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**COVER PHOTOGRAPH**

Coreidae nymph (Hemiptera). Photograph by William Westrate.
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PHENOLOGY OF OVIPOSITION OF DASYNEURA OXYCOCCANA (DIPTERA: CECIDOMYIIDAE) IN RELATION TO CRANBERRY PLANT GROWTH AND FLOWERING

Stephen D. Cockfield and Daniel L. Mahr

ABSTRACT

Eggs of cranberry tipworm, Dasyneura oxycoccana (Diptera: Cecidomyiidae) were sampled in a Wisconsin cranberry marsh from 1990 through 1992. Oviposition began in May within one week after the first cranberry shoots elongated more than 5 mm. Oviposition fluctuated in June, then greatly decreased in July, after over 90% of cranberry flowers had opened. Some oviposition continued into August. Tipworm probably has greatly overlapping generations, as no distinct broods could be detected. Consequently, D. oxycoccana may be difficult to manage without control methods effective against multiple life stages.

Cranberry tipworm, Dasyneura oxycoccana (Johnson), feeds on the youngest leaves of cranberry, Vaccinium macrocarpon, at the apex of growing shoots. Larvae rasp the leaves while feeding, and the cranberry plant responds by growing distorted, cupped leaves. Feeding eventually kills the apical meristem of the shoot (Smith 1890).

Tipworm has been suspected of causing reductions in cranberry yield, although the cranberry plant is able to compensate for the damaged tips. Smith (1890) examined infested cranberry branches and could find no damage to the current year's fruit or to the flower buds forming for the next year. After making more observations, Smith (1905) stated that tipworm feeding does not hinder flower bud formation if damage occurs early in vigorous plants. If feeding occurs late enough on weak plants, however, vegetative buds are formed at the expense of flowering buds. Latter publications on the insect (e.g., Franklin 1948) repeated the same viewpoint. However, D. oxycoccana apparently has caused severe yield reduction in New Jersey (Eck 1990) and many Wisconsin growers believe that tipworm causes economic losses.

The larval stage of D. oxycoccana was observed to last about 10 d, and the pupal stage about 3 days. Therefore, estimating the duration of the life cycle to be about half a month, Smith (1890) believed there were four to five generations per year. However, he reported that most feeding injury occurred in early summer. Franklin (1948) and later authors stated there were two distinguishable broods in early summer, about a month apart. The second brood was believed to be more damaging than the first. There are no published sources that indicate when the broods occur in Wisconsin, and what phenological events could be correlated with the timing of broods.

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Tipworm adults lay tiny, oblong eggs on the innermost leaves of growing cranberry shoots (Franklin 1948). Eggs are not usually laid on dormant buds or branches that have paused in growth (Eck 1990). Oviposition may build and decline along with the abundance of suitable growing tips. The purpose of this study is to determine the phenology of oviposition of cranberry tipworm and relate the time of oviposition to easily-observed events in the cranberry plant.

MATERIALS AND METHODS

Eggs of cranberry tipworm were monitored in 1990–1992 in a commercial cranberry marsh in Warrens, Monroe Co., WI. Within the marsh were beds each about 25 by 75 m, separated by ditches and dikes. The sample bed of ‘Searles’ was not treated with insecticides during the years monitored. Eight quadrats of foliage (each 0.1 m² area) were selected randomly within the bed every 2 or 3 days starting in mid-May until the end of August. A subsample of 50 branch tips was randomly selected from each sample and the terminal buds were examined for eggs under a microscope at 25 X magnification. Sometimes fewer than 50 intact tips could be recovered if other insects had been feeding on the foliage. In 1992, larvae were counted in the tips as well.

Phenology of the cranberry plants was monitored on the same bed. Plastic hoops (10 cm inner diameter) were secured over the vines in early spring. Twelve hoops were distributed over a 2 by 3 m area about 3 m from the edge of the bed. Any branches growing within the hoops were considered sample units, and the total sample area was about 0.12 m². The cumulative number of shoots over 5 mm in length was counted in the hoops every 2 or 3 days in May and June. Flowering is the most visible event to monitor in summer. It is during the summer also that dormant buds are formed for next year’s growth (Eck 1990), potentially reducing the available oviposition sites. We hypothesized that cessation of vegetative growth, and thus of oviposition, would occur sometime during or just after flowering. In the summer, the number of flowers in the hoops that had opened or were past bloom were counted. These numbers could be expressed as a percentage of total inflorescence (% in flower) because the number of cranberry flowers is determined the previous year when primordial buds are formed (Eck 1990). Flower observations were made every week in 1990 and every 2 or 3 days in 1991 and 1992.

RESULTS AND DISCUSSION

In all sample years, *D. oxycocca* adults began oviposition in May, within a week after the first shoots elongated (Fig. 1). In 1992 there appeared to be three or four surges in oviposition before flowering was complete, but no clear peaks could be distinguished in 1990 and 1991 (Fig. 1). The time when 90% of flowers had bloomed occurred in late June one year and in early July in the other two years (Fig. 1). Each year, the majority of oviposition ended soon after most flowers had opened. Occasionally, some eggs were laid throughout the rest of the summer, but not in great numbers (Fig. 1). In 1992, even though there appeared to be cycles in oviposition, the density of larvae gradually increased, then decreased after mid-June, with no apparent separate broods (Fig. 2).

After flowering, the cranberry plant begins to produce the vegetative and flowering buds for the following year (Eck 1990). Oviposition decreases after flowering probably because of the decrease in available growing shoots. As the plants produce some growing shoots in August, perhaps to compensate
for those damaged in June or July, a few females are able to find these and lay eggs on them (Fig. 1).

Scouting for tipworm can be greatly improved by concentrating observations between the time of new growth in the spring and the end of flowering. Eggs can be deposited at any time during this interval. Although it is likely that more than one generation was produced during this time period, we were unable to discern distinct broods. Lack of distinct generations makes the
Figure 2. The density of *Dasyneura oxyccocca* larvae (upper graph) and eggs (lower graph) counted in up to 400 cranberry shoot tips per sample date. Data are from 1992.

phenology of the insect difficult to predict and makes the insect a challenge to manage with stage-specific control agents.

ACKNOWLEDGMENTS

We thank C. Strozewski (Claude Strozewski Marsh) for permitting sampling on his property. M. Gehl, S. Nannapaneni, S. Stern, J. Frost, R. Engelke, and R. Ness (Department of Entomology, University of Wisconsin-Madison), provided technical assistance. Research reported herein was funded in part by Ocean Spray Cranberries, the Wisconsin Cranberry Board, and the College of Agricultural and Life Sciences, University of Wisconsin-Madison.

LITERATURE CITED

ABSTRACT

Two levels of commercially-reared *Trichogramma pretiosum* were released during the oviposition period of the cranberry fruitworm (*Acrobasis vaccinii*) in eight Massachusetts (U.S.A.) cranberry bog sites. Release levels of $4.8 \times 10^5$ *T. pretiosum* per ha or $1.9 \times 10^6$ *T. pretiosum* per ha were made at 3–5 day intervals, with a total of nine releases. Parasitism was estimated by collecting cranberry fruits and examining them for the presence of *A. vaccinii* eggs and *T. pretiosum*. Eggs were classified as unhatched, hatched, parasitized or emergent parasite. Collections of cranberries from four 'neglected' bog sites (not currently under cultivation) were examined and classified similarly, but *T. pretiosum* were not released, to determine the level of parasitism from endemic populations.

Cumulative parasitism from the neglected sites was consistently higher than levels recorded from the release sites throughout the season. Parasitism in the neglected sites was determined to be from natural populations of *T. pretiosum*. Comparisons of cranberries damaged by *A. vaccinii* showed that damage was greatest in the neglected sites, but was not significantly different from fruit damage within either the low release or high release level. Collections of cranberries were also made within bog sites managed under current Massachusetts Cooperative Extension IPM guidelines. Damage to cranberries was lowest in the IPM-managed sites; although this value was less than the other bog sites, it did not differ significantly.

Cranberry fruitworm (*Acrobasis vaccinii* Riley) is a primary, direct pest of cranberries (*Vaccinium macrocarpon*) and also feeds on other *Vaccinium* (Shawa et al. 1984). In the northeastern United States, immature cranberry fruitworm overwinter beneath the cranberry bog surface within hibernaculae and emerge as moths throughout June, dependent upon cranberry variety and environmental conditions (Anonymous 1982). Typically, peak flight of the moths coincides with full bloom (late June) of the cranberry crop (Roberts & Brodel 1985).

Female *A. vaccinii* generally deposit a single, flattened egg in the calyx of the developing cranberry. Larvae hatch, move to the upper berry surface and bore into the green fruit, then begin feeding. Larval development includes five instars (Brodel & Roberts 1985) and is usually completed by August. At this time, this univoltine pest drops to the soil to form a hibernaculum and over-

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winters as a larva. Pupation occurs in the spring. During its feeding period, a larva will enter and feed in 5-8 berries. Thus, high populations can substantially reduce cranberry yields, causing losses which may exceed 50%. This pest is generally controlled by several insecticidal applications.

At the time of these field trials, the ongoing pest management strategy listed first application of an insecticide (parathion, diazinon, chlorpyrifos or carbaryl) at 7-9 days after > 50% of the plants are post-bloom. This timing is determined by sampling 20 cranberry vines ('uprights') per ha and estimating the percentage of flowers that have set fruit. A second spray is applied 10 days later and a third spray is applied if a single fruitworm egg is found in a sample of 100 berries per ha.

Franklin (1950) reported that *Trichogramma pretiosum* Riley were native egg parasites of *A. vaccinii* in Massachusetts. He speculated that these wasps could limit insect pest populations in cranberries. Inundative release of *T. pretiosum* could reduce fruit injury by *A. vaccinii* by eliminating their eggs prior to hatch. The potential for *T. pretiosum* and other *Trichogramma* species to generate significant control against a range of lepidopterous pests has been long promulgated (Stinner 1977, Ridgeway et al. 1981). Prior (Stinner et al. 1974, Oatman & Platner 1978, Burbutis & Koepeke 1981) and more recent control attempts (Gross et al. 1984, Kanour & Burbutis 1984, King et al. 1986, Brower 1988) against several lepidopterans have used an inundative release strategy. Results have been erratic, but encouraging, and these studies have reflected a need for continuing field trials. Commercial rearing techniques have been developed (Morrison et al. 1978) so that at least six *Trichogramma* species are now available.

In this field study, two release levels of *T. pretiosum* were made during *A. vaccinii* oviposition and were compared with parasitism found in four neglected bogs with natural populations of *T. pretiosum*. Cranberry damage was compared between these treatments and with four commercial bogs that used insecticides for control.

**METHODS AND MATERIALS**

Site selection. The field study was conducted in 1988 in Carver, MA. Eight cranberry bogs were selected as sites for parasite release based upon the following criteria: (1) the bog was approximately 0.5 ha in size; (2) it had a history of cranberry fruitworm damage; and (3) it was equipped with a solid-set irrigation system which could be shut off from the main system, thus avoiding accidental contamination from insecticidal sprays. A single 0.25 ha release area was measured and flagged within each selected bog such that it was at least 5m from any bog edge. All data were collected from within this boundary. Thirty release points within the release area were arranged in a grid pattern, with points spaced ca. 10 m apart. Four bogs not currently under production (i.e., 'neglected') were also chosen for comparisons. These sites ranged from < 0.01-0.02 ha and were within the same general area (Carver, MA) as the release treatments, but were at least 100 m from these sites. Four cranberry bogs managed within guidelines established by the MA Cooperative Extension Agency were selected for fruit damage comparisons, but field parasitism was not noted in these treatment bogs.

Parasite release. *Trichogramma pretiosum* were purchased from an insectary (Rincon-Vitova, Oak View, CA) on a weekly schedule. Each shipment was examined to confirm that parasites had not emerged. Production cards, consisting of construction paper with parasitized host eggs (Morrison et al. 1978) were then placed within a refrigerator at 4.5 °C until field release. Cards with
the appropriate number of parasites were divided and transported to field sites within a chilled (< 8 °C) cooler. This technique effectively placed emerging *Trichogramma* on a site within hours following removal from refrigeration (see Morrison 1985, for details of this technique). Four release sites received $1.2 \times 10^5$ *T. pretiosum* per release ('Low level' equivalent to $4.8 \times 10^5$ wasps per ha) and four sites received $4.8 \times 10^5$ *T. pretiosum* per release ('High level' equivalent to $1.9 \times 10^6$ wasps per ha). Each release episode within a site was standardized to include placement of cards with 4,000 wasps or 16,000 wasps, respectively, at each of 30 release points. Cards were arranged with the paper backing topmost to prevent sunscald or egg damage by precipitation. The first release was initiated near the end of bloom (25 June) and releases were made at three to five day intervals thereafter, for a total of nine releases through 30 July 1988. A sample of at least five cards was examined during each subsequent release to ensure that wasps had eclosed.

**Cranberry classification.** At least 100 cranberries were collected at random from each site immediately following every release. Cranberries were examined with a hand lens (10X) and classified as: (1) cranberry without *A. vaccinii* egg; (2) cranberry with egg; or (3) cranberry with parasitized egg; or (4) egg with emergent parasite. Phenology of *A. vaccinii* oviposition was determined by recording the total number of eggs collected during each sampling period from all treatments and expressing this value as the cumulative percentage of all eggs collected throughout the entire sampling period. Eggs with unhatched fruitworm were held individually in petri dishes at ambient temperature until larval hatch or parasite emergence. Cumulative parasitism was recorded for each of these three treatments. *Trichogramma* recovered from the neglected sites (two male specimens) were sent to Mr. Gary Platner (Department of Entomology, University of California, Riverside, CA) for determination.

**Damage estimation.** Damage due to *A. vaccinii* was estimated in early September by selecting ten samples (30 X 30 cm) randomly at each treatment site. Sampling was also conducted on four additional sites that had been treated with insecticidal sprays as recommended by the Massachusetts Cooperative Extension Service integrated pest management strategy (IPM' sites). The ten samples per treatment were made once within each site. All cranberries within the defined area were collected and rated, using the following categories established by Roberts and Brodel (1985). These categories were: (1) sound cranberry, unblemished and marketable; (2) cranberry damaged by another larval Lepidoptera (e.g., *Sparganothis sulfureana* [Clemens]); and (3) cranberry damaged by *A. vaccinii*.

Cranberries were regarded as damaged by *A. vaccinii* only if a feeding entry hole or frass within the cranberry cavity was observed. Cranberries were considered damaged by *S. sulfureana* only if a characteristic external feeding scar was noted. Cranberries that were otherwise damaged or affected by a pathogen were noted, but were not included in these comparisons. The number of damaged cranberries was then expressed as a percentage of the total number per treatment and transformed to arcsine proportion prior to one way analysis of variance. Mean values were separated by Duncan's Multiple Range Test.

**RESULTS**

A total of 11, 278 cranberries were examined and 264 *A. vaccinii* eggs were detected over the entire sampling period. Multiple *A. vaccinii* eggs were not observed on any single cranberry fruit. Over 80% of *A. vaccinii* eggs were
Cumulative parasitism in low and high release levels was similar in pattern throughout the season, but parasitism within the neglected sites was higher consistently than either level (Table 1). There was little difference between the high or low release levels during the season, with a peak cumulative parasitism of 21.4% (6/28) within low release sites, 12.2% (19/156) within high release sites and 46.3% (37/80) within neglected sites. Curiously, while the low level release sites resulted in a higher percentage of cumulative parasitism than the high level releases throughout this study, host density in the low release sites was substantially lower. Parasitism was not estimated in IPM bog sites due to the application of insecticides during the study period. However, application of fungicidal compounds on low and high release bog sites could have interfered with parasite performance, although this variable was not tested here.

Since parasitism was estimated from vacant A. vaccinii eggs that showed an emergence hole, few adult parasites were collected. However, two adult males were recovered from eggs found within the neglected sites and were sent for determination. They were identified as T. pretiosum, using the standard technique of examining male specimens (Pinto et al. 1978). This finding deposited between 7 July and 24 July (Fig. 1), the period of cranberry fruit formation. The early deposition of A. vaccinii eggs is consistent with results from others (Anonymous 1982) and demonstrates that control measures of A. vaccinii must be directed during its earliest appearance since the presence of a larva within a cranberry prevents control materials from contacting and killing the insect. The inundative release strategy used in this trial included three separate releases of parasites, at low and high levels, prior to 2 July, ensuring that adult parasites were released well in advance of the first A. vaccinii eggs. Presumably, these parasites were searching actively for host eggs during the oviposition period.

Figure 1. Cumulative deposition of A. vaccinii eggs during oviposition period from July-August, 1988. Values are combined data from twelve sites (three treatments). Arrow indicates the date of 80% accumulation of eggs.
Table 1. Cumulative parasitism (# parasitized eggs/# host eggs) within low release level, high release level and neglected cranberry bog sites**.

<table>
<thead>
<tr>
<th>Date</th>
<th>Low level sites</th>
<th>High level sites</th>
<th>Neglected sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>7 July</td>
<td>0/ 3 (0.0%)</td>
<td>0/ 19 (0.0%)</td>
<td>2/ 5 (40.0%)</td>
</tr>
<tr>
<td>11 July</td>
<td>1/13 (7.7%)</td>
<td>0/ 56 (0.0%)</td>
<td>5/23 (21.7%)</td>
</tr>
<tr>
<td>14 July</td>
<td>2/17 (11.8%)</td>
<td>3/ 95 (3.2%)</td>
<td>8/32 (25.0%)</td>
</tr>
<tr>
<td>19 July</td>
<td>3/22 (13.6%)</td>
<td>8/112 (7.1%)</td>
<td>19/49 (38.8%)</td>
</tr>
<tr>
<td>24 July</td>
<td>3/23 (13.0%)</td>
<td>15/141 (10.6%)</td>
<td>24/63 (38.1%)</td>
</tr>
<tr>
<td>29 July</td>
<td>3/24 (12.5%)</td>
<td>15/145 (10.3%)</td>
<td>30/69 (43.4%)</td>
</tr>
<tr>
<td>4 Aug</td>
<td>3/24 (12.5%)</td>
<td>15/147 (10.2%)</td>
<td>34/76 (44.7%)</td>
</tr>
<tr>
<td>12 Aug</td>
<td>3/25 (12.0%)</td>
<td>15/161 (9.9%)</td>
<td>35/77 (45.5%)</td>
</tr>
<tr>
<td>20 Aug</td>
<td>6/28 (21.4%)</td>
<td>19/156 (12.2%)</td>
<td>37/80 (46.3%)</td>
</tr>
</tbody>
</table>

**values are combined from four replicates per treatment.

confirms earlier observations in cranberries of endemic levels of this species (Franklin 1950). No other egg parasites emerged from eggs held during the incubation period.

Although the percentage of A. vaccinii-damaged cranberries in the IPM sites was less than in the other sites, means were not significantly different among low release, high release or neglected sites, nor between low or high releases or IPM sites (F= 1.56; df = 3, 12; ns). Cranberry damage by A. vaccinii was low, relative to other damage factors (Table 2). The number of sound, unblemished cranberries was similar among low, high and IPM bog sites, but was significantly lower in neglected sites ($\chi^2 = 36.34$; df = 3; $P<0.01$).

Analysis of the relationship between the level of fruitworm-damaged cranberries and parasitization provided insight into the effect of Trichogramma in suppressing A. vaccinii. A significant, negative correlation ($r^2 = -0.747; Y = -5.37X + 98.31; P < 0.05$) between the percentage of fruitworm-damaged berries and percentage of Trichogramma parasitization was determined from data collected within the neglected sites. No significant correlation was noted in sites with released Trichogramma.

DISCUSSION

Female A. vaccinii deposited 80% of their total complement of eggs during the early fruiting period of cranberry development (from 7–24 July), thus permitting their progeny to develop concurrently with the formation of the cranberries. Because each larva can consume 5–8 cranberries before pupation (Roberts & Brodel 1986), early oviposition would enhance larval survival, as

Table 2. Mean number (± SE) of sound or damaged cranberries from treatments*.

<table>
<thead>
<tr>
<th></th>
<th>Low level sites</th>
<th>High level sites</th>
<th>Neglected sites</th>
<th>IPM sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sound cranberries</td>
<td>183.6 (± 36.0)</td>
<td>173.6 (± 70.5)</td>
<td>96.3 (± 17.6)</td>
<td>192.1 (± 15.2)</td>
</tr>
<tr>
<td>Unidentified damage</td>
<td>36.9 (± 6.8)</td>
<td>32.4 (± 17.8)</td>
<td>28.5 (± 8.4)</td>
<td>27.4 (± 2.9)</td>
</tr>
<tr>
<td>A. vaccinii damage</td>
<td>9.7 (± 3.2)</td>
<td>9.6 (± 5.9)</td>
<td>10.9 (± 1.6)</td>
<td>2.5 (± 0.6)</td>
</tr>
<tr>
<td>Total cranberries</td>
<td>230.2</td>
<td>215.6</td>
<td>135.7</td>
<td>222.0</td>
</tr>
</tbody>
</table>

% damage by A. vaccinii 4.2% 4.5% 8.0% 1.1%

*Mean of ten samples per replicate and four replicates per treatment, except three replicates for neglected bogs.
only a single larva can infest a single cranberry. This fact was supported by the absence of multiple eggs on a single cranberry.

A large population of larval *A. vaccinii* could remove much of a marketable cranberry crop. Overwintering adult parasites, such as *Trichogramma*, would be present in relatively low numbers during the ovipositional period of *A. vaccinii*, and would likely parasitize a low percentage of eggs. However, the high level of parasitism noted in the neglected sites (between 21.7%-38.8% from 7-19 July) would indicate that endemic *Trichogramma* are seeking and locating, and successfully parasitizing, these host eggs. The feeding damage to cranberries in neglected sites was higher than other treatments, however, but could be due to the lower total number of cranberries in these areas.

The relatively low level of parasitism generated by either release (i.e., consistently less than the level found within the neglected bog sites) would indicate that these parasites did not locate and oviposit in their target host eggs. Other trials have demonstrated that even low releases of *Trichogramma* over a 21 day period (62,000 per ha) would generate a parasitization rate of between 11-49% in *Heliothis* spp. (Johnson 1985). In this case, naturally-occurring *Trichogramma* (*T. pretiosum* and *T. exiguum*) were noted to parasitize 59% of eggs on the initial sampling date; the percentage dropped rapidly thereafter.

Lower levels of parasitism were noted in another study, where *Heliothis virescens* (F.) eggs were placed near the edge of a soybean field, and endemic parasitism was between 8-14% during the two seasons of the study (Thorpe 1984). Thus, the levels of parasitization noted in the current trial are relatively high when compared with other studies.

Repeated inducive release of *T. pretiosum* has been attempted within a simulated warehouse of storage peanuts, and parasitism rates here were similar to those noted in the *A. vaccinii* release sites. Weekly release of 500 or 1,000 *T. pretiosum* over an 11 week period resulted in overall suppression of *Cadra cautella* (Walker) at 12.5 and 34.7%, respectively, and of *Plodia interpunctella* (Hübner) at 11.2 and 16.6%, respectively (Brower 1988). The author concluded that these results were promising, but releases should be made prior to the emergence of a pest species.

The relatively low levels of parasitism generated within the release sites may be a result of critical factors from either pre- or post release periods. Production of *Trichogramma* by commercial preparation could result in a significant proportion of 'inferior wasps' unable to locate and parasitize host eggs. Post release factors could include predation of the host eggs by spiders, ants, and other generalist feeders within the bogs, limiting survival of the emergent wasps (Hohmann et al. 1988). Additionally, various fungicides, including copper hydroxide, chlorothalonil, or tribasic copper sulfate are applied as a prophylactic cover spray against several fruit pathogens during the fruiting and developmental period. As such, these compounds could have interfered with the newly eclosed adult *Trichogramma*. Another complicating factor in this release program was the presence of other lepidopteran pests, such as *S. sulfureana*, which feed externally on cranberries during and after bud development. Application of an insecticide (such as carbaryl, azinphos-methyl or chlorpyrifos) is necessary for control when populations of this pest require attention. This treatment could subsequently interfere with *T. pretiosum* released during the *A. vaccinii* egg period.

The higher rate of cumulative parasitism noted in the neglected sites, however, warrants further study. Although the size disparity of neglected and release bogs cannot be dismissed, parasitism generated by the naturally-occuring *T. pretiosum* strain which may have evolved to local environmental conditions, and to the biology of *A. vaccinii*, should receive further attention.

In light of the current IPM insect-pest threshold (e.g., one *A. vaccinii* egg
noted on a sampling of 25 cranberries per ha, the parasitism generated during the season by either the low or high release level would not provide the degree of suppression required to eliminate even a single insecticide application. It thus appears unlikely that an inundative release of *T. pretiosum* will suppress *A. vaccinii* populations to tolerable levels.

**ACKNOWLEDGMENTS**

This work was supported by the Massachusetts Department of Food and Agriculture. Statistical assistance was provided by Barton Matsumoto, and field planning and consultation was provided by Sherri Roberts and Pamela Moran. Great appreciation is extended to cooperating cranberry growers, including John C. Decas, Jack Angley, John Alden, Mary Lou Piscatelli, Paul Piscatelli, Clark Griffith, Willard Rhodes and Dave Engstrom for providing valuable cranberry acreage. William Kauffman (USDA-APHIS) reviewed an earlier draft, and my thanks are extended to him.

**LITERATURE CITED**


The habitats and host plants of buckmoths (Hemileuca: Saturniidae: Hemileucinae) in Michigan are described and compared to those of the three species known from eastern North America, *H. maia*, *H. nevadensis*, and *H. lucina*. Michigan populations show variation in host plant and habitat use spanning the entire range of all three species. The presence of transitional phenotypes and the host plant and habitat data suggest that Michigan populations are a single, variable species. These things combined with the intermediate geographical location of Michigan’s populations call into question the taxonomic distinctness of the three eastern buckmoth species.

The genus *Hemileuca*, with 30 currently recognized species in North America and Mexico, is most diverse in Mexico and the southwestern United States (Seitz 1929, Ferguson 1971, Tuskes 1978, Peigler 1985, Peigler and Stone 1989, Lemaire 1993). Females lay large batches of eggs on host plants and early instar larvae feed in aggregations. Host plant choice varies widely with species, including many plant families and genera (Stone 1991). Populations occur in habitats ranging from dry prairies and upland oak woods to wet meadows and soggy fens (Ferguson 1971, pers. obs.).

All populations occurring in Michigan, as well as the rest of eastern North America, are day-fliers and members of the *maia* group. As traditionally understood, this group consists of three species: (1) *Hemileuca maia* (Drury), occurring over much of the eastern United States from Illinois south to Louisiana and Florida and east to Massachusetts, (2) *H. lucina* Hy. Edw., in the northeast from Maine to Massachusetts [Ferguson (1971) indicated possibly northern Michigan also], and (3) *H. nevadensis* Stretch, throughout western North America and Canada, east in the north to Minnesota and Wisconsin. *Hemileuca maia* has generally been recorded as an oak feeder, *lucina* as a meadowsweet feeder and *nevadensis* as a willow feeder (Ferguson 1971).

Michigan populations of *Hemileuca* are of interest for several reasons. In addition to being located geographically between known populations of *nevadensis* and *maia*, buckmoth populations in Michigan appear to show a variety of phenotypes ranging from types similar to Minnesota and Wisconsin *nevadensis* to others virtually indistinguishable from typical *maia* (pers. obs.). The existence of extensive populations in the Upper Peninsula that very closely resemble *lucina* adds an additional complication. The host plants of Michigan populations of *Hemileuca* have not been well documented, but historical variation in host use suggests a single species.
records from nearby Illinois and Wisconsin suggest an association with willow wetlands (Riley 1873, Worthington 1878, Ely 1954), and records from southern Ohio indicate an upland, oak woodland habitat (Metzler 1980, pers. obs.).

Our objectives in this study were to (1) determine the occurrence and distribution of *Hemileuca* populations in Michigan, (2) document the habitat and host plant associations of the Michigan populations, and (3) compare these associations with those of the described species.

**METHODS**

A check of museum records at The University of Michigan and Michigan State University revealed a paucity of known localities for *Hemileuca* in Michigan. In order to better document the range and variation of *Hemileuca* in Michigan, we traveled over much of the state to locate populations. Our fieldwork was concentrated in the spring and fall each year from 1987 to 1990. During the spring, populations were easily located by driving through appropriate habitats and spotting the large, black masses of larvae feeding after hatching from the egg rings. During fall, populations were located by observing adults flying during the day in potential habitats. This endeavor was supplemented by having caged females emitting pheromone to attract males. These females were either reared from larvae collected as early instars, or captured before mating in known populations. Females could be used for several days if not allowed to mate and kept refrigerated in a humid environment between uses.

For several populations, scattered over the range of buckmoths in Michigan, we recorded information about habitats and host plants. These were located in Schoolcraft Co. in the Upper Peninsula, Roscommon Co. in the upper-middle of the Lower Peninsula, and Washtenaw and Monroe Cos. in the southeastern part of the Lower Peninsula. In addition we compared these populations to ones in Vinton Co., Ohio and outside of Ottawa, Ontario as well as to published accounts of the habitats and host plants for the three described species. Voucher specimens for these populations have been deposited in the collections at the University of Michigan (UMMZ) and the Canadian National Collection (CNC) with additional specimens retained in the authors' collections.

At each locality we made notes on habitat, including topography, moisture conditions, and dominant plant species. Where possible we recorded data on both primary (oviposition) and secondary (used by larvae, but not used for oviposition) host plants. Primary hosts were identified either by finding egg rings during the winter, or more commonly by spotting masses of feeding larvae in the spring and then locating the egg ring from which they emerged (generally only a few feet away). Secondary hosts were documented when late instar larvae were found feeding on them (with no oviposition record) or when a larval mass was located on a plant species other than that on which the adjacent egg mass was located (given that the egg mass was on a known larval host, as occasionally egg masses are laid on dead stems or stems of non-hosts near the actual host). We also recorded behavioral observations on female emergence and mating.
RESULTS

To our knowledge, at the start of the study, buckmoths were known from only 6 counties in the Lower Peninsula (Moore 1955) and one record from the Upper Peninsula (Voss 1969, Ferguson 1971). During our work we added 10 new county records and documented the extensive distribution of buckmoths across the state, including both peninsulas. Figure 1 shows the present known distribution of *Hemileuca* in Michigan by county. The western section of the Upper Peninsula was not explored. The paucity of records in the upper part of the Lower Peninsula cannot be ascribed to lack of surveying; we made many efforts to locate populations in several counties of this area during the spring and fall. This area seems to have extensive areas of appropriate habitat without buckmoth populations. Buckmoths probably occur in every county in the middle and southern parts of the Lower Peninsula.

The range of variation in the habitats and host plants used by *Hemileuca* in Michigan is much more extensive than previous accounts of these buckmoths would indicate. This host diversity is illustrated by describing the habitats and host plants of the four main study populations (Washtenaw, Monroe, Roscommon, and Schoolcraft Cos.) in addition to the Ohio (Vinton
Table 1. Primary host plants of *Hemileuca* populations in this study.

<table>
<thead>
<tr>
<th>Site</th>
<th>Known Primary Hosts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Washtenaw Co. 1</td>
<td><em>Salix petiolaris</em>, <em>S. discolor</em>, <em>S. bebbiana</em>, <em>Spiraea alba</em></td>
</tr>
<tr>
<td>Washtenaw Co. 2</td>
<td><em>Salix exigua</em></td>
</tr>
<tr>
<td>Monroe Co.</td>
<td><em>Populus deltoides</em>, <em>P. tremuloides</em>, <em>S. discolor</em>, <em>S. exigua</em>, <em>S. undet.</em></td>
</tr>
<tr>
<td>Roscommon Co.</td>
<td><em>Salix petiolaris</em>, <em>S. undet.</em>, <em>Spiraea alba</em></td>
</tr>
<tr>
<td>Schoolcraft Co.</td>
<td><em>Betula pumila</em>, <em>Salix petiolaris</em>, <em>S. pedicellaris</em>, <em>S. serrissima</em>, <em>S. candida</em></td>
</tr>
<tr>
<td>Vinton Co., OH</td>
<td><em>Quercus</em> (black oak group)</td>
</tr>
<tr>
<td>Ottawa, Onto</td>
<td><em>Menyanthes trifoliata</em></td>
</tr>
</tbody>
</table>

Co.) and Ottawa (Ontario, Canada) populations. Data on the host plants of our study populations is summarized in table 1.

**Washtenaw County**

Two populations in northwest Washtenaw County were extensively studied during our work. Site 1 is a fen dominated around the periphery by grasses and sedges, grading into a tamarack bog in the center. It is located on Roe Rd. in Section 19 of Lyndon Twp. Buckmoths fly over this entire area, but concentrate oviposition at the edge of the wooded area where willows (*Salix* spp.; *Salicaceae*), meadowsweet (*Spiraea alba*; *Rosaceae*) and bog birch (*Betula pumila*; *Betulaceae*) are the dominant woody vegetation.

Flight records at this locality are from 24 September to 29 October, with the peak flight during the second week of October. Long term monitoring of this population by Wagner indicates that population levels fluctuate considerably from year to year.

The documented oviposition hosts at this site are almost exclusively willows (*Salix petiolaris*, *S. discolor*, and *S. bebbiana*) with only a single egg ring found on *Spiraea alba* over a period of 3 years. Two plant species present, but not used as host plants at this site, *Betula pumila* (bog birch) and *Menyanthes trifoliata* (bog buckbean; *Gentianaceae*), are used as primary hosts in other populations.

Site 2 in Washtenaw County occurs on the rights of way on both sides of the Freer Rd. overpass on Interstate 94, and the area adjacent to a nearby farm pond. Most of this area is willow wetland, some spots being dry and others having standing water nearly year-round. The dominant plants are sedges (*Carex* and *Scirpus* spp.) and cattails (*Typha* spp.) in the wettest sections and willows as the habitat grades into drier areas.

The flight period is virtually identical to the site 1 population, with records of adults from 5 to 16 October. In 1988 we found more than 20 egg rings during a one-day, winter search of the habitat. We returned the next spring to check on these flagged egg masses and found additional ones had gone undetected until the emergence of the larvae. Populations at this site also seem to fluctuate, although we have records only from the years of our study.

The only documented oviposition host at site 2 is also a willow (*Salix exigua*). An additional possibility is *Spiraea*, but only a small number of plants are present in the habitat.
Monroe County

In the Petersburg State Game Area, a population of buckmoths occurs on a much drier site than those in Washtenaw County. The different moisture conditions here may be partly a result of the channeling of the water courses, and there may have been more extensive wetlands in the past. However, now the habitat is dominated by small quaking aspens (Populus tremuloides) and cottonwood (P. deltoides)(Salicaceae), upland willows and other shrubs interspersed with grassy areas and cultivated fields.

Flight times at this site are similar to those of the Washtenaw County localities. The earliest recorded adult flight date is 20 September and the latest 24 October. We flagged 2 egg rings during the winter of 1988 and located 7 additional larval masses the following spring during a quick search. M. C. Nielsen (pers. comm.) and other collectors with experience in the area note that the population size has apparently dropped in recent years, perhaps due to the changing successional age of most of the habitat. Other lepidopteran species that occur on the remnant prairie habitats in the game area have also declined in numbers, and some may now be extirpated (e.g. the butterflies Lycaeides melissa and Incisalia irus, both Lycaenidae). Management of these areas using carefully prescribed burns might reverse this trend.

We recorded Populus deltoides, P. tremuloides, Salix discolor, S. exigua, and an undetermined Salix as the primary larval hosts at this site. On occasion each of these may be used as a secondary host because the branches often grow intertwined and at least one larval mass was found feeding on Populus and Salix simultaneously. Although not abundant in the area, Spiraea and possibly Quercus are potential host plants.

Roscommon County

The habitat in Roscommon County, near Houghton Lake (and extending into adjacent Clare County), consists of extensive willow-meadowsweet wetlands with sedges as the dominant graminoids. Here, virtually the entire habitat has standing water or waterlogged soil throughout the year and is fairly uniform in its composition. At the margins of the wetland the habitat grades into aspen woods.

Adults fly at this locality from the beginning of September almost through the end of the month with the main flight during about the second week of the month. The population in Roscommon County is consistently very large and certainly numbers in the thousands each year. On a suitable fall day hundreds of buckmoths can be seen flying over the habitat.

Both willows (Salix petiolaris and an undetermined Salix) and meadowsweet (Spiraea alba) are used as primary hosts in the habitat, and both are abundant at the site. During one census on 21 May 1988 we counted early instar larval masses in a small area of the habitat and recorded 25 on willow and 3 on meadowsweet. In the main habitat these appear to be the only host genera, but Populus bordering the wetland may be used also. Buckmoths were frequently seen entering and leaving the wooded area, although no egg rings or larval masses were located on aspen.

Schoolcraft County

Although one record of two adult specimens from Manistique exists (Ferguson 1971), the populations in the Upper Peninsula were not relocated until 1987–88. At this time specimens were presented to Wagner for identifi-
cation by colleagues who had been birding early in the fall. He visited the locality shortly thereafter and found extensive buckmoth populations. The previous summer, a larva had been given to Scholtens by Dr. Barbara Madsen, who related that this species was abundant at her Upper Peninsula field site, and seemed to be eating mainly bog birch (*Betula pumila*). The larva completed development on paper birch (*Betula papyrifera*), pupated, overwintered, and emerged the following summer, simultaneous with Wagner’s investigation of the Upper Peninsula buckmoth populations.

The populations in Schoolcraft and Luce Counties in the Upper Peninsula are probably the most extensive in the state, due in large part to the great expanse of available habitat (thousands of acres), much of it inaccessible. Madsen’s field site, for example, is reached by a long hike through wetlands. Much of our work was done at or near Seney National Wildlife Refuge where populations are readily accessible.

The habitat comprises willow-bog birch-alder wetlands broken by sandy ridges, which are forested primarily with pines. The dominant graminoids are sedges, with grasses on the drier areas. These wetlands are permanently soggy, generally with standing water. Wetlands similar to this are found throughout much of the central part of the Upper Peninsula.

At these sites buckmoths fly from mid-August through mid-September, with peak flight during about the first week of September. The population sizes at these sites are comparable to or larger than those at the Roscommon County site, and flights of hundreds of individuals can be observed on even minimally warm (16°–18°C), sunny days.

Both willows and bog birch are used extensively as primary hosts in these habitats. On 9 June 1988 Wagner recorded host plants for larval masses located in one section of Seney National Wildlife Refuge. This count indicated that the two host genera are almost equally used by *Hemileuca* at this site, with 10 masses found on *Betula pumila*, 4 on *Salix petiolaris*, 1 on *S. pedicellaris*, 1 on *S. serrissima*, and 2 on an undetermined *Salix*. Subsequently we located a larval mass on *S. candida*. During this visit, Wagner specifically noted that no larvae were found on *Alnus rugosa* (Betulaceae) (abundant in the habitat), *Spiraea alba* (frequent), *Spiraea tomentosa* (occasional), *Rubus* sp. (Rosaceae) (occasional), or *Potentilla fruticosa* (Rosaceae) (occasional). By 17 June 1988, larvae had dispersed and few were in groups of more than two. They remained most abundant on *Betula* and *Salix*, but a few were found on *Spiraea*, *Vaccinium* (Ericaceae) (on sandy upland), or even grasses. Feeding on these plants was not specifically noted, and larvae may simply have been wandering to locate a pupation site. At appropriate sites in these habitats, either *Spiraea* or *Menyanthes* might be possible alternative hosts.

**H. maia** population from Vinton Co., Ohio

The habitat at this site is an upland, primarily oak woodland. The understory consists of typical deciduous woodland shrubs, notably lacking in willow and spiraeas.

Adults fly at this locality from mid-October through early November. We examined the population on 27 October 1989. In this year the population was very large. During one afternoon, we easily saw several hundred adult buckmoths, and we stopped our search before the afternoon flight ended. Local Ohio collectors report significant fluctuation in the population size from year to year, similar to that seen in some southern Michigan populations (Metzler pers. comm.).

Because we were present only during the adult flight season, we did not
directly observe egg rings or larval masses on host plants. The presumed hosts are oaks in the black oak group, and *Quercus* (Fagaceae) is apparently the only known host genus present in numbers at the site.

We have not located any Michigan populations of *Hemileuca* on sites similar to that in Vinton Co., OH. However, Nielsen reared adults collected from larvae found on black oak in the Barry State Game Area (Barry Co.) in 1969. We revisited this site, which is dominated by oaks on sandy, upland soil, but did not relocate an oak-feeding population.

**Hemileuca** population near Ottawa, Ontario

With the help of Dr. J. Donald Lafontaine at the Canadian National Collection, Scholtens was able to examine two sites near Ottawa during the fall of 1990. Both of these localities are wet fens characterized by graminoids with very little shrubby growth. Sedges dominate much of the habitat, most of the mat consisting of *Carex lasiocarpa* with *Scirpus* also common. At the larger of the two sites, Richmond Fen, the grass *Phragmites* is a significant component. *Thuja* and *Larix* are both present as small trees on the mat. The main shrubs of the habitat are *Betula pumila* (found near the margins) and *Myrica gale* (in hummocks throughout), with only a small amount of *Salix candida* and 1 undetermined *Salix*.

The flight period at these sites is from about mid-September through early October. According to Lafontaine, populations at these sites, especially the second, can be very large. We visited on 3 and 4 October 1990, near the end of the flight period.

The host plant at these localities is bog buckbean, *Menyanthes trifoliata*. Females are apparently unable to locate foliage of the host itself when ovipositing because it has already senesced. This was the case during the trip of 1990. Instead, females search for sturdy stems of grass or sedge, often *Carex*, and place egg rings on these. Upon hatching in the spring, larvae then locate newly flushed plants of buckbean (Lafontaine, pers. comm.). A similar population is known from New York (R. Dirig and J. Cryan, pers. comm.), and M. Nielsen and L. Ferge (pers. comm.) found larvae in a Wisconsin population feeding on buckbean and willow, with the egg ring on a nearby sedge stem. At Richmond Fen, the willows and bog birches present at the periphery of the habitat may be used as primary or secondary hosts on occasion, but neither has been recorded at this locality as a host (Lafontaine, pers. comm.).

**Behavioral Observations**

During the course of our fieldwork we observed emergence and mating behaviors of buckmoths at the main study sites, primarily in Schoolcraft and Roscommon Counties where populations are largest.

On most days during the flight season, night and early morning temperatures are cool or cold, and buckmoths do not become active until late morning. Activity is first indicated by males flying over the habitat in the typical straight-line flight. Females are often found emerging and expanding their wings at the margins of the wet areas of the habitat, just onto higher ground. Mating follows emergence very closely, often occurring before the female’s wings are completely expanded. Emerging females are easily located by watching males follow pheromone trails and tracing their path to the female. Flights by females are observed later in the day, usually in mid-to late afternoon.
We often attracted male buckmoths using unmated females that were reared or captured before mating. We found that Roscommon County females would easily attract both Schoolcraft and Washtenaw County males. Females from other sites were not available at appropriate times to test the reciprocal attraction in each case. Washtenaw County females were taken to Vinton Co., OH, but apparently did not attract males from this population; none were seen approaching and hovering around the cage as they did at other sites.

Although buckmoths are quite apparent during their flight season, we observed only one act of predation (and saw no other attempts), when a dragonfly (*Aeshna* sp.: *Aeshnidae*) took a male buckmoth on the wing at the Schoolcraft Co. site.

**DISCUSSION**

The distribution of buckmoths in Michigan is much more widespread than previously believed (Fig. 1). Populations are most common in the southern part of the Lower Peninsula, but the largest populations occur in the central part of the Lower Peninsula and the Upper Peninsula. In Michigan, populations apparently can occur wherever there are sufficient wetlands of an appropriate type. One exception to this is the unexplained paucity of records from the upper Lower Peninsula. We suspect that few records existed for buckmoths before our study primarily because of the late flight season of these moths. Most lepidopterists have hung up their nets by the time *Hemileuca* is on the wing. Even though the larval masses are very conspicuous, only a few lepidopterists spend time rearing larvae, and the buckmoth larvae may often be passed over as those of the similar appearing Mourning Cloak (*Nymphalis antiopa*; *Nymphalidae*) (Ferguson 1971, pers. obs.).

*Hemileuca* populations in Michigan span nearly the entire range of host plants and habitats previously attributed to the three described species of the *maia* group. For these three species, host plant and habitat specialization has been regarded as a significant factor isolating the species (Ferguson 1971). *Spiraea*, the reported host plant of *H. lucina*, is used in the Roscommon population side by side with *Salix*, the main host plant of the western *H. nevadensis*. In addition, *Populus* and *Betula*, a newly reported host, are also commonly used by at least some populations. Of the host plants of the three described species, *Quercus*, that of *H. maia*, was the only one not documented during the course of our study. This is despite the fact that the populations in Michigan have traditionally been labelled *H. maia*. Even for oak, a record exists documenting its use in Michigan. The recently discovered populations in New York and Ontario that feed on *Menyanthes* add additional complications, and the discovery of Wisconsin larvae on this same host suggests that this association may also be more widespread.

Although there is no obvious link between the known host genera, one possibility is the presence of phenolic glycosides as secondary chemicals. Some species of *Salix*, *Populus*, and *Betula* are known to contain these chemicals (Palo 1984, Rowell-Rahier and Pasteels 1990), but we are presently unaware of their occurrence in *Quercus*, *Spiraea*, and *Menyanthes*. Other insect herbivores are known to specialize on plants containing these chemicals (Rowell-Rahier 1984, Lindroth et al. 1988), and some make use of them for their own protection (Pasteels et al. 1988), an interesting possibility for *Hemileuca* considering its bold, black and white markings. Even if no secondary chemical link can be found among the host plants, the wide diet breadth would not be unexpected when compared to other members of the Saturniidae, which
are often oligophagous feeders on woody plants (Covell 1984, Stone 1991, Tietz 1972).

The habitats in which buckmoths occur in Michigan are most similar to those described for nevadensis or lucina (Fergusen 1971, Covell 1984). Both often occur in wetlands, where their host plants can be found in abundance. Drier habitats, such as those used by typical H. maia, are not entirely excluded from the known sites (e.g. Monroe Co. or, historically, Barry Co.), but, at least in Michigan, they are not as common.

Michigan's buckmoth populations are a puzzle when trying to apply the nomenclature now attached to the three described species in the maia group. These three taxa have been treated as distinct species because of differences in maculation, geographically separated ranges, and divergence in habitat and host plant use (Ferguson 1971). Michigan's populations, historically identified as H. maia (and perhaps H. lucina in the Upper Peninsula), are now known to span most of the gaps between the three described species. In habitat use they most resemble nevadensis and lucina, being found primarily in wetlands. The primary hosts used by these populations include those normally associated with nevadensis (willow and aspen), lucina (meadowsweet), and an historical record includes the typical host of maia (oak). In addition they use the newly reported host, bog birch.

The maculation of Michigan buckmoth populations also spans nearly the entire range of known variation in the three species (Scholtens and Wagner in review). Populations in the southern Lower Peninsula are indistinguishable from more southern or eastern populations of maia, with relatively narrow white bands on dark black, heavily-scaled wings. Those in the Upper Peninsula show only slight differences from typical northeastern populations of lucina, with a somewhat wider white band than typical maia and extremely glassy wings due to smaller, less dense scales (Scholtens and Wagner in review). Populations in the central part of the Lower Peninsula are intermediate between these two extremes in both respects. All populations, however, show a significant amount of variation, and within any one population individuals can be found that very closely match phenotypes typical of other populations. Some individuals even have white bands that approach the extreme width of typical nevadensis, and Roscommon County individuals strongly resemble specimens identified as nevadensis from northwestern Wisconsin and Minnesota (Scholtens and Wagner pers. obs.).

Several possible taxonomic alternatives exist for the Michigan populations. Phenotypically, the three main geographic areas of our study could easily be viewed as different entities, the southernmost fitting nicely into descriptions of maia and the northernmost matching lucina, but our findings on host plant and habitat use as well as the clinical nature of the variation in maculation (Scholtens and Wagner in review) argue against these populations being separate taxonomic entities. Unlike the traditional belief, the habitats and host plants of buckmoth populations may be combined in various ways, depending on the available hosts.

Michigan populations also lie geographically between at least two of the described species ranges, those of nevadensis and maia, in an area where transitions between known phenotypes would be expected to occur. Because all buckmoths have very similar genitalia (but see Ferguson 1971, for possible differences in the genitalia of lucina), this often reliable character is of little help in determining if these populations are taxonomically distinct.

Ultimately, interbreeding and producing viable offspring would be the most convincing argument against separate species, but at this time data of this sort are unavailable. Previous work with buckmoths indicates that cross attraction and interbreeding is indeed possible and hybrids can be produced (Peigler and Williams 1984). The presumed geographic barrier separating the
phenotypically distinct populations is not present in Michigan. All populations in Michigan appear to be capable of genetic exchange with other, phenotypically different populations. Further work relating these populations to others in North America should resolve the status of what name to apply to Michigan's buckmoths.

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David Bay, John Cryan, Robert Dirig, Les Ferge, J. Donald Lafontaine, Barbara Madsen, Robert Masta, Eric Metzler, Mogens Nielsen, Barry O'Connor, and Heidi Appel all contributed in important ways to the completion of the project.

LITERATURE CITED


Scholtens, B. G. and W. H. Wagner, Jr. (in review). An example of clinal variation in eastern North American buckmoths (Saturniidae: *Hemileuca*).


RELATIONSHIPS OF THE GENERA ACANTHAMETROPUS, ANALETRIS, AND SIPHLURISCUS, AND RE-EVALUATION OF THEIR HIGHER CLASSIFICATION (EPHEMEROPTERA: PISCIFORMA)

W. P. McCafferty and T-Q. Wang

ABSTRACT

The historical higher classification of the genera Acanthametropus Tshernova, Analetris Edmunds, and Siphluriscus Ulmer is reviewed. The first comprehensive generic description of Siphluriscus is given, and first figures of wings are provided. A cladistic analysis of adult and larval characters of Acanthametropus and Analetris, and adult characters of Siphluriscus reveal a close relationship between the former two genera, which represent a well-defined clade based on five identified synapomorphies; however, Siphluriscus, which has been classified with them in the past, does not share any apomorphies with them but instead shares apomorphies with the genera of Siphlonuridae sensu stricto. Acanthametropus and Analetris are recombined in the family Acanthametropodidae, suppressing Analetrididae; and Siphluriscus is reassigned to the family Siphlonuridae sensu stricto, although taxon rank for both of these clades is still tentative and awaits comparative cladistic analysis of the entire suborder Pisciforma. The relationship to each other of these clades also remains in doubt. Stackelbergisca Tshernova, a fossil genus formerly classified with the three extant genera apparently does not share any of the 11 apomorphies used in this study, and is placed as family incertae within the Pisciforma.

The relationships and classification of the pisciform mayflies Acanthametropus pecatonica (Burks) from North America, Acanthametropus nikolskyi Tshernova from eastern Russia, Analetris eximia Edmunds from western North America, and Siphluriscus chinensis Ulmer from China have been tentative in the past. We have restudied all known stages of each of these species and are here able to offer a first cladistic analysis of the represented genera within the framework of other pisciform mayflies.

Ulmer (1920) appropriately placed his Siphluriscus genus, which was and still is based on alate stages only, in the family Siphlonuridae sensu lato. Little could be ascertained with respect to its relationships within Siphlonuridae at that time.

Tshernova (1948) described Acanthametropus from larvae from the Amur Basin and placed it in the family Ametropodidae. Burks (1953) independently discovered larvae of Acanthametropus in Illinois, named them Metreturus and also believed this taxon was related to other psammophilous mayflies, such as Ametropus Albarda. Edmunds and Traver (1954) removed Metreturus to Siphlonuridae sensu lato, and Edmunds and Allen (1957) synonymized

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Metreturus with Acanthametropus. Edmunds et al. (1963) created a separate subfamily Acanthametropodinae for the genus. Tshernova et al. (1986) showed that a previous adult description of Isonychia polita Bajkova (1970) was actually of the adult of Acanthametropus. We have confirmed this association. McCafferty (1991a) compared larvae in the Eastern and Western Hemispheres and confirmed that there were two distinct species of Acanthametropus.

Edmunds in Edmunds and Koss (1972) described Analetris based on larvae and placed it in the subfamily Acanthametropodinae. Demoulin (1974), while recognizing Acanthametropus and Analetris in separate subfamilies (erecting the subfamily Analetridinae), could not place Siphluriscus and Stackelbergisca to any subfamily with any certainty. Edmunds et al. (1976) restated the broad concept of Acanthametropodinae, and suggested a strong possibility that Acanthametropus could prove to represent the larval stage of Siphluriscus. This is definitely not the case based on our examination and comparison of Siphluriscus adults (see below).

Families of pisciform mayflies have become more restricted in recent years (see e.g. Campbell 1988, McCafferty 1991c), basically recognizing previous subfamilies of Siphlonuridae sensu lato at the family level. Much of this is related to the hypothesis of McCafferty and Edmunds (1979) that Siphlonuridae sensu lato is, to a large extent, polyphyletic and that a number of lineages within it share apomorphies with other more derived lineages of Ephemeroptera [although some extreme splitting of families can be traced to Riek (1973)]. This hypothesis has since been corroborated cladistically for certain of these previous subfamilies. For example, Coloburiscidae and Isonychiidae (previous subfamilies of Siphlonuridae sensu lato) were shown by McCafferty (1991b) to be in sequential ancestral positions of a major lineage including the Oligoneuriidae and Heptageniidae, and Oniscigastriidae (another previous subfamily of Siphlonuridae sensu lato) appears to be at the base of the suborder Rectracheata (see Landa and Soldán 1985, McCafferty 1991b). Edmunds (see e.g. Edmunds 1973) has long realized the close relationship of the Siphlaenigmatidae (another previous subfamily of Siphlonuridae sensu lato) with the family Baetidae.

McCafferty (1991c), as part of this move to recognize all of the separate lineages represented by Siphlonuridae sensu lato, provisionally recognized families Acanthametropodidae and Analetrididae among several others in the Pisciforma. This particular classification was based on presumed rather than demonstrated cladistic data. We have now discovered data, however, that allow us to resolve cladistically the relationships among the genera Acanthametropus, Analetris, and Siphluriscus. We are publishing this data and analysis at this time at the prompting of co-workers, such as R. D. Waltz, who are preparing keys and synopses of higher taxa of Ephemeroptera and need to know, for example, if the North American genera Acanthametropus and Analetris will fall to the same or separate families.

The only existing description of Siphluriscus was the original by Ulmer (1920). Unfortunately, it did not include characters that we now know are important for comparative generic and cladistic purposes. The concurrent description of S. chinensis Ulmer, the only species known in the genus, was also incomplete. In addition, very important wing venation characteristics were not figured by Ulmer. Therefore we acquired the original, and, to our knowledge, the only material of Siphluriscus from the Berlin Museum and give a description of Siphluriscus based on characters of use in generic level

delineation. This is followed by a cladistic analysis of the three genera. We conclude with a short discussion of the classificatory implications of our analysis.

*Siphluriscus* Ulmer  
*Siphluriscus chinensis* Ulmer, 1920

*Siphluriscus chinensis* Ulmer, 1920:62.  
Syntypes. China, Tsayin San (Tsayin Mountains), S. V. Mell. Berlin Museum. Male adult syntype here designated LECTOTYPE (blue label); one male adult and two male subimagos, same data, designated PARALECTOTYPES. A folded brown label accompanying a specimen reads in part “Aug 10.” This may be a collecting date, but no year is indicated, and other writing on the labels is indecipherable.  
Male Adult. Body length, excluding terminal filaments: ca. 18mm. Forewing length ca. 20mm. Hindwing length ca. 12mm.  
Head: Median ocellus with lateral and hind margins elevated. Frontal aspect of head capsule slightly shorter in length than forecoxae. Thorax: Pronotum emarginate posteriorly. All sterna lacking spines and spine vestiges. Forewings (Fig. 1) without stigmatic anastomoses, with 10-15 parallel cross-veins directly connecting CuA and hind margin. Anal margin of forewings extending ca. one half the length of the wings. Hindwings (Fig. 2) relatively long (ca. one half length of forewings), with MA and MP forked in basal half of wings (note that the hindwing shown in Fig. 2 is drawn from the pinned type specimen without mounting; the hind margin is actually smooth not scalloped or sinuate as it appears in the drawing—that being an artifact of the dried wing). Forefemora each with two blunt projections at exterior apex and only slightly longer than foretibiae (ratio 17:15). Relative ordered length of foretarsal segments (from longest to shortest): 2-3-1-4-5. Relative ordered length of
hindtarsal segments (from longest to shortest): 1–2–5–3–4; segment 1 partially fused with tibia. Claws all similar and sharp. *Abdomen:* Abdomen lacking dorsal and ventral tubercles, armature, or vestiges of such. Median terminal filament short, but slightly longer than abdominal terga 8, 9, and 10 combined. Genitalia (Fig. 3): Forceps with two short terminal segments. Subgenital plate deeply concave. Penes furcate medially.

**Male Subimago** (pinned). Similar to adult, except frontal head capsule subequal to forecoxae, ordered length of foretarsal segments 1–2–3–5–4, and genital forceps with only one short terminal segment.

**PHYLOGENY**

In order to determine the possible relationships of *Acanthametropus, Analetris, and Siphluriscus*, our OTU’s analyzed were *Acanthametropus, Analetris, Siphluriscus*, and also other genera of Siphlonuridae sensu stricto lumped together (*Dipteromimus* McLachlan, *Edmundsius* Day, *Parameletus* Bengtsson, *Siphlonisca* Needham, and *Siphlonurus* Eaton), so that all elements of the problematic higher taxa under consideration were represented. Our outgroup for establishing character state polarity consisted of non-*Acanthametropodidae* and non-*Siphlonuridae* sensu stricto Pisciforma, including all extant genera listed as Baetoidea and Heptagenioidea by Hubbard (1990). These taxa essentially represent all mayflies that have been associated phylogenetically with the OTU’s. Details of the numbered characters used for cladistic analysis and appearing on Fig. 4 are given in Table 1, where both the apomorphic and comparative plesiomorphic states are described.
Table 1. Characters used in cladistic analysis of Acanthametropus, Analetris, and Siphluriscus (see Fig. 4).

<table>
<thead>
<tr>
<th>Apomorphy</th>
<th>Plesiomorphy</th>
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</thead>
<tbody>
<tr>
<td>1. Prosternum with spine (larva) or spine vestige (adult).</td>
<td>- Prosternum without spine.</td>
</tr>
<tr>
<td>2. Claws longer than tibiae (larva)</td>
<td>- Claws shorter than tibiae.</td>
</tr>
<tr>
<td>3. Forefemora 2X foretibiae length (male adult).</td>
<td>- Forefemora less than 2X foretibiae length.</td>
</tr>
<tr>
<td>4. Penes fused medially.</td>
<td>- Penes more-or-less furcated.</td>
</tr>
<tr>
<td>5. Forewings with cubital field short (less than half length of anal margin), with short series of somewhat anastomose veinlets.</td>
<td>- Forewings with cubital field long (one half or more length of anal margin), with long series of simple or forked veinlets.</td>
</tr>
<tr>
<td>6. At least mid- and hindclaws similar, sharp (adult).</td>
<td>- All claws dissimilar, one blunt, one sharp.</td>
</tr>
<tr>
<td>7. Median terminal filament reduced (adult).</td>
<td>- Median terminal filament well developed.</td>
</tr>
<tr>
<td>9. Clypeus minute and triangular.</td>
<td>- Clypeus transverse.</td>
</tr>
<tr>
<td>10. Hindwing with MA forked in basal half of wing.</td>
<td>- Hindwing with MA forked at mid-length or beyond.</td>
</tr>
<tr>
<td>11. Forewing with MP stem connected to CuA by one or more crossveins.</td>
<td>- Forewing with MP stem not connected to CuA by crossveins.</td>
</tr>
</tbody>
</table>

Two unconnected clades (Fig. 4) are indicated by our cladistic analysis. Synapomorphies used to deduce these clades within the Pisciforma are indicated as numbers on the stems of the respective clades. Selected autapomorphies are also indicated for informational purposes on the terminal branches. As can be seen, Acanthametropus and Analetris share at least five significant synapomorphies, including both adult and larval characters. Since these apomorphies are not shared by other Ephemeroptera, they clearly indicate a close relationship between the two genera, as has always been hypothesized on phenetic grounds by Edmunds (see e.g. Edmunds and Koss 1972). Siphluriscus, which has been grouped with latter genera in the past, does not share apomorphies with those genera, but instead shares apomorphies with the genera of Siphlonuridae sensu stricto (see OTU description above).

No apomorphies used in this study connect the two indicated clades, and therefore we have no evidence that they represent sister groups, and we have not arbitrarily connected them in Fig. 4. Only a more exhaustive cladistic analysis of the entire Pisciforma will resolve their exact relationships.

The fossil genus Stackelbergisca cannot be placed to either clade based on its available adult and larval characteristics (see Tshernova 1948). Despite our attempts, we were unable to borrow any material of Stackelbergisca for comparative analysis. However, based on figured forewing venation and larval legs, it apparently does not share forewing apomorphies (see character 5, Table 1) or larval claw apomorphies (see character 2, Table 1) with the Acanthametropus-Analetris clade. It does appear to possess plesiomorphies common in various lineages of the Pisciforma, which are of no aid in cladistic analysis. Unfortunately, it appears from published figures that basal forewing venation is somewhat obscured in the fossil, and thus we cannot decipher whether crossveins are connecting the stem of MP with CuA, a characteristic we propose as an apomorphy that may define at least one branch of the
Siphluriscus—Siphlonuridae sensu stricto clade (see character 11, Table 1 and Fig. 4). In essence, with respect to Stackelbergisca, we cannot find any of the apomorphies indicated in Table 1.

CLASSIFICATION

Based on our phylogenetic findings, we suggest that the genera Acanthametropus and Analetris be recombined in the family Acanthametropodidae. We also suggest that the genus Siphluriscus be replaced in the family Siphlonuridae sensu stricto. The fossil genus Stackelbergisca cannot be placed to any family with any confidence and thus is placed in family incertae at this time, although it is without a doubt a member of the Pisciforma.

In addition to not knowing at this time if Acanthametropodidae and Siphlonuridae sensu stricto share an immediate common ancestor, the taxonomic rank of the clades studied here remains tentative until our cladistic analysis is completed. There is always the possibility that they should be expressed at subfamilial or another level, either within the same family or different families. We would argue, for the time being, that consideration of these clades as families is prudent given the preliminary data before us, most importantly the apotypic cladistic position of the Baetidae, which is appropriate to maintain at the family level (see discussion in McCafferty 1991c). In any case, there are no cladistic data supportive of placing Siphluriscus or Stackelbergisca in the same supergeneric category with Acanthametropus and Analetris unless such a taxon is extremely inclusive in scope.

Acanthametropodidae was placed in the proposed infraorder Arenata, and Siphlonuridae sensu stricto was placed in the proposed infraorder Imprimata by McCafferty (1991c). Arenata included pisciform mayflies whose larvae are adapted more-or-less for psammophilous existence [see review of psammophilous mayflies in McCafferty (1991a)]; however, it appears that such adaptations are subject to homoplasy, bringing such an infraordinal classification into question. For example, Siphlonisca, a member of Siphlonuridae sensu stricto reported by Edmunds et al. (quoting C. P. Alexander) as occurring "along low sandy margins," has independently evolved sternal processes on the thoracic sternum (restricted to meso- and metasternum) paralleling somewhat the sternal processes found more extensively in the Acanthametropodidae, which are also psammophilous. The appropriateness of infraordinal classification of these families should be clarified by further cladistic analysis of the Pisciforma.

ACKNOWLEDGMENTS

We thank Dr. K. K. Günther, of the Museum für Naturkunde der Humboldt-Universität zu Berlin, for the extended loan of Ulmer's type material of Siphluriscus chinensis. This paper has been assigned Purdue Agricultural Research Program Journal No. 14308.

LITERATURE CITED


EFFECTS OF LIGHT AND NUTRIENTS ON 
TOMATO PLANT COMPENSATION FOR HERBIVORY BY 
MANDUCA SEXTA (LEPIDOPTERA: SPHINGIDAE) 

Anita K. Gertz and Catherine E. Bach

ABSTRACT

This preliminary study examined how two resources (light and nutrients) influence the ability of tomato plants to show growth compensation for defoliation by the tobacco hornworm (Manduca sexta). Growth rate and biomass of plants grown under high and low levels of light and nutrients, and exposed to 4 levels of defoliation by Manduca sexta were measured. Nutrients affected plant growth rate much more strongly than did light. Light and nutrients, however, each influenced how herbivory affected plant growth. Defoliation significantly decreased growth rate only under conditions of low light and high nutrients. Biomass, on the other hand, was low under all resource treatments except high levels of both light and nutrients, and defoliation significantly decreased biomass only under high levels of both resources. Thus, plants appeared to compensate for damage, in terms of biomass, only under conditions of either low light and/or low nutrients.

Although herbivory clearly decreases plant fitness in many insect-plant systems (Louda et al. 1990, Huntly 1991), many plants are able to compensate for herbivore damage (Paige and Whitham 1987, Maschinski and Whitham 1989, Hjalten et al. 1993, Meyer and Root 1993, Trumble et al. 1993). Compensation is typically defined as equal growth and/or reproduction of plants experiencing herbivory and control plants experiencing no herbivory. There is much current interest in examining the conditions under which plant compensation occurs (Maschinski and Whitham 1989). Trumble's (1993) review emphasizes the importance of studying the role of exogenous factors in influencing the compensatory ability of plants.

Coley et al. (1985) predicted that herbivory would be a stronger selective force on plant species growing under low resource conditions than under high resource conditions, because foliage lost to herbivory is more expensive to replace. If this hypothesis is applied to plants within the same species, then compensation would be predicted to occur more often under conditions of high resources. Few studies are available to test this prediction, and the results are equivocal; compensation occurs more frequently at higher resource levels in some systems (Cox and McEvoy 1983, Maschinski and Whitham 1989, Piersen et al. 1990, Hjalten et al. 1993), whereas there is a higher incidence of compensation at lower resource levels in other systems (Georgiadis et al. 1989, Oesterheld and McNaughton 1991, Meyer and Root 1993). Despite the importance of interactions between resources in influencing plant growth, few stud-

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ies have examined how two or more resources interact to influence compensation for herbivory.

The purpose of this preliminary study was to investigate the effect of light level and nutrient level on the ability of tomato plants (*Lycopersicon esculentum*) to compensate for damage by the tobacco hornworm, *Manduca sexta* (L.). Welter (1991) compared the effects of simulated and real herbivory by *Manduca sexta* on tomato plants, but did not vary resource levels. In this study, we addressed the following questions: (1) Do tomato plants compensate for herbivory, in terms of growth rate and above-ground biomass?, and (2) If so, does resource level (light and/or nutrients) influence the level of compensation? In particular, do resources interact to influence the level of compensation?

**METHODS**

The experimental design was a 4×2×2 factorial design, with 4 levels of herbivory (0%, 25%, 50%, and 75% defoliation), 2 light levels (low and high), and 2 nutrient levels (low and high). Plants in the low light level treatment (LL) were exposed to fluorescent grow lights for 8h/d, whereas high light level plants (HL) were exposed to the same grow lights supplemented with 75-watt light bulbs for 12h/d. Light levels averaged approximately 100 lumens for the LL treatment and approximately 300 lumens for the HL treatment. We will refer to the combination of increased light intensity/spectrum and increased photoperiod as the high light level condition. Because the incandescent bulbs gave off some heat, temperatures were also slightly higher in the HL treatment (28–30°C) than in the LL treatment (26–27°C). Plants in the low nutrient level treatment (LN) received no fertilizer; plants in the high nutrient level treatment (HN) received liquid fertilizer (standard dilution of 15–30–15 fertilizer) at each watering. There were six replicates of each treatment combination, for a total of 96 plants.

Seeds of *Lycopersicon esculentum* (variety Big Boy) were planted on 20 February, 1992 in a growing medium (Sunshine mix) in 9.5 cm diameter plastic pots. Plants were grown in a greenhouse and fertilized once on 3 March. Defoliation treatments were established on 17 March by placing one larva of *Manduca sexta* on each plant receiving defoliation. Larvae were removed after the desired percentage of leaf area was removed (Welter 1991).

After the defoliations had occurred, all plants were grown for 4 weeks on light benches in a laboratory at Eastern Michigan University. Because low and high light plants were grown on different light/dark cycles, they were grown on separate light benches. For ease of watering, plants receiving each nutrient treatment were placed on the same half of each bench, and position of pots within each light/nutrient treatment was haphazard. At each watering (approximately every 2 d), plants in each nutrient treatment were switched to the other side of the bench, and pot position was again haphazardly determined.

Plant height was measured one week (24 March) and four weeks after defoliation (14 April). Plants were harvested on 14 April, cut at the soil level, and their above-ground dry masses were determined after drying for 72 h at 60°C. Data were analyzed with 3-way ANOVA testing for effects of defoliation level, light level, nutrient level, and all interactions. To compare the four defoliation treatments, 1-way ANOVAs were conducted on final masses and growth rates (change in height) for plants in each treatment combination of light and nutrients. Because biomass is a more accurate indicator of plant growth than is change in height, the lack of a significant difference in biomass
Table 1. Results from 3-way ANOVAs of growth rate (change in height over a 3-week period) and final biomass. F-values, degrees of freedom, and significance levels are presented from ANOVAs testing for effects of defoliation level, light, nutrients, and all possible interactions.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Growth Rate</th>
<th></th>
<th>Biomass</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>df</td>
<td>P</td>
<td>F</td>
</tr>
<tr>
<td>Defoliation</td>
<td>7.1</td>
<td>(3,74)</td>
<td>***</td>
<td>15.2</td>
</tr>
<tr>
<td>Light</td>
<td>29.8</td>
<td>(1,74)</td>
<td>***</td>
<td>200.6</td>
</tr>
<tr>
<td>Nutrients</td>
<td>176.8</td>
<td>(1,74)</td>
<td>***</td>
<td>204.1</td>
</tr>
<tr>
<td>Defoliation × Light</td>
<td>5.6</td>
<td>(3,74)</td>
<td>**</td>
<td>3.4</td>
</tr>
<tr>
<td>Defoliation × Nutrients</td>
<td>2.8</td>
<td>(3,74)</td>
<td>*</td>
<td>14.0</td>
</tr>
<tr>
<td>Light × Nutrients</td>
<td>37.6</td>
<td>(1,74)</td>
<td>***</td>
<td>162.8</td>
</tr>
<tr>
<td>Def. × Light × Nutrients</td>
<td>1.9</td>
<td>(3,74)</td>
<td>*</td>
<td>6.6</td>
</tr>
</tbody>
</table>

* = P<.05; ** = P<.01; *** = P<.001

between control and damaged plants was used as evidence for plant growth compensation.

RESULTS

Plant growth rate, measured as change in height over the 3-week period, was significantly affected by defoliation level, light, and nutrients (Table 1, Fig. 1). Although the significance level for each of these effects was less than .001, the magnitude of the nutrient effect was much greater, as evidenced by

Figure 1. Growth rate (change in height (cm) over a 3-week period) of plants receiving four levels of defoliation and grown under four sets of conditions: low light/low nutrients (LL/LN), low light/high nutrients (LL/HN), high light/low nutrients (HL/LN), and high light/high nutrients (HL/HN). Means and standard errors are presented for six replicates of each treatment. The * indicates a significant effect of defoliation from 1-way ANOVAs within treatment groups.
the fact that the F-value was 25 times greater than for defoliation and 6 times greater than for light. The significant interactions between defoliation and light, defoliation and nutrients, and light and nutrients (Table 1), emphasize that the effect of each of these factors depended on the magnitude of other factors. Growth rates of defoliated and control plants did not significantly differ under conditions of LL/LN, HL/LN, or HL/HN (P>.05 for all comparisons). Only under conditions of LL/HN did defoliation significantly decrease plant growth rate (Fig. 1; F=13.6, df=(3,17), P<.001). Thus, it appears that when light is limiting, damaged plants can not attain the same height as control plants, even when high levels of nutrients are available.

Final biomass of plants was also significantly affected by defoliation level, light, nutrients, and all possible interactions (Table 1). The highly significant light X nutrient interaction is evident from the 3.5-5.4-fold greater biomass of control plants in the HL/HN treatment than in any of the other three treatments (Fig. 2). Biomass of defoliated and control plants did not differ under conditions of LL/LN, LL/HN, or HL/LN (P>.05 for all comparisons). However, defoliation significantly decreased biomass under HL/HN (F=14.7, df=(3,19), P<.001); thus plant compensation occurred under all conditions except under high light and high nutrients.

DISCUSSION

Results from this study clearly demonstrate that resource levels strongly influence the ability of tomato plants to re-grow following defoliation by Manduca sexta. Plants showed growth compensation for damage under low resource conditions, but not under high resource conditions. Under all sets of
conditions in which levels of one or both resources were low, final biomass of defoliated and control plants did not differ; only under high levels of both resources did defoliation significantly decrease biomass. However, the non-significant trend of decreasing biomass with increasing defoliation under low light and high nutrients was similar to that observed for the high light and high nutrient conditions (see Fig. 2). Thus, it appears that: (1) light and nutrients interact to influence plant growth compensation and (2) nutrients were more important than light in influencing plant compensatory ability.

It was interesting that the two aspects of above-ground growth measured in this study, height growth and biomass, exhibited different responses to nutrient levels and different regrowth responses following defoliation. In general, height growth seemed to be mostly nutrient-limited, whereas biomass production seemed to be both nutrient-limited and light-limited. In addition, defoliated plants added as much height as control plants under high resource conditions (see Fig. 1), but did not attain as great a mass as control plants (see Fig. 2). It appears that defoliated plants put more energy into height growth rather than into development of lateral branches under high resource conditions.

The result that plants compensated for herbivory, in terms of biomass, only under low resource levels is in contrast to results from several studies (Cox and McEvoy 1983, Pierson et al. 1990, Hjalten et al. 1993). In fact, Maschinski and Whitham (1989) found overcompensation in *Ipomopsis arizonica* only with nutrient supplementation. However, our results agree with several other studies reporting compensation under low resource conditions (Georgiadis et al. 1989, Oesterheld and McNaughton 1991). Meyer and Root (1993) report that goldenrod plants compensated for herbivory in terms of seed production only under low soil fertility. They further suggest that plants growing under conditions of low soil resource levels would more likely be nitrogen-limited rather than carbon-limited, and thus reduced leaf area would not affect seed production; on the other hand, under high soil resource conditions, plants would be carbon-limited and defoliation would strongly affect seed production. If this line of reasoning is applied to growth compensation in tomato plants, then the lack of compensation at high nutrient levels may result from carbon-limitation. Tomato plants growing at high resource levels appear to be growing so quickly that regrowth can not compensate for damage.

If Coley et al.'s (1985) predictions about the strength of herbivory as a selective force on different plant species growing under different resource levels can be extended to comparisons within plant species, then one would predict that herbivores would have stronger effects on plant fitness when resources are scarce. Maschinski and Whitham's (1989) model also predicts that the degree to which a plant can compensate for herbivory decreases as nutrient availability decreases. Results from this study do not support these predictions; instead, herbivory appears to exert the strongest differential impact on plant growth when resources are abundant. However, conclusions about compensation in terms of reproductive output, the most meaningful measure of plant fitness, can not be made from this preliminary study, because reproduction was not measured.

In conclusion, it appears that herbivore impacts on plant growth are strongly condition-dependent. Many studies report significant negative effects of herbivory on plant growth, survivorship, and fecundity (Louda et al. 1990, Huntly 1991). In a study similar to ours, Welte (1991) found a significant negative correlation between growth of tomato plants and percentage defoliation; this study only found negative effects of herbivory on biomass under high levels of both resources. Further research is needed to determine if the preponderance of studies showing negative effects of herbivory result...
partly from the fact that most studies are conducted with vigorous plants growing under conditions of high resources.

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We thank Gary Hannan, David Karowe, and Robert Neely for their insights about data interpretation, Glenn Walker for his support throughout this project, and Jamin Eisenbach, Brian Hazlett, and Glenn Walker for helpful comments on the manuscript.

LITERATURE CITED

DIFFERENTIAL SHOOT FEEDING BY ADULT TOMICUS PINIPERDA (COLEOPTERA: SColytidae) IN MIXED STANDS OF NATIVE AND INTRODUCED PINES IN INDIANA.

Clifford. S. Sadof, 1 Robert. D. Waltz 2 and Charles. D. Kellam 1

ABSTRACT

The larger pine shoot beetle Tomicus piniperda, a native bark beetle of Europe and Asia, was found in North American Christmas tree plantations in 1992 in Ohio. Subsequent surveys found it in six U.S. states and in one Canadian province. The first natural area where Tomicus was found to be established was at the Indiana Dunes State Park, in northwestern Indiana near the Lake Michigan shoreline. Pine stands were surveyed for fallen shoots to determine the extent and range of shoot feeding in the park. Within the study area adult Tomicus fed on the shoots of all native pines (Pinus banksiana, P. resinosa, and P. strobus), as well as the European species (P. sylvestris). More fallen shoots were collected from both P. resinosa and P. sylvestris than expected from their basal areas in the sampled stands. This contrasted with P. banksiana and P. strobus whose shoots were underrepresented relative to their basal areas. The relatively high numbers of fallen shoots found for P. resinosa suggests that red pines in the Great Lakes region will easily support populations of T. piniperda.

The larger pine shoot beetle, Tomicus piniperda (L.) (Coleoptera: Scolytidae), is an important pest of pines, Pinus spp., throughout Europe and Asia (Bakke 1968). This beetle was probably introduced to the Great Lakes Region of the United States through one or more recent introductions from cargo ships (Anonymous 1993; USDA, APHIS, PPQ 1992). Since being first reported in Lorain County, Ohio, on 1 July 1992, it has been found, as of 20 July 1994, in 107 counties in Illinois, Indiana, Michigan, Ohio, Pennsylvania, New York, and in 7 counties in the province of Ontario, Canada (source: USDA-APHIS-PPQ). We believe that the broad and relatively contiguous distribution of this beetle suggests that it has been in the United States for several years. In Indiana, the known infestation is restricted to 29 counties in the northern one-third of the state (Fig. 1). Delaware County, located approximately 100 miles south of Lake Michigan is currently the southern border of the known infestation in Indiana. Concern about the potential impact of this pest on North American pines has resulted in a federal quarantine designed to slow the spread of this beetle to non-infested areas (USDA, APHIS, PPQ 1992).

Tomicus piniperda has been reported to feed on many species of pine in Europe and Asia (Bakke 1968, Langstrom 1983, Hui 1991). In Europe, adult beetles spend the winter in shallow galleries in the outer bark at the base of their

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host trees. In early spring, when temperatures exceed 12°C, adults fly to stumps or trunks of recently cut or killed pines where they mate and lay their eggs in galleries under the bark. After approximately 6-10 weeks, depending on temperature, a new generation of adults begins to emerge and flies to the tops of pine trees where they feed inside shoots until autumn. This feeding is needed to mature their reproductive systems. Typically, adults enter shoots by boring a circular hole in a lateral twig and excavate it while tunneling toward the shoot tip. Shoot feeding continues until the first hard frost, when adults crawl out of the shoots and move to the base of trees where they construct their overwintering galleries. From autumn, through the winter, excavated shoots break and fall to the ground.

Not all shoot feeding is caused by the new generation of *T. piniperda* that have emerged from brood logs in the spring. Some shoot feeding is caused by the beetles in the parent generation of adults. These individuals may leave brood logs and feed in shoots after they have constructed their first egg gallery prior to finding new sites for depositing the remainder of their eggs (Langstrom 1983, Sauvard 1993, Haack and Lawrence 1994). A substantial portion of parental adults that have mated and depleted their supply of eggs and sperm will also return to feed on shoots to regenerate their reproductive capacity. In cooler regions of northern Europe these beetles can mate and reproduce during the following year (Schroeder and Risberg 1989). In warmer regions, such as in Kunming China, many of these adults can mate and enter new pine to produce new egg galleries after only two months (Hui 1991).

Damage to forest trees occurs primarily when beetles feed in shoots and kill
new growth. Heavy defoliation in northern Europe resulted in up to 70% reduction in the volume of tree growth (Langstrom and Hellqvist 1991). Economic injury is most common in forests containing large quantities of freshly killed or dying pine trees that can serve as breeding material for the larger pine shoot beetle (Langstrom 1984, Langstrom and Hellqvist 1991). Although this beetle is seldom a significant mortality factor of pines in northern Europe, it can kill drought stressed pines in southern Europe and Asia (Hui 1991, Langstrom and Hellqvist 1993).

The establishment of T. piniperda in North America can potentially threaten the productivity of native and introduced pines throughout the continent. To assess this threat on a local level, we have initiated a long-term study on patterns of adult shoot feeding in undisturbed stands of native and introduced pines in northwestern Indiana. In this paper we report on the results of our initial census of pines and shoot feeding by T. piniperda.

MATERIALS AND METHODS

Study site selection. Our study site, the Indiana Dunes State Park (Porter County), is located on the southern shore of Lake Michigan and is bordered on the west by the Port of Indiana in Burns Harbor. Some pine stands in the park are natural, representing post-glacial remnants, while others were planted during the early 1900's through the mid-1960's. Four species of pine are present in the park. These include: jack pine (P. banksiana), red pine (P. resinosa), Scotch pine (P. sylvestris), and eastern white pine (P. strobus). Nineteen pine stands were located throughout the park on maps of existing vegetation (Fig. 1). Twelve of the 19 pine stands were surveyed on 5 and 7 April 1993. At that time, little new growth had occurred on the forest floor, making the fallen pine shoots clearly visible.

Survey methods. At each pine of the 12 pine stands, at least one 25m X 1m transect was sampled to characterize stand composition. When stands were large (> 0.4 ha, or >100 m long), more than one transect was sampled, yielding a total of 28 transects (= 700 m²) for the 12 stands in this study. Along each transect, all trees whose trunks were within 0.5 m of the transect line were identified to species and their diameters at breast height (DBH; 1.4 meters above the ground), were recorded. The total number of live trees was tallied. To estimate the trees cross sectional area at 1.4 m, the basal area for each live tree was calculated as \( \pi \times (\text{DBH}/2)^2 \). Percent of basal area contributed by each species was determined.

Differential Shoot Feeding. During the April surveys, we counted the number of detached pine shoots on the forest floor within each transect described above. Shoots that had a frass-free tunnel bored from the base toward the tip were counted as positive feeding sites for T. piniperda. Each fallen pine shoot within the transect area was identified to species. This method assumes a proportional relationship between adult beetles feeding in shoots and the number of shoots that fall to the ground (Langstrom and Hellqvist 1991). Moreover, in the present study this method assumes that shoots hollowed out by these scolytids break off equally among all pine species.

Differential shoot feeding among the four pine species was examined by comparing the frequency of fallen shoots with the relative basal area contributed by each pine species using a G-test (Sokal and Rohlf 1981). Basal area of pines surveyed was used to approximate the relative numbers of shoots available to adult larger pine shoot beetles. This measure of cross-sectional area has been correlated with canopy size for several pine species (Stephens 1969, Whitehead 1978).
Table 1. Summary data for the 28 transects that were surveyed at Indiana Dunes State Park in April 1993

<table>
<thead>
<tr>
<th>Species of pine</th>
<th>No. of trees</th>
<th>% of total</th>
<th>Average DBH*</th>
<th>Total basal area (BA)</th>
<th>% of total</th>
<th>Fallen Shoots</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>%</td>
<td>x ± SEM</td>
<td>BA in m²</td>
<td>%</td>
<td>No. shoots</td>
</tr>
<tr>
<td>P. sylvestris</td>
<td>64</td>
<td>21.9</td>
<td>16.94±0.54</td>
<td>1.442</td>
<td>19.4</td>
<td>41</td>
</tr>
<tr>
<td>P. resinosa</td>
<td>60</td>
<td>20.5</td>
<td>20.06±0.43</td>
<td>1.896</td>
<td>25.5</td>
<td>57</td>
</tr>
<tr>
<td>P. banksiana</td>
<td>117</td>
<td>40.0</td>
<td>15.08±0.99</td>
<td>2.090</td>
<td>28.1</td>
<td>30</td>
</tr>
<tr>
<td>P. strobus</td>
<td>51</td>
<td>17.5</td>
<td>22.33±1.69</td>
<td>1.997</td>
<td>26.9</td>
<td>2</td>
</tr>
</tbody>
</table>

* Diameter of tree at breast height, in cm.

RESULTS

The overall composition of pine stands sampled in the Indiana Dunes State Park study site is summarized in Table 1. Jack pine was the most common pine (40%) and contributed the most (28%) to the total basal area of pines surveyed. Based on DBH, white pines were the largest of all tree four species sampled.

The overall density of fallen shoots per transect was $0.185 \pm 0.051$ (SE)/m². Densities of shoots in transects ranged from 0 to 1.24/m². A total of 130 shoots was found in the 28 transects (Table 1). The species distribution of fallen shoots did not correspond with the proportional species distribution of cross sectional areas ($G=87.2$, df=3, $p<0.0001$). Overall, more red pine and Scotch pine shoots were found on the forest floor than their percent contribution to the total basal area of sampled pines. In contrast, feeding on both jack pine and white pine was less frequent than expected from their respective basal areas. For example, Tomicus-fed white pine shoots constituted less than 2% of the total shoots found even though white pines represented 27% of the total basal area.

DISCUSSION

Tomicus piniperda shoot-feeds on both native and European pines at the Indiana Dunes State Park. Most of the pine shoots found in this survey (44%) came from red pine, a native species. This suggests that in undisturbed stands native pines can be at least as susceptible to maturation feeding as Scotch pine, the preferred host of this beetle in Europe (Gibbs and Inman 1991). In contrast, many fewer jack pine and especially eastern white pine shoots were found than expected from their relative contribution to the basal area of pines surveyed. This suggests that white pine stands may not be highly susceptible to shoot feeding by T. piniperda. Our findings are consistent with those of Lawrence and Haack (1994) who observed that caged adult beetles in southern Michigan excavated longer tunnels in Scotch pines and red pines than either jack pines or eastern white pines.

Interpretation of the number of fallen shoots that we collected assumes that attacked shoots detach from these 4 species of pines at the same rate. Studies of shoot diameters reveal that red pine shoots are much thicker (6mm) than eastern white pine, jack pine, or Scotch pine (4 mm) at the point of attack by adult beetles (Lawrence and Haack 1994). Thus, our counts of fallen pine shoots may underestimate shoot feeding on red pines because their thicker stems could delay shoot detachment. This bias strengthens our ability to infer that T. piniperda feeds more readily on red pine shoots than on those of jack or white pine.

The under-representation of Tomicus-fed white pine shoots may be related
to the quantity and quality of oleoresins that these trees produce in response to shoot feeding. Caged field experiments show 30-40% of adult *T. piniperda* attempting to enter eastern white pine shoots were trapped in resin flows compared to only 5-10% in Scotch pine (Lawrence and Haack 1994). The abundance of non-crystallizing resins in eastern white pines has been shown to confer resistance to *Pissodes strobi* (Peck), a weevil that enters actively growing shoots as an adult (van Buijtenen and Santamour 1972).

Differences in monoterpene composition of the four pine species in the park may also contribute to the distribution of *Tomicus*-fed shoots among species. "East Anglia" Scotch pine, a strain commonly planted in northern Indiana, is reported to have a monoterpene profile that is lower in both alpha-pinene and limonene when compared to eastern white pine (Hanover 1975, Tobolski and Hanover 1971). Limonene has been associated with resistance of *P. ponderosa* to another scolytid, *Dendroctinus brevicomis* LeConte (Smith 1965). However, both the more and lesser preferred species in our study, red pine and jack pine respectively, are reported to have a relatively low content of limonene (Mirov 1961, McCullough and Kulman 1991a, b). Clearly, there is a need for direct studies to examine the relation of shoot feeding and monoterpene composition. Compared with European conditions, the intensity of shoot feeding was relatively light at our study area. In Sweden, when densities of fallen shoots are below 1 shoot/m² of forest floor, stands are considered to be well managed and are not likely to experience growth loss from *T. piniperda* (Langstrom and Hellqvist 1991). Densities of fallen shoots exceeded this level in only 1 of the 28 transects. This density of 1.24 shoot/m² of forest floor occurred in a mixed pine transect of 50% red pine and 50% Scotch pine. Using data from Sweden (Langstrom and Hellqvist 1991) to estimate a possible linear relationship between density of fallen shoots (x) and tree volume growth loss (y), \( y = 5.641 + 0.711x \), \( R^2 = 0.97 \), this density is not likely to affect tree growth. It is almost 5 times less than the density of 6.12 shoots needed to reduce tree volume by 10% in Sweden.

In conclusion, we found that *T. piniperda* shoot-feeds on both native and introduce pines at the Indiana Dunes State Park. The relatively high frequency of *Tomicus* -fed red pine shoots collected in this survey suggests that red pine stands in the Great Lakes region will easily support *Tomicus piniperda* populations. In contrast, jack pine and especially white pine stands may be less at risk.

**ACKNOWLEDGMENTS**

We thank T. Hall of the Pennsylvania Department of Agriculture for finding the first larger pine shoot beetle at the Indiana Dunes National Lakeshore, E. Childers of the Indiana Dunes National Lakeshore for producing maps of pine stands in the Park; Indiana Department of Natural Resources, Division of State Parks for their cooperation; and R. Haack of the United States Forest Service, as well as four anonymous reviewers for comments on a preliminary draft of this manuscript. This paper is published as Journal No. 13990 of the Indiana Agricultural Experiment Station, Purdue University.

**LITERATURE CITED**


A BAIT ATTRACTANT STUDY OF THE NITIDULIDAE (COLEOPTERA) AT SHAWNEE STATE FOREST IN SOUTHERN OHIO

R. N. Williams,1 M. S. Ellis,1 and G. Keene2

ABSTRACT

Four baits were tested for efficacy in attracting sap beetles (Nitidulidae) at two sites in the Shawnee State Forest over two collection periods in 1992. Species taken were categorized into three groups: abundant, moderate, and uncommon. At Site 1, nitidulids displayed a strong preference for whole wheat bread dough, followed by fermenting brown sugar, and fermenting malt/molasses solution, and vinegar, respectively. Site 2 collections showed a similar trend to Site 1, but the order of preference was switched for brown sugar and malt/molasses solution. Of the 20 species collected, six species were abundant, seven species were moderate, and seven species were locally uncommon.

Two sites in Shawnee State Forest (extreme southern Ohio) were used to test efficacy of four trap baits for Nitidulidae (Coleoptera) during the 1992 season. The baits tested included whole wheat bread dough (WWBD), fermenting brown sugar, a mixture of fermenting malt/molasses and vinegar. WWBD has been our preferred nitidulid bait since we began using it in the late 1970's as it was found to be quite successful in luring Stelidota geminata (Say) (Miller and Williams, 1982). Frost and Dietrich (1929), who reported the other three baits as successful nitidulid attractants, caught nineteen species of nitidulids within nine genera in both fermenting sugar and molasses traps. After achieving good results with these baits in a survey in Portage County, Ohio (Williams et al. 1992), we decided to systematically compare efficacy of these four baits for attractancy to the nitidulid complex in the Shawnee State Forest.

MATERIALS AND METHODS

The trapping sites were located within 8 km of the Ohio River in the south central area of the 24,000 ha Shawnee State Forest in Nile Township (Scioto Co.). The four treatments (baits) were replicated four times at each location in a randomized block. Site 1 was in a low ravine about 6.5 km from State Route 52 just off of State Forest Road 1 near Pond Run, while Site 2 was located about 140 m higher on a ridge about 3.2 km NNW of the first site, near State Forest Road 2. Spacing between traps was 10 m. Treatments consisted of fermenting malt/molasses solution, fermenting brown sugar solution, vinegar and WWBD.

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The malt/molasses solution was prepared using liquid Maltsupex® malt
soup extract (Wallace Laboratories Division of Carter-Wallace Inc., Cranbury,
NJ) and livestock feed molasses obtained from a local feed company. The
preparation of the malt/molasses solution was as follows: 45 ml of Maltsupex®,
45 ml of molasses, 35 g of granulated sugar and a pinch of active dry
yeast per liter of warm water. One hundred fifty ml of the above solution of
malt/molasses were placed in each trap.

The brown sugar solution was prepared using approximately 340 g of
brown sugar and a pinch of active dry yeast per liter of warm water. About
150 ml of this mixture was used in each brown sugar trap.

The vinegar traps were baited with 150 ml of apple cider vinegar per trap.
The WWBD was made by mixing 450 g of whole wheat flour, 15 ml of sugar,
300 ml of warm water and a 7 g package of dry active yeast. A small piece of
dough (ca. 30 g) was rolled into a ball and wrapped in a piece of fiberglass
screen to prevent beetles from becoming imbedded in the dough. This screen-
covered ball was then placed in the trap.

The trap chosen for this study was the nitidulid inventory technique (NIT)
trap (Williams et al. 1993), which is a modification of the trap used by
Skalbeck (1976). The NIT trap consists of a 1-liter wide-mouth canning jar
with a plastic cone (a tapered drinking cup with bottom removed) inserted in
the mouth of the jar and held in place by the canning band. A 15 cm square of
Masonite (6.5 mm thick) was attached about 2 cm above the mouth of the jar
as a rain cover. A golf course cup cutter was used to dig a hole deep enough to
hold the entire jar. The top edge of the jar remained slightly above the soil
surface. Once the traps were set in the ground, they were covered with a 0.6 m
square piece of "chicken wire", which was anchored to the ground using 25 cm
landscaping spikes. This prevented pilfering by raccoons and other mammals.

Four collections were made: two early season and two late season. The
early season traps were set out on 18 April and collected on 25 April and 2
May. The late season traps were set out on 1 August and collected on 8 and 15
August. After collection, contents of jars were placed in plastic bags and
frozen. They were thawed at a later time, separated from the bait, and pre-
served in 70% ethyl alcohol. Data were analysed using the Wilcoxon rank sum
test (SAS Institute 1985) at a level of \( P < 0.05 \).

RESULTS AND DISCUSSION

Nitidulids taken in these collections were separated into three abundance
categories. The categories were defined as: abundant = > 80 specimens col-
clected during the season; moderate = between 8 and 80 specimens; and
uncommon = 7 specimens or fewer.

Abundant species were Carpophilus lugubris Murray, Epuraea helvola
Erichson, Glischrochilus fasciatus (Olivier), G. quadrisignatus (Say), Stelidota
geminata (Say) and S. octomaculata (Say) (Table 1). All except E. helvola are
pests that are quite common throughout Ohio. E. helvola is primarily a wood-
land dweller in northern and southern Ohio.

Species caught in moderate numbers were Colopterus sp., Cychramus
adustus Erichson, Epuraea alternata Parsons, E. peltoides Horn, E. rufa
(Say), Glischrochilus sanguinolentus (Olivier) and Pallodes pallidus (Beauvois)
(Table 1). In this group, all are woodland insects which congregate at sap flows
(Connell 1956), with the possible exceptions of Cychramus adustus and Pal-
loides pallidus. The latter two species are primarily fungus feeders which were
encountered less frequently in a similar 1991 study (Keeney et al. 1994).

Uncommonly collected species were: Carpophilus corticinus Erichson, C.
<table>
<thead>
<tr>
<th>SPECIES CAUGHT</th>
<th>SITE 1*</th>
<th></th>
<th></th>
<th>SITE 2*</th>
<th></th>
<th></th>
<th>GRAND TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>WWBD</td>
<td>BS</td>
<td>M/M</td>
<td>VIN</td>
<td>TOT</td>
<td>WWBD</td>
<td>BS</td>
</tr>
<tr>
<td>Carpophilus corticinus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Carpophilus freemani</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<td>Carpophilus lugubris</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>288</td>
<td>119</td>
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<tr>
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<td>0</td>
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<td>1</td>
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<td>Epuraea rufa</td>
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<td>Epuraea sp.</td>
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<td>Glischrochilus quadrignatus</td>
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<td>Glischrochilus sanguinolentus</td>
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<td>0</td>
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<td>Pallodes pallidus</td>
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<td>0</td>
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<td>0</td>
</tr>
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<td>Phenolla grossa</td>
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<td>0</td>
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<td>0</td>
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<td>2</td>
</tr>
<tr>
<td>Stelidota geminata</td>
<td>374</td>
<td>162</td>
<td>223</td>
<td>113</td>
<td>872</td>
<td>506</td>
<td>297</td>
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<tr>
<td>Stelidota octomaculata</td>
<td>20</td>
<td>20</td>
<td>39</td>
<td>43</td>
<td>122</td>
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<tr>
<td>Total Species:</td>
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<td>7</td>
<td>8</td>
<td>8</td>
<td>15</td>
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<td>15</td>
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<tr>
<td>Total Specimens:</td>
<td>478</td>
<td>219</td>
<td>313</td>
<td>172</td>
<td>1,182</td>
<td>1,076</td>
<td>618</td>
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</table>

* For each site:
WWBD = Whole Wheat Bread Dough.
BS = Brown Sugar.
M/M = Malt/Molasses.
VIN = Vinegar.
TOT = Individual Site Totals.
Figure 1. Response of all nitidulid species to four attractants using NIT traps in Shawnee State Forest, Scioto County, Ohio, over the entire season. Letters are used to indicate statistical separation.

freemani Dobson, Carpophilus sp., Epuraea sp., Glischrochilus obtusus (Say), Phenolia grossa (F.), and Stelidota ferruginea Reitter (Table 1). In a 1991 study of this area, 137 specimens of Glischrochilus obtusus were taken during June 2–6 in brown sugar traps (Keeney et al. 1994). In that study, traps were located 1 m above the ground, whereas in our current study traps were at ground level. Furthermore, the 1991 collections were made a month earlier than in 1992. Location and timing may have reduced the number of G. obtusus collected. Stelidota ferruginea was unexpected in this study. This species is an invader of acorns in southeast U. S. (Galford et al. 1991a), and although it has been reported as far north as Wisconsin and Michigan, Galford et al. (1991a) did not report it in southern Ohio during five years of extensive studies. We concur with Galford et al. (1991a) suggestion that these northern encounters appear to be limited migrations. Several specimens were collected from our traps in the Cleveland area in 1993. The other uncommon species, though frequently found in northern Ohio's agricultural habitats, were also uncommon in our earlier study of Shawnee State Forest (Keeney et al. 1994).

In all, 20 species in nine genera were taken over the season. Species are listed in Table 1 with their respective baits and locations. A great majority of the nitidulid species responded more strongly to WWBD rather than the other three baits. Brown sugar, malt/molasses solution, and vinegar followed in descending order, as shown in Figure 1. Individually, most of the nitidulid
species followed the same pattern of attraction to the baits, with the exception of: E. helvola, E. rufa and S. octomaculata; the most significant being in Stelidota octomaculata Say. This species was first reported in red oak acorns in Illinois by Winston (1956). More recently it has been deemed a pest of red oak in northeastern North America. The beetles are attracted to red oak acorns and hinder red oak regeneration (Galford et al. 1991b). At both sites, this species showed a preference for the vinegar bait, after which S. octomaculata responded to the remaining three baits differently at each site. At Site 1, the second preference of this species was the malt/molasses bait followed by an equal representation in the WWBD and brown sugar bait. Based on numbers caught in descending order at Site 2, S. octomaculata chose WWBD, brown sugar, and malt/molasses, respectively.

Another species which deviated from the common bait response is Epuraea helvola. Little is known of the biology of this species, although it was reported by Skalbeck (1976), along with E. peltoides, as the most prevalent Epuraea species found in his Minnesota forest collections. We have encountered this species in extreme northeastern Ohio (Williams, unpub. data). However, this species has not been taken in Wayne, Crawford, or Knox counties using similar collecting methods. E. helvola appeared to favor the brown sugar followed by WWBD, malt/molasses, and vinegar, respectively.

Although not statistically significant, 12 specimens of Epuraea helvola were captured with baits in a manner similar to S. octomaculata. This species has been reported in leaf litter, at sap and in fungi, and has also been reared on the fallen seeds of sugar maple, Acer saccharum (Parsons 1943).

As shown in Table 1, several species were represented differently at each trapping site. However, Carpophilus lugubris, Colopterus sp., and Epuraea helvola were the only species collected in significantly higher numbers at Site 2 than at Site 1 (P < 0.05). Although worthy of note, no direct conclusions can be drawn from these differences due to the complexity of the many factors involved (i.e. elevation, vegetation, weather conditions, etc.).

ACKNOWLEDGMENTS

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LITERATURE CITED

Keeney, G., M. S. Ellis, D. Richmond, and R. N. Williams. 1994. A preliminary study of


TILLERING RESPONSE OF ‘MONON’ AND ‘NEWTON’ WINTER WHEATS INFESTED WITH BIOTYPE L HESSIAN FLY (DIPTERA: CECIDOMYIIDAE) LARVAE

Stanley G. Wellso¹ and Robert P. Hoxie²

ABSTRACT

Two wheat, Triticum aestivum, cultivars that differed in their ability to tiller were infested by ovipositing Hessian flies, Mayetiola destructor, under similar controlled conditions. Since a larva typically stunts and kills the stem where it feeds and develops, tiller development of fly infested-wheat seedlings is an important plant trait relative to grain yield. ‘Monon’ tillered more than ‘Newton’ at the 0 infestation level (control). ‘Monon’ had about the same number of tillers at 0, 1, 2, and 3 puparia (indicative of the number of feeding larvae) per plant; and ‘Newton’ had fewer tillers at 0 than 1, 2, or 3 puparia per stem. However, tillering of both cultivars was less at 4 or more puparia per stem, perhaps due to the depletion of plant nutrients. In general, for both cultivars there was a decrease in leaf length, number and wet weight as the number of puparia increased per tiller.

Wheat, Triticum aestivum, is not as susceptible to damage by phytophagous arthropods as many other crops. It is a very resilient crop, and usually produces secondary tillers (shoots or stems). Wheat usually has eight tiller buds, but typically only three or four develop into full sized tillers (Williams et al. 1975). A few winter wheat tillers develop in the autumn or winter, but more tillers appear under warm spring temperatures (Simmonds 1987). Kirby (1983) noted that the main shoot and early formed tillers (those formed when leaves 4 to 6 emerge on the main shoot) are most likely to complete development and form grain.

An arthropod may feed on the primary tiller and destroy it, while later-developing tillers may be undamaged and produce seeds. Like other grasses, wheat can compensate for damage or injury by producing more stems per unit of area (tillering), seeds and/or heavier seeds per head, and heads per plant (Schlehuber & Tucker 1967). Wheat is thus very adaptable and tolerant of insect attack and rarely requires insecticide treatment. In dollar value in the United States in 1984 it ranked fourth among crops in acreage (Anon. 1984), while in insecticidal usage it ranked tenth (Anon. 1988).

Both biotic and abiotic conditions influence tillering. Studies of the tillering process or the production of additional culms in the Gramineae have focused primarily on cultivar differences and the effects of a wide range of

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environmental factors. The physiology of tillering has been investigated by studying the effects of various growth substances and inhibitors (Williams et al. 1975, Williams & Langer 1975). In barley, *Hordeum vulgare*, a reduction of auxin depressed tillering; however, an application of auxin naphthaleneacetic acid (NAA) to plants with destroyed apexes increased tillering (Leopold 1964).

Little information is available about the interaction of insect numbers and wheat tillering. Multi-tillering wheat varieties may tolerate heavier infestations of the wheat bulb fly, *Delia coarctata* (Fallin), but this represents greater pest survival in the following season (Oakley 1980).

Successful Hessian fly, *Mayetiola destructor* (Say), larval infestation of the main stem usually results in stem death, and may result in the production of tillers. The economic threshold values for the Hessian fly in Central Europe are 1 to 6 larvae per plant (Wetzel and Freier 1981) and 20% larval infestation of stems in North America (Hill et al. 1943). If the infestation is severe, young plants do not tiller, but wheat cultivars that tiller freely survived better (Barnes 1956). The main resistance mechanism of wheat to the Hessian fly is larval antibiosis, resulting in the death of young larvae due to their inability to maintain sustained feeding (Gallun 1965, Shukle et al. 1990); the resistant plant continued to grow with little evidence of the previous insect infestation. However, Hessian fly biotypes able to overcome host plant resistance are becoming common.

Two cultivars that differed in tillering were evaluated under known Hessian fly puparia (larvae) numbers under controlled growth chamber conditions to evaluate the relationship between Hessian fly numbers and wheat tillering, leaf length, fresh weight, and leaf numbers.

**MATERIALS AND METHODS**

**Test Plants.** 'Newton' (less tillering) and 'Monon' (greater tillering compared to 'Newton') were selected for study, as they were found previously to differ in their tillering response under controlled conditions (authors unpublished data). 'Monon' (H3 gene for resistance, but susceptible to biotype L) and 'Newton' (H0, susceptible) seeds were germinated in moist vermiculite in single seed containers. Seedlings of each cultivar were transplanted after 5 to 7 d to soil in 24 pots (10 cm diameter), three plants per pot, and held at 15°C at 14:10 (L:D) photoperiod. The plants were provided with Hoagland's solution once weekly and watered when needed. The experiment was replicated four times.

**Test Insects.** Biotype L Hessian flies virulent to all Hessian fly resistant commercial cultivars currently deployed were used in this study. Hessian flies were originally collected from Indiana wheat fields and maintained by the USDA, ARS Insect and Weed Control Research Laboratory, Purdue University. In general, 26 pots per cultivar, 3 plants per pot were planted and 24 pots with plants 7 days in age were infested with biotype L Hessian flies. This design was replicated four times. Seven days after planting, virulent biotype L Hessian flies were placed to oviposit for 2–7 h on 'Monon' and 'Newton' caged wheat seedlings with the duration of oviposition dependent upon the the number of eggs observed per plant. The number of eggs per plant were recorded the day after oviposition, and if more eggs than 5–10 were found per plant, the excess eggs were removed with a brush, so that the eggs laid on plants of the two cultivars were about equal. The numbers of puparia (indicative of the previous larval infestation), tillers, and the total plant length from
**Table 1. Tillering and other plant responses of 'Newton' and 'Monon' winter wheats to biotype L Hessian fly larval feeding**

<table>
<thead>
<tr>
<th>No. of Puparia</th>
<th>No. of Eggs</th>
<th>Puparia per Egg (%)</th>
<th>No. of Plants</th>
<th>Tiller no.</th>
<th>Length mm.</th>
<th>Weight mg.</th>
<th>Leaves no.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>'Monon'</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0 d</td>
<td>0 f</td>
<td>24</td>
<td>3.8ab</td>
<td>343a</td>
<td>2056a</td>
<td>10.7a</td>
</tr>
<tr>
<td>1</td>
<td>4.7c</td>
<td>31.7d</td>
<td>57</td>
<td>3.8a</td>
<td>280b</td>
<td>1457b</td>
<td>10.2a</td>
</tr>
<tr>
<td>2</td>
<td>6.0b</td>
<td>42.5c</td>
<td>32</td>
<td>3.8a</td>
<td>271bc</td>
<td>1448b</td>
<td>9.9a</td>
</tr>
<tr>
<td>3</td>
<td>6.3b</td>
<td>52.2c</td>
<td>27</td>
<td>3.4ab</td>
<td>252cd</td>
<td>1113c</td>
<td>8.2b</td>
</tr>
<tr>
<td>4</td>
<td>6.7b</td>
<td>65.8ab</td>
<td>26</td>
<td>3.3bc</td>
<td>229e</td>
<td>834d</td>
<td>7.3c</td>
</tr>
<tr>
<td>5</td>
<td>8.9a</td>
<td>58.0bc</td>
<td>10</td>
<td>2.7c</td>
<td>238de</td>
<td>959cd</td>
<td>8.0bc</td>
</tr>
<tr>
<td>6-8</td>
<td>9.3a</td>
<td>79.6a</td>
<td>12</td>
<td>3.1bc</td>
<td>251cde</td>
<td>1043cd</td>
<td>8.3bc</td>
</tr>
<tr>
<td>F-ratios</td>
<td>41**</td>
<td>14**</td>
<td></td>
<td>3*</td>
<td>32**</td>
<td>27**</td>
<td>18**</td>
</tr>
</tbody>
</table>

|               |             |                     |               | 'Newton'  |            |            |            |
| 0             | 0 e         | 0 e                 | 24            | 2.6b      | 336a       | 1568a      | 9.0a       |
| 1             | 4.6d        | 35.4d               | 55            | 3.3a      | 268b       | 1091b      | 8.7a       |
| 2             | 5.5cd       | 46.9c               | 31            | 3.4a      | 251bc      | 909bc      | 7.5b       |
| 3             | 5.8c        | 56.7bc              | 45            | 3.2a      | 243cd      | 784cd      | 7.7b       |
| 4             | 7.1b        | 59.8b               | 24            | 2.7b      | 227e       | 637e       | 6.4c       |
| 5             | 6.9b        | 75.8a               | 20            | 2.4b      | 228de      | 680de      | 6.4c       |
| 6-13         | 8.2a        | 85.7a               | 31            | 2.4b      | 217e       | 597e       | 6.3c       |
| F-ratios     | 43**        | 26**                |               | 7**       | 50**       | 32**       | 20**       |

Puparia (includes 3rd instars) were removed from the stem 21 d after oviposition.

aMonon: 6-8 puparia (mean=6.75), Newton: 6-13 puparia (mean=6.90), no significant difference (t-test).

F-ratios from a one way ANOVA of larval-damage levels within each cultivar; significance: *, P < 0.05; **, P < 0.01.

the crown to apex of the longest leaf per plant were recorded 21 d after oviposition.

**Statistical Analysis.** A one-way analysis of variance (SPSS 1988) was used to test the effects of different levels of Hessian fly infestation on the two cultivars on a per plant basis relative to number of tillers, number of leaves, plant length and weight. Differences in significance were identified at the P < 0.05 and P < 0.01 levels and separated by Least Significant Difference Tests.

**RESULTS AND DISCUSSION**

Based upon the greater values above ground of the four control plant parameters (leaf and tiller numbers, and plant length and weight) measured under controlled conditions, 'Monon' is a more robust cultivar than 'Newton' (Table 1). Both cultivars were susceptible to virulent biotype L larvae; within each cultivar, the number of tillers and leaves, and plant length in general decreased as the infestation level increased. An exception occurred with the plant weight of 'Monon,' where the greatest weight loss occurred at the four puparia per plant level.

The cultivars differed in their tillering response to similar Hessian fly levels, which are related to the genetics and physiology of the wheat cultivars. The numbers of tillers of 'Newton' were lower at 0, and 3 or more puparia infestation level than at 1–2 puparia per plant, indicating that Hessian fly at the 1 or 2 puparia per plant level promoted tillering in this cultivar. This was different than the tillering response of 'Monon'. For 'Monon' within the 0 to 3
Table 2. Analysis of variance of tillering and other plant responses to winter wheat cultivars 'Newton' and 'Monon' to biotype L Hessian fly larval feeding.

<table>
<thead>
<tr>
<th>Sources of Variation</th>
<th>No. of Eggs</th>
<th>Puparia per Egg</th>
<th>Plant Response</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Cultivar</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Puparia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cultivar-Puparia</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Interaction</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Replicate (Date)</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

| Puparia levels: 0, control; 1, 2, 3, 4, 5-number of puparia; 6, ≥ 6 puparia. For variables no. of eggs and % puparia/egg, only puparia levels 1 through 6 were used in the ANOVA, because controls were constant zeros. Plant weight was transformed for homogeneity.

puparia levels, tillering remained constant, but at greater than 3 puparia, there was less tillering.

Although the number of eggs and puparia for both cultivars within each replicate were similar, the percentages of puparia per egg oviposited were greater for all infestation levels on 'Newton' than on 'Monon' (Table 1). The resistance associated with the H3 gene of 'Monon' may have adversely affected virulent biotype L larvae or the 'Monon' plants may have been more tolerant to Hessian fly feeding damage. This may also reflect infestation with an impure Hessian fly biotype. The percentages of puparia per egg were lower than expected, especially at the lower infestation levels.

Stunting of the main stem due to Hessian fly larval feeding might have caused more nutrients to be available for tillering. Thus, Hessian fly feeding not only stopped elongation of both cultivars, but may have also promoted some tillering. Perhaps as the number of larvae (puparia) per plant increased, more nutrients were removed (Weiss et al. 1989), and eventually the ability to tiller decreased.

The multiple analysis of variance (Table 2) shows that the cultivars and puparia factors significantly affected all of the parameters examined. The greatest effect of Hessian fly infestation on both cultivars was on plant wet weight, portraying the detrimental effect of this insect on the growth of infested wheat. There was no significant interaction between cultivar-puparia levels; however, the replicates differed significantly due to different egg deposition ranges.

Sosa & Foster (1976) evaluated the resistance of 'Arthur 71', 'Knox 62', 'Monon', and 'Seneca' (H5, H6, H3, and H7H8 genes for resistance, respectively (Gallun 1977) to Hessian fly biotypes GP (Great Plains), B, C, and D at 15 to 27°C. They noted that tillering varied with the Hessian fly biotype, cultivar, and temperature, with most cultivars exhibiting a greater fly infestation and tillering at higher temperatures. Greater tillering could be a potentially important form of tolerance in some cultivars, offsetting fly induced losses. Increased tillering might be particularly beneficial, if used in conjunction with antibiosis.

To use Hessian fly infested wheat as a forage crop because it may have more tillers may not be a valid option, as Buntin & Raymer (1989) noted that low to moderate levels of Hessian fly damage reduced wheat forage yield primarily by reducing tiller size and weight rather than tiller density.

This experiment establishes that the response of wheat to virulent Hes-
sian fly damage varied relative to the capacity of the cultivar to tiller. If an insect such as the Hessian fly infests and destroys the main stem, tillering becomes an important response for wheat survival. Tillering of these two cultivars varied in response to infestation of similar numbers of Hessian fly puparia (larvae), and plants that tiller more at lower infestation levels may have a survival and yield advantage.

LITERATURE CITED

Anon. 1988. Division of Contaminants Chemistry, FDA.
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