Oct.</td>
</tr>
<tr>
<td><em>Cryphula trimaculata</em> (Distant)</td>
<td>1</td>
<td>1.00</td>
<td>—</td>
</tr>
<tr>
<td><em>Cymus angustatus</em> Stål</td>
<td>4</td>
<td>3.00±1.41 1–7</td>
<td>31 March–25 Aug.</td>
</tr>
<tr>
<td><em>Cymus discors</em> Horvath</td>
<td>7</td>
<td>4.43±0.61 2–7</td>
<td>31 March–1 Sept.</td>
</tr>
<tr>
<td><em>Eremocoris herus</em> (Say)</td>
<td>3</td>
<td>5.00±1.00 3–6</td>
<td>31 March–30 June</td>
</tr>
<tr>
<td><em>Geocoris punctipes</em> (Say)</td>
<td>78</td>
<td>2.37±0.20 1–7</td>
<td>31 March–13 Oct.</td>
</tr>
<tr>
<td><em>Geocoris uliginosus</em> (Say)</td>
<td>9</td>
<td>5.22±0.52 3–7</td>
<td>20 May–9 Sept.</td>
</tr>
<tr>
<td><em>Heraeus plebejus</em> Stål</td>
<td>3</td>
<td>5.33±0.88 4–7</td>
<td>30 June–22 July</td>
</tr>
<tr>
<td><em>Kleidoceris resedae</em> (Panzer)</td>
<td>28</td>
<td>5.39±0.34 1–7</td>
<td>29 April–13 Oct.</td>
</tr>
<tr>
<td><em>Kolenetrus plenus</em> (Distant)</td>
<td>1</td>
<td>1.00</td>
<td>—</td>
</tr>
<tr>
<td><em>Ligyrocoris diffusus</em> Uhler</td>
<td>7</td>
<td>3.86±0.94 1–7</td>
<td>29 April–15 Sept.</td>
</tr>
<tr>
<td><em>Lygaeus kalmii</em> Stål</td>
<td>19</td>
<td>1.68±0.20 1–4</td>
<td>9 June–29 Sept.</td>
</tr>
<tr>
<td><em>Lygaeus turcicus</em> (Fabricius)</td>
<td>1</td>
<td>2.00</td>
<td>—</td>
</tr>
<tr>
<td><em>Myodocha serripes</em> Olivier</td>
<td>10</td>
<td>4.20±0.77 1–7</td>
<td>22 April–7 July</td>
</tr>
<tr>
<td><em>Neacoryphus bicrucis</em> (Say)</td>
<td>2</td>
<td>5.00±0.00</td>
<td>7 July–14 July</td>
</tr>
<tr>
<td><em>Nysius niger</em> Baker</td>
<td>10</td>
<td>4.70±0.72 1–7</td>
<td>7 April–13 Oct.</td>
</tr>
<tr>
<td><em>Ortholomus scolopax</em> (Say)</td>
<td>12</td>
<td>2.58±0.68 1–7</td>
<td>10 June–25 Aug.</td>
</tr>
<tr>
<td><em>Pachybrachius basalis</em> (Dallas)</td>
<td>12</td>
<td>4.00±0.71 1–7</td>
<td>1 April–13 Oct.</td>
</tr>
<tr>
<td><em>Pachybrachius bilobatus</em> (Say)</td>
<td>13</td>
<td>3.00±0.39 1–5</td>
<td>17 June–13 Oct.</td>
</tr>
<tr>
<td><em>Phlegyas abbreviatus</em> (Uhler)</td>
<td>1</td>
<td>1.00</td>
<td>29 July</td>
</tr>
<tr>
<td><em>Pseudocnemodus canadensis</em> (Provancher)</td>
<td>2</td>
<td>5.50±1.50 4–7</td>
<td>30 June–14 July</td>
</tr>
<tr>
<td><em>Piochiomera nodosa</em> Say</td>
<td>45</td>
<td>3.80±0.32 1–7</td>
<td>3 June–13 Oct.</td>
</tr>
<tr>
<td><em>Xyonysius californicus</em> (Stål)</td>
<td>9</td>
<td>4.11±0.77 1–7</td>
<td>7 April–6 Oct.</td>
</tr>
<tr>
<td><em>Zeridoneus costalis</em> (Van Duzee)</td>
<td>1</td>
<td>7.00</td>
<td>—</td>
</tr>
<tr>
<td><em>Piesmatidae</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Jalysus spinosus</em> (Say)</td>
<td>1</td>
<td>6.00</td>
<td>26 May</td>
</tr>
<tr>
<td><em>Jalysus wickhami</em> Van Duzee</td>
<td>30</td>
<td>3.40±0.38 1–7</td>
<td>3 June–8 Sept.</td>
</tr>
<tr>
<td><em>Neides muticus</em> (Say)</td>
<td>1</td>
<td>3.00</td>
<td>14 April</td>
</tr>
<tr>
<td><em>Piesma cinerea</em> (Say)</td>
<td>32</td>
<td>3.72±0.44 1–7</td>
<td>14 April–13 Oct.</td>
</tr>
</tbody>
</table>

Overwintered adults emerged in late March and were most active during the first two weeks of April. Their adult offspring were present from about July to the end of the season and were particularly active in August, and in October just before entering overwintering sites. *C. disconotus* has been collected from pine (Slater and Baranowski 1978), goldenrod (Slater and Baranowski 1978, Torre-Bueno 1925, Van Duzee 1894) and oak (Torre-Bueno 1912). We have found no published information on its field life cycle.

In the present study, *C. disconotus* adults were found from the third week of May to mid-October (Table 1). They were collected at all seven flying heights with almost 66% captured at 1–3 m (Fig. 2). This species overwintered as adults and was apparently univoltine (Fig. 5). Adults began to emerge from overwintering sites in late May and were present to late June. Their adult offspring occurred from late September to the end of the season. It is possible that other
Fig. 1-3. Flying height distributions of three lygaeid species during 1977-78 in a North Carolina black walnut plantation: (1) Antillocoris pilosulus, (2) Crophius discnotus, (3) Geocoris punctipes.

Fig. 4-6. Seasonal flight activities of three lygaeid species during 1977-78 in a North Carolina black walnut plantation: (4) Antillocoris pilosulus, (5) Crophius discnotus, (6) Geocoris punctipes.

generations were produced during the season that did not exhibit flight activity (e.g., overwintering adults may actually have emerged in March-April and the May-June activity is that of their adult offspring) but this could not be determined from the available data.

G. punctipes has been collected on alfalfa (Townsend 1894) and cotton (McGregor and McDonough 1917), and by sweeping low weeds and searching under objects on the ground (Froeschner 1944); it is known to feed on spider mites (McGregor and McDonough 1917). We have found no published information on its field life cycle other than it is known to overwinter as adults (Froeschner 1944).

In the present study, G. punctipes adults were found from late March to mid-October (Table 1). They were collected at all seven flying heights with almost 50% captured at 1 m.

This species overwintered as adults and was apparently bivoltine although the fluctuations in flight activity during the season make this difficult to determine. Nevertheless, the follow-
ing life cycle seems probable. Adults began to emerge from overwintering sites in late March (Fig. 6). Their adult offspring (summer generation) occurred from about June to late July or early August, and peaked in early July. Adults of the second (overwintering) generation occurred from August to the end of the season. It is possible that the peak in October represents an additional generation but since the time between this peak and that in September is only one month, the drop at the end of September probably resulted from random variation or was a response to some environmental factor (e.g., temperature).

ACKNOWLEDGMENTS

We wish to thank Dr. J. A. Slater, Biological Sciences Group, University of Connecticut, Storrs, and Dr. R. C. Froeschner, National Museum of Natural History, Washington, D.C., for confirming our identifications of these lygaeids and berytids, respectively. We also wish to acknowledge Mr. D. Brenneman and the staff of the North Carolina Division of Forestry, Morganton, for their help in collecting data and maintaining the window traps. This research was partially supported by the USDA Forest Service, North Central Forest Experiment Station.

LITERATURE CITED


SEASONAL FLIGHT PATTERNS OF HEMIPTERA IN A NORTH CAROLINA BLACK WALNUT PLANTATION.
6. TINGIDAE AND ARADIDAE

J. E. McPherson¹ and B. C. Weber ²

ABSTRACT

The seasonal flight patterns of 11 species of Tingidae and six species of Aradidae collected in window traps in a North Carolina black walnut plantation are described. Flying height distributions and seasonal flight activities of Corythucha ciliata (Say) and Gargaphia solani Heidemann are considered in detail.

This is the sixth in a series of papers on seasonal flight patterns of Hemiptera in a black walnut (Juglans nigra L.) plantation near Asheville, North Carolina, and deals with the families Tingidae and Aradidae; earlier papers dealt with the Pentatomoidae (1980), Coreoidea (1981a), Reduvioidae (1981b), Cimicoidea (1981c) and Lygaeoidea (1981d). The study was conducted from 24 March to 14 October in 1977, and from 24 March to 13 October in 1978. Specimens were collected weekly by window trapping; traps were suspended at 1, 2, 3, 4, 5, 6 and 7 m. The study site and trap construction were discussed in detail by McPherson and Weber (1980). All hemipteran specimens collected during this study are deposited in the Entomology Collection, Zoology Research Museum, Southern Illinois University, Carbondale.

RESULTS AND DISCUSSION

Eleven tingid and six aradid species were collected during the two years of this study; numbers of specimens collected for all taxa ranged from one to 91 (Table 1).

Most of the species were collected in numbers too low to permit conclusions about seasonal flight patterns. However, Corythucha ciliata (Say) and Gargaphia solani Heidemann were collected in sufficient numbers (Table 1) to allow a more detailed discussion of flying height distributions and seasonal flight activities.

C. ciliata occurs primarily on sycamore (e.g., Bailey 1951, Barber and Weiss 1922, Blatchley 1926, Drake 1919, Froeschner 1944, Horn et al. 1979, Morrill 1903, Wade 1917) but has also been collected from cypress (Froeschner 1944), ash, hickory, mulberry (Blatchley 1926, Drake 1919) and leather-leaf (Bailey 1951). It overwinters as adults (e.g., Bailey 1951, Barber and Weiss 1922, Froeschner 1944, Wade 1917); in central New England, overwintering adults may be found in abundance under loose tree bark in October and may not emerge until early June (Bailey 1951). Barber and Weiss (1922) felt this species probably has "two broods" (is bivoltine?) in New Jersey.

In the present study, C. ciliata adults were found from early April to early September (Table 1). They were collected at all seven flying heights with over 55% captured at 3-5 m (Fig. 1).

¹Department of Zoology. Southern Illinois University, Carbondale, IL 62901.
²USDA Forest Service. North Central Forest Experiment Station, Forestry Sciences Laboratory, Carbondale, IL 62901.
Table 1. Seasonal flight activity of Tingidae and Aradidae during 1977–78 in a North Carolina black walnut plantation.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>No. Collected</th>
<th>Collection Height (m)</th>
<th>Range of Collection Dates</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>TINGIDAE</strong></td>
<td></td>
<td><strong>x±SE</strong></td>
<td></td>
</tr>
<tr>
<td>Corythucha ciliata (Say)</td>
<td>70</td>
<td>4.27±0.21</td>
<td>1–7</td>
</tr>
<tr>
<td>Corythucha cydoniae (Fitch)</td>
<td>1</td>
<td>3.00</td>
<td>—</td>
</tr>
<tr>
<td>Corythucha juglandis (Fitch)</td>
<td>26</td>
<td>4.62±0.35</td>
<td>1–7</td>
</tr>
<tr>
<td>Corythucha marmorata (Uhler)</td>
<td>3</td>
<td>3.67±1.45</td>
<td>1–6</td>
</tr>
<tr>
<td>Corythucha pallida Osborn &amp; Drake</td>
<td>2</td>
<td>6.50±0.50</td>
<td>6–7</td>
</tr>
<tr>
<td>Gargaphia solani Heidemann</td>
<td>91</td>
<td>1.85±0.16</td>
<td>1–7</td>
</tr>
<tr>
<td>Gargaphia tiliae (Walsh)</td>
<td>1</td>
<td>6.00</td>
<td>—</td>
</tr>
<tr>
<td>Leptopypha costata Parshley</td>
<td>8</td>
<td>4.75±0.25</td>
<td>4–6</td>
</tr>
<tr>
<td>Melanorhopala infuscata Parshley</td>
<td>1</td>
<td>4.00</td>
<td>—</td>
</tr>
<tr>
<td>Physatocheila brevirostris Osborn &amp; Drake</td>
<td>2</td>
<td>2.50±1.50</td>
<td>1–4</td>
</tr>
<tr>
<td><strong>ARADIDAE</strong></td>
<td></td>
<td><strong>x±SE</strong></td>
<td></td>
</tr>
<tr>
<td>Aradus cinnamomeus Parshley</td>
<td>3</td>
<td>3.67±0.67</td>
<td>3–5</td>
</tr>
<tr>
<td>Aradus crenatus Say</td>
<td>1</td>
<td>1.00</td>
<td>—</td>
</tr>
<tr>
<td>Aradus niger Stål</td>
<td>1</td>
<td>6.00</td>
<td>—</td>
</tr>
<tr>
<td>Mezira granulata (Say)</td>
<td>30</td>
<td>4.07±0.33</td>
<td>1–7</td>
</tr>
<tr>
<td>Mezira lobata (Say)</td>
<td>1</td>
<td>4.00</td>
<td>—</td>
</tr>
<tr>
<td>Neuroctenus sp. *a</td>
<td>2</td>
<td>3.50±1.50</td>
<td>2–5</td>
</tr>
</tbody>
</table>

*Genus is currently being revised (Froeschner, pers. comm.).

This species overwintered as adults and was apparently bivoltine (Fig. 3). Adults began to emerge from overwintering sites in early April and were present to mid-May. Their adult offspring (summer generation) occurred from late June to late July or early August. Adults of the second (overwintering) generation were present in September (and possibly in August).

*G. solani* occurs primarily on eggplant (e.g., Bailey 1951, Fink 1915, Froeschner 1944, Horn et al. 1979) but has also been collected from horse-nettle (Blatchley 1926, Fink 1915, Froeschner 1944, Somes 1916), white horse-nettle (Froeschner 1944) and sunflower (Horn et al. 1979). It overwinters as adults (Bailey 1951, Fink 1915, Froeschner 1944). Fink (1915) stated that *G. solani* may have 7–8 generations per season in the vicinity of Norfolk, Virginia, with apparently six generations on eggplant and the remainder on horse-nettle.

In the present study, *G. solani* adults were found from early June to mid-October (Table 1). They were collected at all seven flying heights with almost 70% collected at 1 m (Fig. 2).

This species apparently overwintered as adults but the number of generations per year is unclear from the available data (Fig. 4). It appears that during spring (i.e., April and May), adults were either not flying or were not in the plantation. However, adults were quite active from early July to the end of the season.


ACKNOWLEDGMENTS

We wish to thank Dr. R. C. Froeschner, National Museum of Natural History, Washington, D.C., for confirming our identifications of these tingids and aradids. We also wish to acknowledge Mr. D. Brenneman and the staff of the North Carolina Division of Forestry, Morganton, for their help in collecting data and maintaining the window traps. This research was partially supported by the USDA Forest Service, North Central Forest Experiment Station.

LITERATURE CITED


DEVELOPMENT OF ORIUS INSIDIOSUS (HEMIPTERA: ANTHOCORIDAE) IN RELATION TO TEMPERATURE

P. C. Kingsley and B. J. Harrington

ABSTRACT

A developmental threshold of 10.3°C and a thermal constant of 307 day-degrees C were estimated for a Wisconsin population of Orius insidiosus (Say) (Hemiptera: Anthocoridae) by rearing eggs and nymphs at various constant temperatures.

Orius insidiosus (Say) is a small (~3 mm) widely distributed predaceous bug, commonly associated with flowers. It is generally considered a polyphagous predator feeding on a wide variety of economically important arthropods including thrips, aphids, mites and eggs of various Lepidoptera.

This study estimates the two developmental parameters, thermal constant (K) and developmental threshold (t), or base temperature, for a population of insidiosus in Wisconsin. To date, estimations of t and K for insidiosus have not been reported although some studies have dealt with developmental times for this bug or related species (Askari and Stern 1972 a, b; Barber 1936; Marshall 1930; Rajasekhar and Chatterji 1970; Salas-Aguilar and Ehler 1977). Cambell et al. (1974) stated that the developmental threshold is "the temperature below which no measurable development occurs" and Pearis (1927) defined the thermal constant as "the total of effective temperatures expressed in day-degrees to which the organism is subjected during the developmental period under consideration." These parameters, estimated from laboratory rearing experiments, are necessary to predict the number of day-degrees required by insidiosus to complete a generation in the field and thereby better understand the phenology of this important predator.

MATERIALS AND METHODS

A total of 316 eggs were collected from several females reared at 28°C and under a long-day photoperiodic regime of 8 hours dark and 16 hours light (8D:16L). These females, after being denied ovipositional material for one day, were introduced to alfalfa sprouts (four to five days old) and allowed to oviposit for three hours. Sprouts with eggs were placed in 5-cm plastic petri dishes with two moist filter paper discs lining the bottom. These dishes, each with approximately 20 eggs, were distributed among four temperature treatments (15, 20, 28, 33°C) in Percival incubator cabinets. All treatments were maintained at 8D:16L photoperiod. Eggs were checked every 12 hours until the development of eyespots and thereafter at three hour intervals for eclosion.

In a separate experiment, to determine nymphal development time, first instar nymphs were collected at 12-hour intervals as they eclosed from eggs maintained at 28°C, 8D:16L. Two hundred and six nymphs were distributed among five temperature treatments (15, 20, 28, 30 and 33°C; all at 8D:16L). A large proportion of the nymphs were assigned to the 15°C treatment to compensate for a high mortality which was expected from the results of pre-
liminary rearing experiments. Rearing cages consisted of 9-cm by 5-cm Pyrex® crystallizing dishes with a filter paper disc lining the bottom and a Teflon® coating painted around the upper edge to prevent climbing and escape of the insects. Water was supplied from a 3-dram vial with a dental wick inserted into a hole in the cap. An average of five nymphs was placed in each cage and both checked for mortality and fed a more than adequate supply of eggs of *Trogoderma glabrum* (Herbst) (Coleoptera: Dermestidae), daily. These eggs had been killed by freezing and stored at -20°C for approximately one month. After *Orius* nymphs reached the fifth instar, cultures were checked every 12 hours for adult eclosion.

Thermal constant and developmental threshold parameters were estimated following the procedure used by Cambell et al. (1974), except that, from our experiments with *Orius*, values for t and K were determined for egg and nymphal stages separately.

To study the relationship between temperature and development of *insidious* eggs and nymphs, a linear regression, \( y = a + bx \), was calculated for each stage as follows. The developmental times for each egg and nymph were converted to a rate of development (1/days) \( y \), and plotted against the corresponding temperature treatment \( x \). For clarity, only mean rates for each temperature treatment are indicated in Figure 1. A developmental threshold for each stage was calculated as the x-intercept of the corresponding regression line. Thermal constants (expressed in day-degrees C) were calculated as the reciprocal of the slope \( b \) of each regression line (Cambell et al. 1974).

**RESULTS AND DISCUSSION**

The duration and mortality of *O. insidiosus* eggs maintained at four constant temperature treatments are given in Table 1 and the computed regression line is shown in Figure 1.

The developmental threshold, estimated by extrapolation, for the egg stage was 8.8°C. A thermal constant of 66.5 day-degrees was required to complete development from oviposition to egg hatch.

Eggs maintained at 15°C showed very slow development and after 23 days the experiment was terminated. The expected duration for eggs maintained at 15°C (estimated from the regression line computed from the three remaining temperature treatments) is approximately 11 days. Yet, after at least twice this long, the experimental eggs had still not completed development, suggesting that the actual egg developmental threshold may be higher than the estimated 8.8°C.

Nymphs reared at 15°C were also very slow to develop and showed a high degree of mortality. The experiment was terminated after 35 days, by which time 96% (109 of 114) of the nymphs had died. The five surviving nymphs were in the fifth stadium.

The estimated nymphal developmental threshold was 10.7°C and 240.4 day-degrees were required to complete the nymphal development (egg hatch to adult eclosion). Duration and mortality of nymphs reared at the various temperatures are given in Table 2 and the computed regression line for nymphal development is shown in Figure 1.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Initial No. eggs</th>
<th>Mortality (%)</th>
<th>Duration of egg stage (days)</th>
<th>Rate (1/days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>88</td>
<td>—</td>
<td>23a</td>
<td>—</td>
</tr>
<tr>
<td>20</td>
<td>36</td>
<td>17</td>
<td>6.69 0.082 30 6.0–7.3 0.149</td>
<td>—</td>
</tr>
<tr>
<td>28</td>
<td>73</td>
<td>25</td>
<td>3.22 0.023 55 3.0–3.3 0.311</td>
<td>—</td>
</tr>
<tr>
<td>33</td>
<td>119</td>
<td>10</td>
<td>2.84 0.015 107 2.5–3.3 0.352</td>
<td>—</td>
</tr>
</tbody>
</table>

*aExperiment terminated, see text for explanation.*
Fig. 1. Regression lines of developmental rate (y) on temperature (x) for Orius insidiosus (Say) eggs and nymphs maintained at constant temperatures. Points represent mean developmental rates with vertical bars indicating ranges.

Table 2. Mortality and total nymphal duration of Orius insidiosus (Say) reared at five constant temperatures and 8D:16L photoperiod.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>No. 1st Mortality</th>
<th>Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>instars</td>
<td>Mean</td>
</tr>
<tr>
<td>15</td>
<td>114</td>
<td>96</td>
</tr>
<tr>
<td>20</td>
<td>29</td>
<td>14</td>
</tr>
<tr>
<td>28</td>
<td>24</td>
<td>21</td>
</tr>
<tr>
<td>30</td>
<td>23</td>
<td>30</td>
</tr>
<tr>
<td>33</td>
<td>16</td>
<td>19</td>
</tr>
</tbody>
</table>

*aExperiment terminated. see text for explanation.

Under the conditions of these experiments an overall K of 307 day-degrees, for insidiosus, development from oviposition to adult eclosion, can be approximated by summing the values obtained for the egg and nymphal stages. From separate experiments on egg and nymphal development, different developmental threshold values were calculated for the egg (t = 8.8°C) and nymphal (t = 10.7°C) stages. However, a single intermediate developmental threshold value of 10.3°C was estimated by interpolation

\[
\frac{(\text{egg } t \times \text{ egg } K) + (\text{nymphal } t \times \text{nymphal } K)}{\text{overall } K} = \text{overall } t.
\]
This overall t, utilized with minimal and maximal daily temperature information, can be used to calculate accumulated day-degrees in the field for *insidiosus* populations.

Two important limits to interpretation of the results of such experiments must be considered, however, when laboratory estimated values for t and K are applied to the phenology of field populations. First, and most obviously, the inherent differences between laboratory and field conditions must be remembered. Second, even though *Orius* is considered a generalist as a predator, developmental times may vary with different prey species and/or stages. The degree of omnivory also may play an important role in a predator's development. Recently, Salas-Aguilar and Ehler (1977) have reported that *O. tristicolor* (White) developed significantly faster when a diet of thrips was supplemented with pollen.

With these possible limitations in mind, our laboratory obtained developmental parameters may be used, with the addition of a preovipositional interval, to predict the number of generations and approximate time of population peaks for *insidiosus* in the field in Wisconsin. Such predictions for the single growing season of 1979 coincided quite closely with the actual field phenology of *insidiosus* obtained by regular sampling of soybeans and alfalfa at Arlington Experimental Farms, Arlington, Wisconsin, where two generations reached adult population peaks on 6 August and 27 September (Kingsley 1980).

**ACKNOWLEDGMENTS**

We thank D. M. Benjamin for helpful comments regarding the manuscript. Research supported by the College of Agricultural and Life Sciences, University of Wisconsin-Madison and by Federal Hatch Support, Project No. 2391.

**LITERATURE CITED**


THE INFLUENCE OF REFLECTIVE MULCHES AND LETTUCE TYPES 
ON THE INCIDENCE OF ASTER YELLOWS AND ABUNDANCE OF ITS 
VECTOR, MACROSTELES FASCIFRONS (HOMOPTERA: 
CICADELLIDAE), IN MINNESOTA

Frank G. Zalom

ABSTRACT

Five commercial lettuce cultivars representing different genetic types were grown through 
aluminum-coated paper, through black polyethylene film, and on bare soil. For each variety, 
the aluminum mulch reduced the numbers of Macrosteles fascifrons (Stål), reduced the 
incidence of aster yellows, and increased yields when compared to uncovered controls. The 
head lettuce cultivar ‘Minetto’ was most susceptible on unmulched plots (74.3%) while the 
leaf cultivar ‘Grand Rapids’ was least susceptible (33.8%). The latter also had the greatest 
infestation of leafhoppers which may indicate either resistance to the aster yellows agent or 
shorter feeding times by the vector leafhopper. The abundance of aster leafhoppers on the 
romaine cultivar ‘Valmaine’, the butter head cultivar ‘Buttercrunch’, and the bibb cultivar 
‘Summer Bibb’ was much lower than that of the other two and might explain the lower 
percentage of aster yellows on these types as compared with ‘Minetto’.

Aster yellows is one of the most destructive plant diseases of the upper Midwest and the 
prairie provinces of Canada. It has become the limiting factor in the production of lettuce, 
carrots, and celery in Minnesota. Lettuce fields have been reported as suffering 100% loss in 
some years (Schultz 1973).

The principal vector of aster yellows is the aster leafhopper, Macrosteles fascifrons (Stål). The vector leafhoppers which migrate from southern breeding areas each spring are the 
principal source of primary inoculum. The number of migrants and the percentage infected 
with aster yellows has been used to predict early-season loss potential in Wisconsin, allowing 
growers to delay initiation of spray programs (Chiykowski and Chapman 1965). Both the 
vector and the disease have a wide host range. However, lettuce seems to be preferred 
vegetable host in the Midwest (Peterson and Saini 1964, Schultz 1973). No cultivars of 
commercial lettuce have been developed which are highly resistant to the leafhopper or the 
disease.

Frequent insecticidal applications are often required for commercial production of lettuce 
(Richardson and Westdal 1964, Thompson 1967). Though typically effective (Chapman 
1973), the failure of insecticides to adequately protect plants from insect transmission has 
been reported (e.g., Lee and Robinson 1958).

Reflective mulches can decrease the incidence of nonpersistent viruses on lettuce by 
reducing the number of alate aphids alighting upon plants (e.g., Nawrocka et al. 1975, 
Toscano et al. 1979). Aluminum foil has been most successfully utilized for this purpose; however, black polyethylene plastic was more effective than yellow or white plastic in field 
tests (Jones and Chapman 1968). Similarly, reflective mulches may lower the number of 
aster leafhoppers in lettuce and reduce infection by aster yellows (Chapman 1973).

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1This research was supported by the Minnesota Agricultural Experiment Station Project 17-48. Scientific Journal Series Paper No. 11491.
2Statewide IPM Project-Implementation Group, Department of Plant Pathology, University of California, Davis, CA 95616.
This study evaluated the effect of aluminum and black plastic mulches on the abundance of aster leafhoppers, the incidence of aster yellows, and yield for five commercial lettuce types in Minnesota during the 1980 season.

METHODS

Five cultivars of lettuce, representing five distinct genetic types were selected for study: 'Valmaine', a deep green romaine type; 'Buttercrunch', a larger growing butter head type making a dense cluster of leaves; 'Grand Rapids', a heavy leaf type with light green, well frilled leaves; 'Minetto', a small, firm head lettuce with short cores; and 'Summer Bibb', a longer standing bibb type with tight clusters of medium dark green leaves. The plants were seeded in wooden flats in a greenhouse, and transplanted to field plots on the St. Paul campus of the University of Minnesota four weeks after seeding (early June). The bed was disced and leveled prior to planting.

One third of the plots were covered with Reynolds® aluminum-coated construction paper, one third with black polyethylene plastic film, and one third remained uncovered. Each plot measured 5.4 m on a side, with 1 m between plots. There were four replications of each mulch type. The reflective mulches were held in place by 12-gauge galvanized steel wires 100 cm long, bent at the ends to pierce the mulch and continue into the soil. Circular holes, 15 cm diam, were cut out of the mulches through which the lettuce was transplanted. Plants within a row were spaced at 45 cm, with 10 plants in a row. Rows within plots were spaced at 75 cm. Each of the five rows within a plot was planted with a different cultivar selected at random. No insecticides, herbicides, or fertilizers were applied to the plots. Weeds were rogued from the plots when necessary.

One week after transplanting and twice weekly thereafter, the plots were sampled for aster leafhoppers and aster yellows. The relative abundance of aster leafhoppers was estimated by sweeping each lettuce plant in a row four times with a standard 40-cm insect net. Therefore, insect abundance was obtained on both a cultivar and plot basis. The abundance of aster leafhoppers among the five cultivars for each mulch treatment was compared by Friedman's analysis of variance by ranks. The cultivar most heavily infested with the insect on a given sampling date was assigned the rank of 1.

The lettuce was hand harvested by cultivar 5.5 weeks after transplanting (mid-July), weighed individually, and examined for symptoms of aster yellows. After determining the percentage of plants with aster yellows in each cultivar for the reflective mulch treatments and among all replications, the differences between the cultivars and between the reflective mulch treatments were analyzed by Duncan's multiple range test. The mean weight of lettuce from the reflective mulch plots and the uncovered controls was compared by one-way analysis of variance.

RESULTS

Leafhopper abundance. The mean number of aster leafhoppers per 40 sweeps from lettuce grown on bare soil exceeded that from lettuce grown through plastic and aluminum mulch on each sampling date (Fig. 1). Their abundance over plastic was greater than over aluminum mulch. The peak abundance of aster leafhoppers on the lettuce plants occurred in mid-July.

The difference in aster leafhopper abundance between the five lettuce cultivars grown on bare soil and through the plastic mulch was significant ($P < 0.05$). The leaf lettuce (Grand Rapids) and the head lettuce (Minetto) had the greatest infestations (Table 1). No significant difference ($P > 0.05$) was found among cultivars grown through the aluminum mulch.

Aster yellows. At harvest, the percentage of plants with aster yellows in each cultivar for the reflective mulch treatments among all replications was determined. A significant difference ($P < 0.05$, $F = 21.0626$) was found by mulch treatment but no significant difference ($P > 0.05$, $F = 2.2345$) was found by cultivar. Aphid-borne lettuce viruses were not present in the study area.
Fig. 1. Mean (n = 4) number of aster leafhoppers per 40 sweeps on lettuce grown through aluminum mulch, plastic mulch, or no mulch.

Table 1. Abundance of aster leafhoppers on five lettuce cultivars grown on bare soil and through reflective mulches.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Treatment</th>
<th>Bare soil</th>
<th>Plastic mulch</th>
<th>Aluminum mulch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buttercrunch</td>
<td></td>
<td>3.40</td>
<td>3.65</td>
<td>3.19</td>
</tr>
<tr>
<td>Grand Rapids</td>
<td></td>
<td>1.65</td>
<td>1.05</td>
<td>1.44</td>
</tr>
<tr>
<td>Minetto</td>
<td></td>
<td>1.85</td>
<td>2.25</td>
<td>2.69</td>
</tr>
<tr>
<td>Summer Bibb</td>
<td></td>
<td>4.20</td>
<td>4.70</td>
<td>3.75</td>
</tr>
<tr>
<td>Valmaine</td>
<td></td>
<td>3.90</td>
<td>3.35</td>
<td>3.44</td>
</tr>
<tr>
<td></td>
<td>( x^2 )</td>
<td>22.22(^a)</td>
<td>31.20(^a)</td>
<td>1.05</td>
</tr>
</tbody>
</table>

\(^a\)\( p < 0.05 \).

The head lettuce (Minetto) exhibited significantly higher incidence of aster yellows than did the other cultivars when grown on bare soil (Table 2). The leaf lettuce (Grand Rapids) had the lowest incidence. For each cultivar, the percentage of plants with aster yellows was significantly reduced when grown through aluminum mulch instead of bare soil. Aster yellows did not occur on 'Valmaine', 'Buttercrunch', and 'Summer Bibb' when grown through aluminum mulch and was greatly reduced on 'Grand Rapids' and 'Minetto'. The effect of the plastic mulch was variable with respect to cultivar and the other mulch treatments.
Lettuce yields. Lettuce plants of each cultivar were significantly larger (P < 0.01) from reflective mulch plots than from uncovered control plots. In every instance, the weight of a plant grown through aluminum mulch was greater than a plant of the same cultivar grown through plastic mulch or on bare soil. When plants infected with aster yellows were eliminated from the calculation of yield per plant, the differences were still significant (Table 3).

Table 2. Mean (± SD; n = 4) percentage of aster yellows infected plants among five lettuce cultivars grown on bare soil and through reflective mulches.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Cultivar</th>
<th>Bare soil</th>
<th>Plastic mulch</th>
<th>Aluminum mulch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Buttercrunch</td>
<td>41.0±17.2a</td>
<td>30.0±16.9a</td>
<td>0.0±0.0b</td>
</tr>
<tr>
<td></td>
<td>Grand Rapids</td>
<td>33.8±11.1a</td>
<td>8.3±9.1b</td>
<td>8.3±9.1b</td>
</tr>
<tr>
<td></td>
<td>Minetto</td>
<td>74.3±16.9c</td>
<td>38.5±16.5a</td>
<td>2.8±4.8b</td>
</tr>
<tr>
<td></td>
<td>Summer Bibb</td>
<td>42.3±11.0a</td>
<td>5.5±9.5b</td>
<td>0.0±0.0b</td>
</tr>
<tr>
<td></td>
<td>Valmaine</td>
<td>41.8±14.2a</td>
<td>19.5±15.7d</td>
<td>0.0±0.0b</td>
</tr>
</tbody>
</table>

a, b, c, d No significant difference between values with same superscript. Values with different superscripts significantly different (P < 0.05).

Table 3. Mean (± SD, n = 4) weight (g per plant) of (1) all plants and (2) all plants excluding those infected with aster yellows.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Cultivar</th>
<th>Bare soil</th>
<th>Plastic mulch</th>
<th>Aluminum mulch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Buttercrunch</td>
<td>249.4±84.9</td>
<td>458.1±50.5</td>
<td>733.9±165.2</td>
</tr>
<tr>
<td></td>
<td>Grand Rapids</td>
<td>368.5±24.2</td>
<td>675.2±60.1</td>
<td>868.2±165.2</td>
</tr>
<tr>
<td></td>
<td>Minetto</td>
<td>255.2±68.3</td>
<td>526.1±109.5</td>
<td>775.9±145.4</td>
</tr>
<tr>
<td></td>
<td>Summer Bibb</td>
<td>142.3±19.4</td>
<td>357.0±61.0</td>
<td>488.7±64.7</td>
</tr>
<tr>
<td></td>
<td>Valmaine</td>
<td>440.8±78.8</td>
<td>849.3±110.5</td>
<td>1258.8±152.5</td>
</tr>
</tbody>
</table>

(2) PLANTS NOT INFECTED WITH ASTER YELLOWS

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Cultivar</th>
<th>Bare soil</th>
<th>Plastic mulch</th>
<th>Aluminum mulch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Buttercrunch</td>
<td>296.0±95.1</td>
<td>544.0±46.7</td>
<td>783.0±72.2</td>
</tr>
<tr>
<td></td>
<td>Grand Rapids</td>
<td>411.7±32.0</td>
<td>702.9±41.3</td>
<td>932.6±133.6</td>
</tr>
<tr>
<td></td>
<td>Minetto</td>
<td>381.4±37.9</td>
<td>654.0±85.8</td>
<td>806.0±147.1</td>
</tr>
<tr>
<td></td>
<td>Summer Bibb</td>
<td>182.3±22.6</td>
<td>372.4±69.2</td>
<td>488.7±64.7</td>
</tr>
<tr>
<td></td>
<td>Valmaine</td>
<td>569.8±151.4</td>
<td>894.5±116.8</td>
<td>1258.8±152.5</td>
</tr>
</tbody>
</table>

DISCUSSION

The results indicated that reflective mulches would lower the abundance of aster leafhoppers, lower the incidence of aster yellows, and increase yields with respect to uncovered controls. In most cases, the aluminum-coated construction paper was superior to black plastic.

The greatest abundance of the aster leafhopper in this study occurred in early July. This might have been the result of planting date and hostplant attractiveness. As the plants increased in size more aster leafhoppers would be drawn to them. The numbers would fall as
the plants reached maturity. No nymphs were found on the lettuce plots until adults were present for 3.5 weeks.

Although both reflective mulch treatments significantly lowered the incidence of aster yellows on the lettuce plantings, no significant difference was found in cultivar susceptibility to the disease. In New York, Linn (1940) determined that romaine and head lettuce were similarly susceptible to aster yellows. The data obtained in Minnesota indicated that the head lettuce cultivar ‘Minetto’ was more attractive to leafhoppers, which might explain the higher incidence of aster yellows on the cultivar. Interestingly, the leaf lettuce variety ‘Grand Rapids’ had the greatest infestation of leafhoppers, yet the lowest incidence of aster yellows on the uncovered plots. Perhaps ‘Grand Rapids’ was resistant to the aster yellows agent, or the leafhoppers had a shorter feeding time, preventing a high level of transmission of the disease agent. The relative abundance of aster leafhoppers on the cultivars ‘Valmaine’, ‘Buttercrunch’, and ‘Summer Bibb’ was much lower than that of ‘Minetto’ and ‘Grand Rapids’, and might explain the lower percentage of aster yellows on these cultivars as compared with ‘Minetto’.

Yield for each cultivar was greatest on the aluminum mulched plots even when the plants infected with aster yellows were eliminated, indicating additional benefits to the plant from the treatment. In Maine, Hilborn et al. (1957) found that head weight of lettuce grown through black plastic was ca. 33% greater than head weight from nonmulched plots owing to higher soil temperature, weed suppression, moisture conservation, and lack of plant contact with the soil which reduced plant diseases such as bottom rot and bacterial soft rot. Additional advantages to the plant from an aluminum soil covering might include increased light reflection to leaf surfaces, and higher air temperatures immediately over the mulch.

Aluminum mulching is routinely used on a commercial scale for aphid management on tomatoes and peppers in Florida. The benefits derived from the technique including reduced disease incidence, increased yield, and weed suppression lend promise to the technology for production of high value crops and home gardens elsewhere.

ACKNOWLEDGMENT

The contribution of D. W. Davis, Professor of Horticulture and Landscape Architecture, University of Minnesota, to this study is gratefully acknowledged. M. A. Ascerno critically reviewed the manuscript.

LITERATURE CITED


Richardson, H. P. and P. H. Westdal. 1964. Experiments on control of the six-spotted
RESOURCE PARTITIONING BY TWO SPECIES OF STREAM MAYFLIES (EPHEMEROPTERA: HEPTAGENIIDAE)

William O. Lamp and N. Wilson Britt

ABSTRACT

We compared the phenology of nymph development, food type, and habitat selection of two stream mayflies, Stenacron interpunctatum (Say) and Stenonema pulchellum (Walsh) in Big Darby Creek, Ohio. Both species, which grow principally from autumn through early spring, emerged from the stream throughout the summer. The nymphs consumed the same sizes and types of food particles from deposits on stones, mostly in the form of detritus. As a result of morphological and behavioral adaptations, S. pulchellum lived on stones in swift water whereas S. interpunctatum lived on stones in a slower current.

Closely-related coexisting species often have similar resource needs, but because of divergent evolution they may differ in their use of resources. Such resource partitioning is common in ecological communities (Schoener 1974). In streams, for example, similar insect species partition the resources of time (Illies 1952, Hynes 1961, Grant and Mackay 1969), food (Sheldon 1971, Mackay 1972, Wallace 1975, Resh 1976), and space (Cummins 1964, Ulfstrand 1967, Madsen 1968, Mackay and Kalff 1973, Allan 1975).

Heptageniid mayflies are important components of the benthic invertebrate community of streams. They feed on algal and detrital particles deposited on stones and vegetation. Extensive systematic and biological studies of the Stenonema and Stenacron species, common in the eastern United States, have been made (Needham et al. 1935, Spieth 1947, Jensen 1974, McCafferty and Huff 1978); however ecological studies have been limited. Although the nymphs of these species have been used as indicators of water quality and pollution levels (Lewis 1974), comparative ecological studies of coexisting species have not been reported.

The purpose of this study was to compare two coexisting mayfly species, Stenacron interpunctatum (Say) and Stenonema pulchellum (Walsh), which inhabit central Ohio streams. We will discuss whether the species partition the resources of time, food, and space, and the morphological and behavioral differences that cause this partitioning.

METHODS

Field studies were conducted on Big Darby Creek (2 km south of Amity, Madison Co.) in central Ohio from May 1975 to September 1976. The stream is third order and flows through a 1437 km² watershed of the high-lime Wisconsin till region. Although organic wastes and soil sediments are present, the macroinvertebrates indicate that the stream is relatively pollution-free (Olive and Smith 1975).

Phenology of nymph development. From July 1975 to June 1976 nymph development was followed by obtaining samples from stones dipped in a white pan containing a weak acid-alcohol mixture (Britt 1955). Samples were obtained from 10 stones in each of four habitats (defined in Results section). Any nymphs that were dislodged by the removal of the stone
from the stream bed were caught with an aquatic insect net. The specimens were killed in KAAD, and taken to the laboratory. At a later date, they were identified to species and the head capsule width was measured with an ocular micrometer mounted in a dissecting microscope.

**Food type.** On 28 April, large nymphs were killed in 80% ethanol. Analyses of the gut contents were made according to the method of Cummins (1973) within two days of collection. Briefly, this involved dispersing the contents of the gut in water, filtering the mixture through a millipore funnel fitted with a 0.45μ filter, and mounting the cleared filter on a permanent slide. Counts of the particles on the filter were made for five arbitrary categories which included algal cells and four size classes of detritus particles. The particle counts from six nymphs of each species were statistically compared using a multinomial chi-square test.

**Habitat selection.** A colonization experiment at the study site was used to compare habitat selection by the two mayflies. Common red brick (6 x 9 x 20 cm), which was found to be readily colonized by the nymphs, was used as an artificial substrate. Nine bricks were placed in a 3 x 3 grid pattern over 4 m² of stream bed in each of four habitats (defined in Results section). Current speeds were measured weekly by timing a float over a known distance (Welch 1948) and depths were also recorded. The bricks were placed on the stream bed on 19 April and were colonized for three months before their removal. During sampling the bricks were individually lifted from the stream and any loosened organisms were caught with an aquatic insect net. All organisms remaining on the brick and in the net were removed and transferred to 70% ethanol. In the laboratory all macroinvertebrates were identified and counted.

**Morphological comparison.** Twenty-five nymphs of various sizes of each species were fixed in KAAD to maintain proper measurements (Britt 1953). Measurements of head width, body length, profemur length, protibia length, and protarsus length were made using an ocular micrometer mounted in a dissecting microscope. Other structural differences were also noted.

**Behavioral comparison.** An aquarium simulating running water was used to explore behavioral differences. The aquarium contained a divider in the center and 19-litre/min pump to generate a current around the perimeter. To compare the ability of nymphs to land on substrate while drifting, two nymphs, one of each species, were released from a 2-dram vial just above and up-current of the brick substrate. Repeated with 25 different pairs of nymphs, the number of successful landings by each species was recorded.

**RESULTS AND DISCUSSION**

**Phenology of nymph development.** The youngest instars of both species were abundant in the autumn and most nymphs developed from autumn through early spring (Fig. 1). *S. pulchellum* nymphs were larger than *S. interpunctatum* nymphs on each of the sample dates except midsummer, which indicates some difference in their period of recruitment or time of maximum growth. Nonetheless, nymphs of all sizes of both species were found all year except during midsummer. Thus, the two species were not segregated by time of growth.

Adult emergence of both species began in late April and peaked in late May and early June. No *S. pulchellum* adults were collected after mid-August, although *S. interpunctatum* adults were collected through September. Both species appeared to be univoltine with recruitment and maturation spread over a long period of time.

**Food type.** The mouthparts of feeding heptageniid nymphs, armed with numerous spines and hairs, scrape and collect detrital and algal particles into the gut. Gut analyses indicated the size and type of food particles ingested by the nymphs. The counts of particles, classified by size and type, were totaled for each species (Table 1). Detritus particles accounted for 97% of the particles ingested. Using conversions for caloric content (Cummins 1973), the detritus composed 90.4% and 91.6% of the energy intake for *S. interpunctatum* and *S. pulchellum* respectively.

A significant difference in these enumeration data would be expected if the nymphs of each species preferentially fed in different microhabitats on the stone surface or if the
mouthparts were sufficiently different to scrape different sizes of particles into the mouth. However, a multinomial chi-square test indicated no significant difference between species in the size and type of food particles (P > 0.20), thus the species did not partition the available food.

![Graph showing head width frequency distribution for nymphs at each sample date.](image)

**Fig. 1.** Nymph development of the two mayflies illustrated by the head width frequency distribution for nymphs at each sample date. Very small nymphs could not be identified. Head width unit 1 is less than or equal to 0.50 mm, and each unit larger increases by 0.18 mm.

### Table 1. Comparison of gut contents by particle counts.

<table>
<thead>
<tr>
<th>Type</th>
<th>Size (μ)</th>
<th>Number of particles (%)</th>
<th>S. interpunctatum</th>
<th>S. pulchellum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Algae</td>
<td>&gt; 2</td>
<td></td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Detritus</td>
<td>1.4–2.8</td>
<td></td>
<td>58</td>
<td>56</td>
</tr>
<tr>
<td>Detritus</td>
<td>2.8–5.6</td>
<td></td>
<td>27</td>
<td>26</td>
</tr>
<tr>
<td>Detritus</td>
<td>5.6–11.2</td>
<td></td>
<td>10</td>
<td>12</td>
</tr>
<tr>
<td>Detritus</td>
<td>11.2–22.4</td>
<td></td>
<td>2</td>
<td>3</td>
</tr>
</tbody>
</table>

Note: Based on total counts of 1710 particles for *S. interpunctatum* and 1427 for *S. pulchellum*.

**Habitat selection.** Four habitats were subjectively defined by relative current speed. Habitat A was in the slowest section of the stream in a shallow pool area along one edge. Habitats B and C were intermediate in current speed, with C having the faster current of the two. Habitat D was in the swiftest section of the stream. Measured water depths and current
speeds illustrated that these habitats were not distinct (Table 2), but rather that they existed on a continuum from slow to fast current. Since the habitats were in close proximity most chemical characteristics would have remained approximately constant, however some chemical and physical characteristics correlated with current rate would have varied (Hynes 1970). Biological data from the colonization experiment reflected the difference between the habitats. Each invertebrate species maximally colonized a particular habitat while their numbers diminished in the faster or slower habitats (Table 3). Of the 14 species collected, one was collected most in habitat A, two in habitat B, four in habitat C, and seven in habitat D.

Table 2. Characteristics of the four habitats during the colonization experiment.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Current Speed (cm/s)</th>
<th>Water Depth (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range</td>
<td>Mean</td>
</tr>
<tr>
<td>A, shallow pool</td>
<td>3–29</td>
<td>8</td>
</tr>
<tr>
<td>B, run</td>
<td>8–55</td>
<td>18</td>
</tr>
<tr>
<td>C, run</td>
<td>25–72</td>
<td>33</td>
</tr>
<tr>
<td>D, riffle</td>
<td>80–150</td>
<td>94</td>
</tr>
</tbody>
</table>

Table 3. Number of each species collected in the four habitats during the colonization experiment.\(^a\).

<table>
<thead>
<tr>
<th>Order</th>
<th>Species</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ephemeroptera</td>
<td>Stenacron interpunctatum</td>
<td>54</td>
<td>200</td>
<td>115</td>
<td>66</td>
<td>435</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td>Stenonema pulchellum</td>
<td>0</td>
<td>1</td>
<td>14</td>
<td>44</td>
<td>59</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td>Caenis sp.</td>
<td>1</td>
<td>16</td>
<td>5</td>
<td>3</td>
<td>25</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td>Isonychia sp.</td>
<td>2</td>
<td>0</td>
<td>8</td>
<td>11</td>
<td>21</td>
</tr>
<tr>
<td>Odonata</td>
<td>Argia sp.</td>
<td>4</td>
<td>6</td>
<td>16</td>
<td>3</td>
<td>29</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>Psephenus herricki</td>
<td>1</td>
<td>6</td>
<td>8</td>
<td>6</td>
<td>21</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>Stenelmis sp.</td>
<td>49</td>
<td>56</td>
<td>95</td>
<td>136</td>
<td>336</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>Protoptila sp.</td>
<td>0</td>
<td>1</td>
<td>27</td>
<td>0</td>
<td>28</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>Hydropsyche sp.</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>13</td>
<td>15</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>Cheumatopsyche sp.</td>
<td>0</td>
<td>1</td>
<td>58</td>
<td>315</td>
<td>374</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>Chimarra sp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>Diptera</td>
<td>Chironomidae</td>
<td>0</td>
<td>7</td>
<td>37</td>
<td>1</td>
<td>45</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>Goniobasis sp.</td>
<td>8</td>
<td>17</td>
<td>18</td>
<td>21</td>
<td>64</td>
</tr>
<tr>
<td>Amphipoda</td>
<td>Hyalella azteca</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>8</td>
</tr>
</tbody>
</table>

\(^a\)Species of which less than five individuals were collected are not shown.

The colonization experiment showed a highly significant difference in the selection of habitats by the two heptageniid species (Table 3, multinomial chi-square test, \( P < 0.001 \)). \textit{S. interpunctatum} was collected in all habitats, but was most numerous in habitat B where current speed was relatively low. \textit{S. pulchellum} was almost completely absent from habitats A and B, but was most numerous in habitat D with a high current speed. Although the colonization experiment only sampled the summer distribution, the nymph development samples during the other seasons produced similar results. With one exception, \textit{S. pul-
chellum was mostly confined to areas of fast current, while *S. interpunctatum* was usually distributed throughout the stream. During the winter and early spring the current speed and volume increased greatly in Big Darby Creek. Samples taken at that time showed *S. pulchellum* distributed more generally across the stream bed, while *S. interpunctatum* was largely found in areas of slower current near the stream edge.

In habitat D, 89% of the nymphs were collected from bricks with both species. Moreover, the distribution of nymphs on the nine bricks showed an insignificant correlation (Spearman's test, \( P > 0.20 \)) between the number of each species on each brick. Thus, the distribution of one species was independent of the other.

**Morphological comparisons.** *S. pulchellum* nymphs were significantly wider than *S. interpunctatum* nymphs of the same body length (ratio of head width to body length for *S. pulchellum*, 0.315; for *S. interpunctatum*, 0.289; Rank Sum Test, \( P < 0.01 \)). Thus, for *S. pulchellum* the ventral surface area in contact with the substrate and thus frictional resistance to the current was greater. Also, *S. pulchellum* measurement of the profemora, protibiae, and protarsi in comparison to body length were significantly shorter than *S. interpunctatum* measurements (\( P < 0.05 \)), which also increased frictional resistance.

*S. pulchellum* nymphs had a ring of hairs around the anterior margin of the head. This ring was absent in *S. interpunctatum* nymphs (Fig. 2). Normally, the nymphs faced the current and these hairs helped seal off the ventral side of the head from the current. Thus, *S. pulchellum* was able to withstand a greater current speed than *S. interpunctatum*.

**Behavioral comparisons.** When nymphs of both species were placed in an aquarium with moving water, *S. pulchellum* landed on the substrate sooner than *S. interpunctatum*. A controlled experiment (see Methods section) tested this response. Out of 25 paired trials in a 35 cm/sec current, seven *S. pulchellum* successfully landed on the substrate while only one of the *S. interpunctatum* nymphs was successful. A Fisher Sign Test for paired replicate
data showed a significant difference between the species responses (P = 0.035, one-tailed test). Characteristics on the nymphs' legs explained the difference. *S. pulchellum* legs were hairy and in particular had several stiff spines laterally on the tibia, whereas *S. interpunctatum* legs lacked spines (Fig. 3). When the *S. pulchellum* nymphs drifted, they kept their legs against their body and the tibiae parallel to the substrate. Thus, when contact with the substrate was made, the nymphs could use the tibial spines to land on the substrate.

Fig. 3. Dorso-lateral view of the right hind legs of nymphs, illustrating the presence of spines on the tibia of *S. pulchellum*: (A) *S. pulchellum*, (B) *S. interpunctatum*.

CONCLUSIONS

These two mayfly species in Big Darby Creek significantly differed in their use of the space resource. *S. pulchellum* inhabited stones in swift water whereas *S. interpunctatum*, because of behavioral and morphological differences, primarily inhabited stones in calm water. Thus, the partitioning of the resource dimension of space by the two species resulted in fewer interactions between *S. interpunctatum* and *S. pulchellum*.

ACKNOWLEDGMENTS

This research was conducted by the senior author in partial fulfillment of the requirements for the degree, Master of Science, Department of Entomology, Ohio State University. The authors gratefully acknowledge the assistance of Philip A. Lewis, US-EPA, Cincinnati, for verifications of mayfly identifications.
LITERATURE CITED


TRUE AND FALSE FOODPLANTS OF CALLOSAMIA PROMETHEA
(LEPIDOPTERA: SATURNIIDAE) IN SOUTHERN MICHIGAN

W. H. Wagner, Jr., Michael K. Hansen, and Michael R. Mayfield

ABSTRACT

A survey in 1980 of the associations of over 400 cocoons of Callosamia promethea Drury in vegetation along and adjacent to southern Michigan roadides gave evidence for seven species of true larval foodplants (not including two others known in the area from other studies) and 17 species of false foodplants, the latter determined by the (1) rarity of their association with cocoons, (2) only one or two cocoons per plant, and (3) their proximity to a well known true foodplant. Three species, sassafras, black cherry, and buttonbush, are evidently the most important true foodplants in this area. Comparisons are made of the foodplants in terms of past literature, geography, and taxonomic relationships.

Reports of false larval foodplants cause a number of difficulties. By creating misleading impressions about the biology of both the plant hosts and their herbivores, which are persistent once they get into the literature, they interfere with the steady progress of basic research. For example, biologists today are much interested in the nature of those chemical substances in plants which may serve as a means of herbivore defense and are seeking general principles underlying this type of adaptation (Feeny 1976, Janzen 1973, Rhoades and Cates 1976). Also, by correlating the phylogenetic relationships of herbivores and their hostplants, it is possible to gain insights into their co-evolutionary patterns (cf. Ehrlich and Raven 1964). The "parasitological method" in phylogenetic systematics, which may aid in the working out of cladistic patterns (cf. Hennig 1966), is critically reliant on accurate herbivore-hostplant information. In each of these cases, use of false foodplant information can potentially lead to great error. For these reasons it is most desirable that extreme caution be exercised in reporting larval foodplants.

For our purposes, we define "true foodplants" as those plant species upon which larval development occurs in nature, and usually upon or near which the eggs are actually laid. As eggs and larvae are often difficult to find, we adopted the standard convention of using site of pupation as an indicator of the true foodplant. We realize, however, that though highly reliable, site of pupation is not an infallible indicator. Just prior to pupation, a larva may fall from, be knocked off, or leave a true foodplant, crawl to another plant and pupate there. A field worker encounters such a "wanderer" or pupa, jumps to the conclusion that an unrecorded foodplant has been found, and so reports it. In Antheraea polyphemus (Cramer), for example, 25% of the cocoons we found were spun entirely in grass, which is definitely not a true foodplant (Wagner and Mayfield 1980).

In connection with the study of cocoons of the endemic North American genus of giant silkworms, Callosamia (Lepidoptera: Saturniidae), we have become interested in their variation in relation to species-taxonomy, geography, and foodplants. The work reported here is part of that study. Nearly 30 genera of plants have been reported to be hosts of C. promethea Drury (see Table 3), most of which occur in Michigan, but a number of which we suspected were not true foodplants for this species. We therefore made a field survey during the period January to May 1980 in an effort to establish what species C. promethea actually utilizes in

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southern Michigan and, if possible, whether there are any clear-cut false foodplants, i.e. plants erroneously thought to be true foodplants.

The survey was conducted along roadsides, adjacent fields, and hedgerows as the majority of alleged foodplant species occur there. The cocoons themselves are readily visible, their pendent outlines conspicuous on the branchlets and twigs of their leafless hosts. The foodplant results obtained are representative of the occurrence of cocoons in relation to the respective foodplant species, with one notable exception. The spicebush (Lindera benzoin [L.] Blume), a well known true foodplant, tends to grow in rich, shaded swamps and is therefore underrepresented. We have, however, frequently encountered *C. promethea* cocoons on spicebush during field studies of swamp plants, and do not question that it is an important host in southern Michigan. At all sites we collected complete samples of the cocoons, as well as recording host plant species. This totalled 487 cocoons from an estimated 130 plants, including both true and false foodplants.

**RESULTS**

The results of our field studies are outlined in Tables 1 and 2. As can be seen from Table 1, the distribution of cocoons was highly clumped. Of the 487 collected, approximately 55% (26) of them occurred on the 16 species of false foodplants, while three of the eight species of true foodplants, sassafras (*Sassafras albidum* [Nutt.] Nees), black cherry (*Prunus serotina* Ehrh.), and buttonbush (*Cephalanthus occidentalis* L.), together accounted for 80% of the total cocoons collected. In fact, sassafras alone accounted for 38.6% of the total cocoons.

The taxonomic unrelatedness of these foodplants will be discussed below. In terms of plant habit, however, we are dealing with a group of plants that have in common a shrubby life form, as can be seen from Table 1. Even those which are trees, black cherry, white ash, (*Fraxinus americana* L.), tulip tree (*Liriodendron tulipifera* L.), and sassafras are utilized as young saplings or stump sprouts, or small shrubs in the case of sassafras. This commonality in growth form suggests that it may be an important factor used in hostplant selection by the promethea moth. Within this growth form the cocoons tended to be located centrally; the vast majority of them occurred between 1-2 m above the ground. A few high cocoons occurred at 5 m up in the branches of white ash and tulip tree. On buttonbush and the introduced lilac (*Syringa vulgaris* L.) cocoons, sometimes numerous, often were hung on branches close to the ground. We sometimes found the same conditions in black cherry where bushy stump sprouts occurred.

The habitats of these foodplants may appear to be strongly different *inter se*, as can be seen in Table 1, although there are some ecological commonalities. Tulip tree tends to be found at the edge of low, rich, hardwood forests. Sassafras occurs most commonly on sterile, upland soils. Lilac does not reproduce in southern Michigan, but is remarkably persistent, remaining for many years after a homestead where it has been cultivated has crumbled away. Large clones are common along roadsides in second-growth places in southern Michigan, but the best cocoon populations are usually in yards and gardens, associated with well-kept landscapes around houses still occupied. The most distinctive habitat for a true foodplant is that of the buttonbush, which is the only aquatic foodplant for *C. promethea*, with edges of marshes, openings in large hardwood swamps, and roadside ditches providing typical sites. All the other foodplants occur along roadsides, hedgerows, and in old fields. Ecologically speaking, these habitats are all early successional ones characterized by a high degree of disturbance. Thus, *C. promethea* appears to be an early successional species.

We looked at the leaf morphology in the different true foodplants to see whether there was a common denominator as this has been shown to be an important component of host plant selection for some Lepidoptera (Rausher 1978). As shown in Table 1, the leaf morphology is strikingly different. The size of the blade varies from large in tulip tree and white ash to small in choke cherry (*Prunus virginia* L.) and spicebush. The case of white ash, however, is unusual in that the large blade is actually compound. Botanically speaking the whole unit is a morphological blade, but both tulip tree and sassafras have a strong tendency toward more
Table 1. True foodplants of *Callosamia promethea*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Description</th>
<th>Habitat</th>
<th>Cocoons (Approx. No. of plants)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cephalanthus occidentalis</em></td>
<td>Clonal shrub, lvs., small, unlobed, simple, opp., entire</td>
<td>Open ditches, marshes, and swamp edges</td>
<td>99 (20)</td>
</tr>
<tr>
<td><em>Fraxinus americana</em></td>
<td>Small tree, lvs. large, comp’d, opp., nearly entire</td>
<td>Roadbanks, hedgerows</td>
<td>22 (6)</td>
</tr>
<tr>
<td><em>Liriodendron tulipifera</em></td>
<td>Small tree, lvs. large, simple, 4-lobed, alt., entire</td>
<td>Forest edges, plantings</td>
<td>25 (10)</td>
</tr>
<tr>
<td><em>Prunus serotina</em></td>
<td>Stump sprouts, saplings, small trees, lvs. small, simple, unlobed, alt., toothed</td>
<td>Roadsides old fields</td>
<td>101 (30)</td>
</tr>
<tr>
<td><em>P. virginiana</em></td>
<td>Clonal shrub, lvs. large, simple, unlobed, alt., toothed</td>
<td>Roadsides old fields</td>
<td>8 (2)</td>
</tr>
<tr>
<td><em>Sassafras albidum</em></td>
<td>Clonal shrub or tree, lvs. large, simple, unlobed to 3-lobed, alt. entire</td>
<td>Roadsides, hedgerows, forest edges</td>
<td>188 (40)</td>
</tr>
<tr>
<td><em>Syringa vulgaris</em></td>
<td>Clonal shrub, lvs. medium, simple, unlobed, opp., entire</td>
<td>Gardens, old homesteads</td>
<td>18 (4)</td>
</tr>
<tr>
<td><em>Lindera benzoin</em></td>
<td>Shrub, lvs. small simple, unlobed alt., entire</td>
<td>Shaded, mainly hardwood swamps</td>
<td>— (—)</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td></td>
<td></td>
<td>461 (112)</td>
</tr>
</tbody>
</table>

or less deeply lobed leaves. The others are unlobed. Three of the eight species have opposite leaves, the remainder alternate. Only two of the species, black cherry and choke cherry, have toothed leaf margins, but the margins of the leaflets in white ash may show shallow teeth. The remainder of the species have perfectly entire blade margins. Thus, there is little similarity in the foliar morphology of the true foodplants suggesting it is an unimportant factor in hostplant selection.

We based our conclusion that the plants listed in Table 2 are false foodplants on circumstantial evidence. Whether or not the larvae of *C. promethea* can be induced to feed upon any of them in captivity is not the question as induction is a well known phenomenon in the lab. We were concerned with what actually happens in the wild; what do the caterpillars normally feed upon in the natural state? For the true foodplants listed, the majority have actually been observed with *C. promethea* caterpillars feeding upon them, and all have been reported previously by authors elsewhere in the range of this moth (Ferguson 1972, Tietz 1952). Our criteria for false foodplants were as follows: (1) observations of cocoons on the plant exceedingly rare, (2) cocoons 1-2 per plant, and (3) the plant growing next to well known true foodplants upon which there are *C. promethea* cocoons.

With one exception there were no more than two cocoons per false foodplant, and the average was 1.1. For the true foodplants, however, the average number of cocoons per plant
Table 2. Probable false foodplants of *Callosamia promethea* in Southern Michigan.

<table>
<thead>
<tr>
<th>Species</th>
<th>Provenance and Habit</th>
<th>Number of Cocoons</th>
<th>Nearby True Foodplant</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acer rubrum</em> (1)</td>
<td>Native tree</td>
<td>2</td>
<td>Cephalanthus</td>
</tr>
<tr>
<td><em>A. saccharum</em> (1)</td>
<td>Native tree</td>
<td>1</td>
<td>Sassafras</td>
</tr>
<tr>
<td><em>Berberis thunbergii</em> (1)</td>
<td>Exotic shrub</td>
<td>1</td>
<td>Sassafras</td>
</tr>
<tr>
<td><em>Carya ovalis</em> (1)</td>
<td>Native tree</td>
<td>1</td>
<td>Sassafras</td>
</tr>
<tr>
<td><em>Celtis tenuifolia</em> (1)</td>
<td>Native tree</td>
<td>1</td>
<td>Sassafras</td>
</tr>
<tr>
<td><em>Cornus racemosa</em> (1)</td>
<td>Native shrub</td>
<td>1</td>
<td>Prunus</td>
</tr>
<tr>
<td><em>C. stolonifera</em> (1)</td>
<td>Native shrub</td>
<td>1</td>
<td>Cephalanthus</td>
</tr>
<tr>
<td><em>Corylus americana</em> (1)</td>
<td>Native shrub</td>
<td>1</td>
<td>Sassafras</td>
</tr>
<tr>
<td><em>Lonicera tatarica</em> (1)</td>
<td>Exotic shrub</td>
<td>1</td>
<td>Cephalanthus</td>
</tr>
<tr>
<td><em>Quercus alba</em> (1)</td>
<td>Native tree</td>
<td>1</td>
<td>Sassafras</td>
</tr>
<tr>
<td><em>Q. coccinea</em> (1)</td>
<td>Native tree</td>
<td>1</td>
<td>Sassafras</td>
</tr>
<tr>
<td><em>Q. rubra</em> (1)</td>
<td>Native tree</td>
<td>2</td>
<td>Sassafras</td>
</tr>
<tr>
<td><em>Rhus typhina</em> (2)</td>
<td>Native shrub</td>
<td>2</td>
<td>Sassafras</td>
</tr>
<tr>
<td><em>Thalictrum dasycarpum</em> (3)</td>
<td>Native herb</td>
<td>6</td>
<td>Cephalanthus</td>
</tr>
<tr>
<td><em>Ulmus americana</em> (2)</td>
<td>Native tree</td>
<td>2</td>
<td>Prunus (1)</td>
</tr>
<tr>
<td><em>Vitis riparia</em> (2)</td>
<td>Native vine</td>
<td>2</td>
<td>Cephalanthus (1)</td>
</tr>
</tbody>
</table>

*aIn all cases, those listed as trees were actually saplings or stump sprouts, none over 3 m tall.*

was 4.1 for all species (range 2.5 [*Liriodendron*] to 4.9 [*Cephalanthus*]). As will be discussed below, all of the false foodplant species were associated with one or another of the three most common true foodplants, sassafras, buttonbush, and black cherry, which in all cases had several cocoons. The black cherry was the least common of the true foodplants associated with false foodplants, but it is also the plant, being non-clonal, that is most likely to occur isolated from other woody plants in fields and hedgerows. The other two, sassafras and buttonbush, are notable cloneformers, the clones abutting upon and intergrowing with other species.

All of the false foodplants are woody with the exception of the tall herb, *Thalictrum dasycarpum* Fisch. and Lall. Also, in early winter 1980, R. Stewart and K. Gover discovered an herbaceous vine, the yam (*Dioscorea villosa* L.) in Jackson County, Michigan, serving as a support for a *C. promethea* cocoon near a sassafras clone. This is an unusual record not only because it is an herbaceous plant but also because it is the only monocot we have encountered that was a false foodplant. All of the rest of the species are trees or shrubs with the exception of riverside grape (*Vitis riparia* Michx.), which is a woody vine. All of the false foodplants are natives with the exception of Japanese barberry (*Berberis thunbergii* DC) and Tatarian honeysuckle (*Lonicera tatarica* L.), both of which are becoming naturalized in southern Michigan and spreading widely, especially in second-growth woods. All of the species are common except for dwarf hackberry (*Celtis tenuifolia* Nutt.), a highly localized species known from only a few counties.

Three genera are well represented among the false foodplants: *Acer* (red maple [*A. rubrum* L.] and sugar maple [*A. saccharum* Marsh.]), *Cornus* (gray dogwood [*C. racemosa* Lam.] and red osier [*C. stolonifera* Michx.]), and *Quercus* (white oak [*Q. alba* L.], scarlet oak [*Q. coccinea* Muenchh.] and red oak [*Q. rubra* L.]). It is interesting to note that several of the genera we here interpret as false foodplants have previously been reported as true foodplants, including *Acer*, *Berberis*, *Corylus*, and *Quercus* (Ferguson 1972, Teitz 1952). To our knowledge, the other taxa have not previously been reported to have promethea cocoons hanging on them.
SUMMARY AND DISCUSSION

In addition to the true foodplants listed in Table 1 for southern Michigan, R. Stewart has kindly given us a report of two collections of *C. promethea* cocoons on privet (*Ligustrum vulgare* L.) in Jackson County. We do not consider this a case of wandering as none of the true foodplants were found in the immediate vicinity. This brings the number of species confidently regarded as true foodplants to nine, of which only three, sassafras, black cherry, and buttonbush, are of major importance. Judging from the incidence of cocoons and the nature of their occurrence, we conclude that there are at least 17 species (including *Dioscorea villosa*) upon which wandering larvae may pupate. The potential number of false foodplants is much greater, of course, since the association is probably casual, and based upon chance. Ferguson (1972) has given a valuable discussion of this phenomenon in connection with the buck moth, *Hemileuca maia* (Drury), "reported to feed on a variety of other plants, almost certainly in error. This is partly explained by the habits of the larvae, which, when about half-grown, lose their gregarious nature and disperse widely in all directions. They are then often found resting on plants upon which they do not normally feed, and in some instances these may have been wrongly assumed to be the host plants." In our studies we based our conclusions upon the incidence of cocoons. It is possible indeed that some of our reports deal actually with secondary foodplants i.e. in which wandering larvae adopted after leaving the primary foodplants. It is also possible that at least some of our "false" foodplants are actually primary foodplants which are very rarely utilized, although the likelihood seems remote.

We should caution that our statistics are based primarily upon roadside observations in which cocoons were recognized from a moving automobile and the site subsequently investigated. We thus mainly surveyed plants growing along the road and in nearby fields and hedgerows. In all likelihood the bulk of *C. promethea* cocoons do, in fact, occur in such habitats, but we did miss one conspicuous foodplant by making our survey in this way, the spicebush.

All of the true foodplants for which we have reports are listed in Table 3. Those marked with question marks are ones which, in our opinion, need further confirmation. Those marked with asterisks are ones that we find to be probable false foodplants in southern Michigan. Ferguson (1972) stated that *C. promethea* has "definite preferences that seem to vary geographically." Based on our correspondence with lepidopterists over the range of this moth, we surmise that the three most important foodplants in southern Michigan are consistently the most utilized throughout the eastern United States. However, as we go farther south, new true foodplants are utilized, including sweet gum (*Liquidambar styraciflua* L.), silverbells (*Halesia carolina* L.), storax (*Styrax americana* Lam.), and sweet leaf (*Symlocos tinctoria* [L.] L'Her.). Heitzman (in Ferguson 1972) reported persimmon (*Diospyros virginiana* L.). We have no reason to question any of these as true foodplants, but more evidence would be welcomed for some of them.

Although the true foodplants can be characterized as possessing a shrubby growth form and occurring in highly disturbed and/or secondary succession sites, from a taxonomic viewpoint they are incredibly diverse. As can be seen from Table 3, the actual taxonomic relationships, following current opinion (e.g. Cronquist 1968), are remote indeed. Represented are five widely separated subclasses, and the families seem almost to have been chosen at random. The pair Lauraceae and Magnoliaceae are obviously interrelated; and the trio Ebenaceae, Styracaceae, and Symplocaceae are also interrelated. However, Oleaceae and Rubiaceae are probably quite divergent. Of all the possible woody Rosaceae, why is it that *Prunus* are preferred, indeed the one species, *P. serotina*, against all others? The most isolated foodplant is the sweet gum, the relationships of which to any of the others are probably very distant. Perhaps the plants are similar chemically, such as in nitrogen content in the leaf, percent leaf water content, leaf toughness, or presence of a chemical which acts as a feeding stimulant; all traits which are important components of the nutritive value of the plants. And differences in feeding and growth of larvae have also been shown to be more dependent on the nutritive value than on the taxonomic range of plants used (Fox and Macauley 1977, Onuf et al. 1977).
Table 3. True and false foodplant genera of *Callosamia promethea* in Southern Michigan

PINOPSIDA | MAGNOLIOPSIDA cont. | MAGNOLIOPSIDA cont.
--- | --- | ---
Pinidae | | |
Pinaceae ? | Styracaceae | Hamamelidae |
*Pinus* ? | *Styrax* | *Hamamelidaceae*
*Thuja* ? | *Halesia* | *Liquidambar*
MAGNOLIOPSIDA | | |
Magnoliidae | | |
Berberidaceae ? | Salicaceae ? | Anacardiaceae *
*Berberis* *?* | *Populus* ? | *Rhus* *
Lauraceae | Rosidae | Juglandaceae *
*Lindera* | *Rosaceae* | *Carya* *
Sassafras | *Prunus* | *Fagaceae* *
Magnoliaceae | *Amygdalus* ? | *Quercus* *?*
*Liriodendron* | *Malus* ? | Betulaceae *
*Magnolia* ? | *Pyrus* | *Corylus* *
Ranunculaceae * | Cornaceae * | Myricaceae *
*Thalictrum* *| | *Myrica* *
Dilleniiidae | | |
Tiliaceae ? | Vitaceae * | Ulmaceae *
*Tilia* ? | *Vitis* | *Ulmus* *
Ebenaceae | Aceraceae *? | *Celtis* *
*Diospyros* | *Acer* *?* | Asteridae

---

as = considered a probable false foodplant in the present survey. ? = previously listed by Elliot and Soule (1902), Ferguson (1972) and/or Tietz (1952), but dubious in light of recent reports.

The situation with regard to *C. promethea* is considerably different from another giant silkworm moth we have studied in southern Michigan. The polyphemus, *Antheraea polyphemus*, has 13 known foodplant species in this area belonging to nine genera (Wagner and Mayfield 1980), but not one of them is the same as any of those we regard as true foodplants for promethea. In general, *C. promethea* feeds on low shrubs, saplings, and stump sprouts, while *A. polyphemus* feeds, with one exception, on full-sized trees. Also *A. polyphemus* forms and attaches its cocoon in several different ways, unlike *C. promethea*, which forms its cocoons in a uniform manner. *A polyphemus* is a much more widely ranging species than *C. promethea*, occurring from Canada to Mexico and from coast to coast, while *C. promethea* exists only in the eastern part of North America. *C. promethea* does have a wider range, however, than its congeners, *C. angulifera* and *C. securifera*, both of which, in nature at least, tend to be confined to single foodplants, tulip tree and sweet bay respectively. Thus part of the success of *C. promethea*, which is a much more abundant species than the tulip tree or the sweet bay moths, may be due to its polyphagous nature.

ACKNOWLEDGMENTS

We thank all of the following individuals who contributed to this study: A. E. Brower, M. Gumina, J. R. Heutzman, B. Mather, D. Bagget, C. Byron, K. Gover, R. Kargosien, T. Manley, S. Nicolay, M. Nielsen, R. Piegler, R. Stewart, and J. Tuttle.
LITERATURE CITED


THE RESPONSE OF ASPEN (POPULUS TREMULOIDES) TO ARTIFICIAL DEFOLIATION

A. C. Hodson

In the summers of 1939 and 1940 hand defoliation of trembling aspen, Populus tremuloides Michx., was carried on in a young stand located a few miles north of Itasca State Park. This study was undertaken to determine the response of aspen trees to several amounts of defoliation at four different times during the summer. Other similar artificial defoliation studies have been reported by Wallace (1945), Giese et al. (1964), Skilling (1964), Kulman (1971), and Heichel and Turner (1976).

Leaf clusters, including the petioles, were removed without injuring the terminal shoots. The procedure was different from that caused by insect defoliation because clusters were taken uniformly over a tree starting with the first cluster on the lowest branch. The basal diameter of the trees ranged from 1.2 to 1.8 inches. Three similar trees were selected to be defoliated 50, 60, 70, 80, 90, and 100%. Groups of three trees were defoliated once during the summer on four dates, 3 June, 30 June, 14 July, and 19 August. Before the leaves were removed the number of leaf clusters was counted, the average number of leaves per cluster determined, and sample of leaves were measured to determine average leaf areas in square inches. From these data it was possible to calculate the average total leaf area on each of the trees. The same measurements were taken for the regenerated leaves produced soon after defoliation, and again for the leaves on the same trees in each of the following two years. In addition, the number of dead branches was recorded the first year after defoliation. The results presented in Table I are average values for three-tree samples.

The most striking feature is the response of the trees to defoliation after the middle of August. There was no refoliation after any level of defoliation. Also, leaf production each of the following two years was not significantly different from that of the undefoliated check trees, and the average leaf area of 1.4 to 1.6 square inches was the same as on check trees.

The percentage of leaf area regenerated was greatest following 90 and 100% defoliation with trees defoliated on 30 June generally showing the most refoliation. With the exception of 50% defoliation on 3 June and 100% on 14 July, the 14 July defoliation resulted in the smallest area regenerated. The size of the regenerated leaves also differed depending on the amount of foliage removed. For example, when the trees were defoliated on 30 June, the average leaf area in square inches, as compared with the original areas, was 72, 64, 61, 46, 33, and 35 for 50, 60, 70, 80, 90, and 100% defoliation respectively. The areas of leaves produced the year following defoliation showed a similar gradation of 100, 94, 86, 80, 53, and 43 for the same amounts of defoliation, and by the second year, the trees defoliated 90 and 100% still had average-sized leaves of only 75 and 53% of their original areas.

Heichel and Turner (1976) reported remarkably similar results after removing 100, 75, and 50% of the foliage from red oak and red maple trees. For example, these trees produced regrowth leaves with leaf areas only 39 and 33% of the primary leaves for oak and maple respectively after 100% defoliation. The leaf areas of the regrowth leaves in aspen were 35% as large as the original leaves. At the other extreme, after 50% defoliation, their regrowth leaves had areas 60 and 66% as large for oak and maple while the aspen leaves averaged 72% the size of normal leaves.

There was a gradation in recovery of the defoliated trees exhibited in each of the two years following the defoliation treatments. Because of the considerable variation in response with

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1Paper No. 11,635, Scientific Journal Series, Minnesota Agricultural Experiment Station, University of Minnesota, St. Paul, MN 55108.
2Department of Entomology, Fisheries, and Wildlife, University of Minnesota, St. Paul, MN 55108.
Table 1. Effects of defoliation on average leaf area in square inches and average number of dead branches.

<table>
<thead>
<tr>
<th>Defol. Date</th>
<th>Orig. Area</th>
<th>Area Regenerated</th>
<th>% of area removed</th>
<th>1 yr. later Regenerated</th>
<th>2 yrs. later % of Orig.</th>
<th>Dead Branches 1 yr. later</th>
</tr>
</thead>
<tbody>
<tr>
<td>50% Defoliation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 June</td>
<td>2385</td>
<td>49</td>
<td>4</td>
<td>124</td>
<td>177</td>
<td>2.3</td>
</tr>
<tr>
<td>30 June</td>
<td>2381</td>
<td>83</td>
<td>7</td>
<td>164</td>
<td>203</td>
<td>4.0</td>
</tr>
<tr>
<td>14 July</td>
<td>1051</td>
<td>79</td>
<td>15</td>
<td>106</td>
<td>137</td>
<td>2.1</td>
</tr>
<tr>
<td>19 Aug.</td>
<td>1498</td>
<td>0</td>
<td>0</td>
<td>210</td>
<td>281</td>
<td>0.0</td>
</tr>
<tr>
<td>60% Defoliation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 June</td>
<td>2777</td>
<td>436</td>
<td>27</td>
<td>137</td>
<td>140</td>
<td>5.0</td>
</tr>
<tr>
<td>30 June</td>
<td>2988</td>
<td>378</td>
<td>22</td>
<td>121</td>
<td>109</td>
<td>8.0</td>
</tr>
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<td>14 July</td>
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<td>115</td>
<td>16</td>
<td>161</td>
<td>227</td>
<td>1.3</td>
</tr>
<tr>
<td>19 Aug.</td>
<td>1176</td>
<td>0</td>
<td>0</td>
<td>197</td>
<td>315</td>
<td>0.0</td>
</tr>
<tr>
<td>70% Defoliation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>3 June</td>
<td>3106</td>
<td>543</td>
<td>25</td>
<td>90</td>
<td>96</td>
<td>5.0</td>
</tr>
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<td>30 June</td>
<td>3756</td>
<td>761</td>
<td>29</td>
<td>64</td>
<td>75</td>
<td>7.6</td>
</tr>
<tr>
<td>14 July</td>
<td>696</td>
<td>53</td>
<td>10</td>
<td>105</td>
<td>153</td>
<td>6.0</td>
</tr>
<tr>
<td>19 Aug.</td>
<td>2040</td>
<td>0</td>
<td>0</td>
<td>134</td>
<td>216</td>
<td>0.0</td>
</tr>
<tr>
<td>80% Defoliation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 June</td>
<td>2162</td>
<td>406</td>
<td>23</td>
<td>82</td>
<td>102</td>
<td>4.6</td>
</tr>
<tr>
<td>30 June</td>
<td>2750</td>
<td>818</td>
<td>37</td>
<td>113</td>
<td>155</td>
<td>7.3</td>
</tr>
<tr>
<td>14 July</td>
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<td>146</td>
<td>16</td>
<td>100</td>
<td>134</td>
<td>5.3</td>
</tr>
<tr>
<td>19 Aug.</td>
<td>1795</td>
<td>0</td>
<td>0</td>
<td>198</td>
<td>258</td>
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<tr>
<td>90% Defoliation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 June</td>
<td>2705</td>
<td>792</td>
<td>33</td>
<td>81</td>
<td>88</td>
<td>8.6</td>
</tr>
<tr>
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<td>3386</td>
<td>1017</td>
<td>33</td>
<td>51</td>
<td>83</td>
<td>15.0</td>
</tr>
<tr>
<td>14 July</td>
<td>1271</td>
<td>313</td>
<td>27</td>
<td>81</td>
<td>89</td>
<td>11.5</td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>161</td>
<td>213</td>
<td>0.0</td>
</tr>
<tr>
<td>100% Defoliation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 June</td>
<td>2331</td>
<td>886</td>
<td>38</td>
<td>66</td>
<td>74</td>
<td>14.5</td>
</tr>
<tr>
<td>30 June</td>
<td>2520</td>
<td>1092</td>
<td>43</td>
<td>35</td>
<td>45</td>
<td>16.0</td>
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<tr>
<td>14 July</td>
<td>2038</td>
<td>1143</td>
<td>56</td>
<td>50</td>
<td>89</td>
<td>28.0</td>
</tr>
<tr>
<td>19 Aug.</td>
<td>1471</td>
<td>0</td>
<td>0</td>
<td>179</td>
<td>214</td>
<td>0.0</td>
</tr>
<tr>
<td>Check</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 June</td>
<td>2325</td>
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<td>250</td>
<td>2.0</td>
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<tr>
<td>30 June</td>
<td>2651</td>
<td>0</td>
<td>0</td>
<td>168</td>
<td>232</td>
<td>0.0</td>
</tr>
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</table>

respect to defoliation date no consistent significant differences are evident. However, a marked reduction in recovery, given as percentage of the original leaf areas, occurred after 90 and 100% defoliation. In both cases there was significantly less total leaf area produced than by trees defoliated on 19 August and for the check trees. This condition persisted into the second year following the defoliation treatments.
Heichel and Turner (1976) also observed the response of their trees the year following defoliation and the results were much the same as found for aspen in this study. There was one marked difference. For their trees the reduction in total leaf area was imperceptible as compared to the total area of the previous year’s primary foliage. In the present study, as mentioned above, there was a significant reduction in total leaf area after the most severe defoliation treatments. The number of dead branches observed the first year after defoliation also was much greater after 90 and 100% defoliation, though there were many more at all levels than for the checks and for the trees defoliated in August.

There was another phenomenon associated with different amounts of defoliation. In the year following the defoliation treatments leaves distorted in size and form, as the result of infestation by an unidentified eriophyid mite, appeared on some of the trees. These galls were found only on trees with 90 and 100% defoliation. Buds infested by these mites could be recognized in the fall by their large size and the presence in them of many overwintering mites. Galled leaves caused by this mite also have been commonly observed in years following complete defoliation of aspen by the forest tent caterpillar.

LITERATURE CITED

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