

Leaf ties as colonization sites for forest arthropods: an experimental study

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Abstract. 1. Secondary colonization of leaf shelters constructed by caterpillars has been reported from a number of systems. Both the mechanism (larval or adult movement vs. oviposition) and the cues used by arthropods in locating leaf shelters, however, have received little attention.

2. Artificial leaf shelters (i.e. leaf ties or pairs of leaves clipped together to form sandwiches) were constructed on understory white oak (*Quercus alba* L.) trees and the abundance and species composition of arthropods colonizing and ovipositing on leaf pairs was examined in three treatments: occupied leaf ties (containing a leaf-tying caterpillar), unoccupied leaf ties, and non-tied control leaves.

3. The density of arthropods present in the occupied and unoccupied leaf ties after two weeks was seven and four times greater respectively, than non-tied controls. The guild composition of these early colonists differed among treatments, with the highest densities of leaf chewers, scavengers, and predators in occupied ties and the lowest densities in non-tied controls.

4. The densities of all arthropods ovipositing on leaf pairs in the occupied and unoccupied leaf tie treatments were four and three times greater than non-tied controls. Leaf-chewing insects (including leaf-tiers and non-tying inquiline species) and scavengers showed strong oviposition preferences for tied leaves. However, most species of leaf-tying caterpillars and the psocids (Psocoptera) did not distinguish between occupied and unoccupied ties, suggesting that these groups do not use occupancy-related cues in selecting oviposition sites.

Key words. Community structure, ecosystem engineering, indirect interactions, leaf shelter, oviposition, *Quercus alba*.

Introduction

To explain variation in abundance of insect herbivores on individual plants, ecologists have traditionally focused on variation in nutrient status and/or defensive chemistry of edible plant parts, since these can influence insect performance measures linked to fitness (e.g. preference–performance linkages; Price *et al.*, 1995). While nutrition and secondary chemistry play an important role in host selection for some herbivorous insects (especially butterflies; Renwick & Chew, 1994), a variety of other ecological

factors, including plant morphology, the density of conspecifics, and the presence of natural enemies, also influences host plant choice (reviewed in Thompson & Pellmyr, 1991). For predaceous arthropods, such as ladybird beetles, the presence of herbivorous prey (e.g. aphids) has been shown to have a large influence on oviposition site selection (Evans & Dixon, 1986). As a consequence, many models of plant–herbivore, predator–prey, and host–parasitoid population dynamics either implicitly or explicitly include information (or assumptions) about arthropod movement and oviposition site selection (Myers, 1976; Ives, 1992; Dwyer, 1995). For most arthropods, however, the understanding of the cues used to locate feeding and oviposition sites is poor.

Implicit in many studies of herbivore oviposition behaviour is the idea that during some phase of its life cycle, an insect has both the opportunity and ability to distinguish differences in quality among potential plants or plant parts

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as a food source for itself or its offspring. Some species do indeed make oviposition choices and feeding site choices that positively influence their fitness or that of their offspring (Singer *et al.*, 1988; Thompson, 1988; Brody & Waser, 1995). Many insects, however, are highly constrained in their ability to select among host plants owing to their mode of dispersal. In particular, species that disperse as juveniles (recently hatched or post-diapause) often have limited mobility, offering few avenues for host plant assessment (Dethier, 1959; Cain *et al.*, 1985; Hunter & Elkinton, 2000). Many generalist caterpillar species may also hatch in the canopy and passively disperse by ballooning, letting wind and gravity determine their eventual destination (Holmes & Schultz, 1988). Even for individuals that arrive at a suitable plant via oviposition, encounters with natural enemies or physical disturbance may often cause them to fly, drop off, or spin down on a silk thread to a new plant (Gross, 1993). Thus, understanding the factors that structure communities of arthropods found on different plants would be enhanced by consideration of the various colonization routes employed by the resident species.

One ecological factor that has been shown to positively influence arthropod colonization is the presence of leaf shelters. Many different kinds of arthropods (e.g. spiders, weaver ants, caterpillars, sawflies, and beetles) create leaf shelters by binding, tying, rolling, or webbing leaves together with silk (Wagner & Raffa, 1993; Berenbaum, 1999; Anderson & McShea, 2001; Fukui, 2001). These shelters often are secondarily colonized by a variety of arthropods that use them as a refuge and/or a feeding site (Carroll & Kearby, 1978; Damman, 1987; Cappuccino, 1993; Cappuccino & Martin, 1994; Martinsen *et al.*, 2000; Lill & Marquis, 2003; Lill, 2004). As such, the arthropods that build these leaf shelters are acting as physical ecosystem engineers, organisms that modify the biotic or abiotic environment which in turn, influences resource availability for other organisms (Jones *et al.*, 1994, 1997). In her study of the birch tube-maker, *Acrobasis betulella* (Hulst), Cappuccino (1993) demonstrated that adult oviposition is an important means of secondary colonization of existing leaf rolls. With the exception of this study, however, the mode of colonization by the secondary occupants has not been explicitly examined. An understanding of the mode(s) of colonization of leaf shelters is important because it provides an insight into the potential mechanisms underlying observed increases in local arthropod abundance on plants containing shelters (Lill & Marquis, 2003).

In the present study, the effects of leaf shelters on colonization of white oak (*Quercus alba* L.) leaves by a diverse community of leaf-dwelling arthropods were examined for a site in eastern Missouri (U.S.A.). Once leaves have fully expanded and hardened (late spring/early summer), white oak is colonized by a rich caterpillar fauna (22 species in six families; Lill & Marquis, 2003) that constructs leaf ties by binding overlapping leaves into *leaf sandwiches* using silk (Carroll & Kearby, 1978). For most species, these leaf ties serve as both room and board for the constructors. A few species, however, such as the skippers *Erynnis juvenalis* (F.)

and *E. brizo* (Bdv. & Leconte), appear to use the ties only as a shelter, feeding outside of the shelter at night. Most species feed primarily by skeletonizing the leaf epidermis inside the shelter, where they typically spend their entire larval development, occasionally adding leaves as food becomes scarce. Occupied ties usually contain frass and insect remains (exuvia, head capsules, etc.) amidst the silk webbing, which probably provides food for scavenging arthropods. Upon reaching the pre-pupal stage, the caterpillars usually exit the leaf ties and drop to the litter where they pupate. Secondary colonization of these leaf ties by other leaf-tying species and by non-tying inquilines (herbivores, scavengers, predators, and parasitoids) is extremely common, resulting in sequential occupation by an array of arthropods over the course of a season (Lill, 2004).

Previous work in this system showed that the presence of leaf ties on white oak trees significantly increased both the abundance of total arthropods (R. J. Marquis & J. T. Lill, unpubl. data) and the species richness of insect herbivores (Lill & Marquis, 2003) at the whole plant level. It was not clear, however, whether these increases were due to increased oviposition in/on the ties or to some other effect, such as increased survival or decreased emigration of insects on trees with shelters. Furthermore, for those species that were observed recruiting by oviposition into existing leaf ties, the cues used to locate and/or select among oviposition sites are unknown. The approach used in this study was to compare the colonization of pairs of leaves in three experimental treatments: (1) leaf ties that initially contained a shelter-building caterpillar; (2) leaf ties that were initially unoccupied; and (3) non-tied leaves. It was predicted that both colonization and oviposition would be higher on tied leaves than on non-tied leaves, and that moths (and other arthropods) would either show a preference for, or would have an easier time locating, occupied ties, due to occupancy-related cues (leaf damage, frass, silk, etc.). It is believed that this study is one of the first to characterize colonization patterns for an entire assemblage of arthropods.

Methods

Study site

This experiment was conducted at Cuivre River State Park, located near Troy, Missouri, U.S.A. The park is a northern extension of the Ozark plateau and is a second growth mixed oak-hickory forest with an understorey of flowering dogwood (*Cornus florida* L.), sassafras (*Sassafras albidum* Nees), sugar maple (*Acer saccharum* Marsh), redbud (*Cercis canadensis* L.), and various oak saplings, and an overstorey consisting mostly of white oak (*Quercus alba* L.), black oak (*Q. velutina* Lamarck), and hickory (*Carya* spp.).

Oviposition experiment

In late June 2000, experimental leaf ties were created on each of 20 white oak trees, including a mix of large saplings

and larger trees with low-hanging branches, all of which were located under closed canopy along a single south-south-west-facing slope in the Big Sugar Creek Natural Area, a 678 ha section of unmanaged forest located within the park. On each tree, 10 replicates of each of three treatments (occupied leaf tie, unoccupied leaf tie, and non-tied control) were established by locating adjacent pairs of undamaged (< 5% leaf area missing) and unoccupied leaves (no arthropods visible) on terminal branches and alternating treatment assignments such that the 30 leaf pairs were spread throughout the accessible understorey foliage (< 3 m). The occupied leaf ties were created by placing a single mid-late instar *Psilocorsis* caterpillar [either *Psilocorsis quercicella* (Clem.), *P. reflexella* (Clem.), or *P. cryptolechiella* (Cham.)] into an artificial leaf tie created by clipping two adjacent undamaged leaves together with a spring-loaded, lightweight plastic hair curler clip (Brentwood Beauty Laboratories International, Hillside, Illinois, U.S.A.). Caterpillars used in this treatment (referred to as TIE + CAT treatment hereafter) were collected from non-study trees at the study site. Unoccupied leaf ties (referred to as TIE treatment hereafter) were created similarly, but no caterpillar was added. For leaf pairs in the non-tied control treatment, clips were placed on each of the paired leaves to control for the presence of the clip.

After 14 days, all leaf ties and pairs of control leaves were harvested and individually placed in plastic storage bags. In the laboratory, all leaves were searched, recording the identity and abundance of all arthropod inhabitants, excluding oak spider mites [*Oligonychus bicolor* (Banks)], found within each leaf tie or on each pair of control leaves. All leaf-chewers were identified to species and non-chewers were identified to family (most insects) or morphotype (non-insect arthropods). For the leaf-chewers, each individual was classified as small, medium, or large, based on its instar at the time of collection and prior knowledge of the size ranges of these species. When small caterpillars were found, the leaves were searched for the remains of eggs as evidence of colonization via oviposition. For each TIE + CAT leaf pair, it was recorded whether the caterpillar originally placed in the tie had successfully established. This was possible because the skeletonization damage caused by *Psilocorsis* caterpillars is easily recognized, as are the characteristic silk and frass feeding tunnels/chambers they form inside the leaf tie. All arthropods that had hatched and/or colonized the leaves prior to inspection (*early colonists*) were removed at this time, and clipped leaves containing any eggs that had not hatched were placed in individual 500 ml clear plastic snap-top containers lined with moist filter paper to maintain high humidity. The containers were randomly placed on shelves under fluorescent lights set to a 14:10 h LD cycle at lab temperature ($\approx 22^\circ\text{C}$). The containers were inspected every 2–3 days for arthropods, and the identity and abundance of all individuals hatching was recorded. The final inspection was performed 2 weeks after harvesting the leaves, at which time the experiment was terminated. Photographs of the more common eggs were taken during the initial inspection by R.J.M.

Data analysis

The number of leaf pairs in each treatment colonized by one or more juvenile or adult arthropod at the time of collection was compared with a *G*-test (Zar, 1999). The abundance of arthropods colonizing leaf pairs in each treatment was $\log(x + 1)$ transformed to normalize the residuals and analysed using mixed-model analysis of variance (PROC MIXED; Littell *et al.*, 1996), with treatment as a fixed effect and tree as a random effect. The individual leaf tie was used as the unit of replication for all abundance data. The LSMEANS statement with the pdiff option was used for means comparisons (Littell *et al.*, 1996). In addition, these early colonists were assigned to one of four feeding guilds (leaf chewers, scavengers, sucking insects, and predators) and the abundance of arthropods in each of the four guilds was summed across the 10 replicates/treatment for each tree. These data were log-transformed and analysed with canonical discriminant analysis [(CDA), PROC CANDISC; SAS Institute, 1989] to examine treatment effects on the composite guild structure of the early colonists. When the treatment effect was significant in the multivariate main effects model, treatment means were compared with pairwise *F*-tests based on Mahalanobis distances (SAS Institute, 1989). Because data from all three treatments were collected from each tree, the response variables may have violated assumptions of independence. However, these tree effects, if they were present, should have *decreased* the ability to detect treatment effects; this test was therefore viewed as a conservative approach to examining treatment effects on community structure.

The abundance of arthropods hatching in each treatment, including both those hatching in the lab and small caterpillars that hatched in the field and for which hatched eggs could be located, was $\log(x + 1)$ transformed and analysed with PROC MIXED as described above for the early colonists. The oviposition patterns of specific groups of arthropods (leaf-chewers, leaf-tying caterpillars, psocids, and thrips) were examined in further detail using nonparametric ANOVA (Friedman's test, including tree as a random blocking factor; Zar, 1999) because the data contained zeros in many cells and could not be transformed to meet assumptions of ANOVA. Post-hoc means separation was performed as outlined in Zar (1999). Because oviposition by predators and sucking insects was rare, these data were analysed with a *G*-test using presence/absence data rather than abundance.

Results

Of the 600 leaf pairs originally marked, five were missing at the time of collection (three from the control treatment and one each from the TIE and TIE + CAT treatments). Ninety percent of the ties in the TIE + CAT treatment showed evidence of successful establishment by the *Psilocorsis* caterpillar placed in the tie at the beginning of the experiment, and 60% ($n = 120$ ties) still contained a medium or large *Psilocorsis* caterpillar at the time of collection (the remaining 30%

showed evidence of establishment but the caterpillar was no longer present). A total of 1288 arthropods were removed from the 595 leaf pairs at the time of collection; given that a maximum of 120 of these were the *Psilocorsis* caterpillars remaining from the TIE + CAT treatment, at least 1168 arthropods colonized these leaves during the 14 day time period. Of these, 98 (8.4%) were small caterpillars that hatched prior to collection (i.e. chorion remains were found on the leaves); these individuals were included with the oviposition data. The remainder was a mix of arthropods that moved onto (or landed on) the leaves or for which oviposition occurred but could not be definitively established (i.e. remains of eggs were not found). Following removal of the early colonists, 2036 additional arthropods hatched from the harvested leaves in the laboratory.

Colonization

At the time of collection, 81% and 91% of the TIE and TIE + CAT leaf ties, respectively, had been colonized by at least one arthropod, compared with 31% of the control leaf pairs. This difference was highly significant ($G_{\text{adj}} = 186.75$, d.f. = 2, $P = 0.0001$), and does not include *Psilocorsis* sp. caterpillars remaining from the TIE + CAT treatment. The total number of arthropods found on a leaf pair ranged from 0 to 15 (median = 1). There was an approximate 4-fold and 7-fold increase in the numbers of arthropods colonizing leaves in the TIE and TIE + CAT treatments compared with controls respectively ($F_{2,573} = 210.1$, $P = 0.0001$; Fig. 1, early colonists). The tree effect (random block) was marginally significant ($Z = 1.36$, $P = 0.09$). In total, insects from 10 different orders were found colonizing the leaves: Collembola, Coleoptera, Diptera, Hemiptera, parasitoid Hymenoptera, Lepidoptera, Neuroptera, Phasmida, Psocoptera, and Thysanoptera. Non-insect colonists included various spiders (from at least five families), an arboreal centipede, and a snail. The most abundant early colonist, comprising 22% of all individuals, was a scavenging psocid (unidentified sp.).

Of the 28 early colonizing leaf-chewing species (Table 1), 20 (71%) were recorded only from leaf ties (TIE and/or TIE + CAT treatments), whereas the non-tied control treatment attracted only a single unique species, *Acrionicta increta* (Morr.), as a colonist (Table 1; note that this species was, however, found hatching in ties). A few control leaf pairs (5 or < 3%) were colonized by leaf-tying caterpillars because one of the control leaves came into contact with a non-study leaf (and a tie was initiated). In the CDA analysis of the early colonists' guild structure, treatment was highly significant (Wilk's lambda = 0.105, $F_{8,108} = 28.20$, $P = 0.0001$). The means of the first canonical variable (CAN1) differed significantly among the treatments ($F_{8,108} = 28.20$, $P = 0.0001$), with treatment explaining 87% of the variation in CAN1 (Fig. 2a). In contrast, treatment had no effect on CAN2 ($F_{3,55} = 1.56$, $P = 0.21$). Examination of the Mahalanobis distances indicated that all three treatments differed significantly from one another ($P < 0.0001$ for all treatment pairs). The leaf-chewing guild

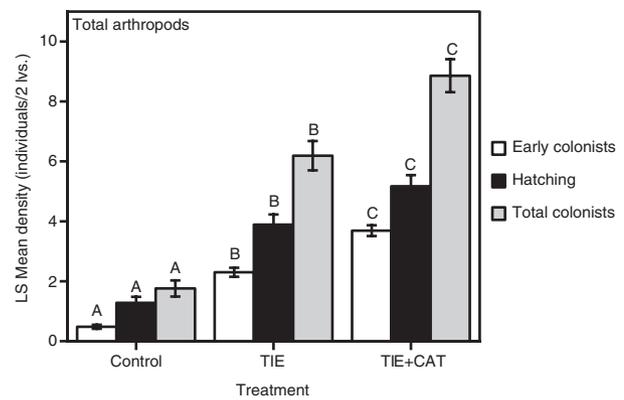


Fig. 1. Least square mean (\pm SE) densities of arthropods colonizing and hatching from leaf pairs in three treatments. Data were analysed with mixed-model ANOVA and means were adjusted for the random block effect. The depicted means are untransformed for presentation purposes (all analyses, including means separation were performed on $\log(x+1)$ transformed data). Clipping leaves together (TIE treatment) significantly increased the densities of both early colonists and hatching arthropods over non-clipped (Control) leaves, with leaf ties that initially contained a caterpillar (TIE + CAT treatment) attracting the highest densities of colonists.

contributed the most to CAN1, followed by scavengers and predators (Fig. 2b), all of which followed the same ranking: TIE + CAT > TIE > control. Sucking insects, however, contributed almost entirely to CAN2, which was unaffected by treatment in both the multivariate analysis and in follow-up univariate ANOVAS.

Oviposition

The number of arthropods hatching from a leaf pair ranged from 0 to 27 (median = 2). The mean densities of total arthropods hatching differed significantly among treatments ($F_{2,573} = 83.31$, $P = 0.0001$) in the mixed-model analysis. There were approximately 3-fold and 4-fold more arthropods hatching from leaves in the TIE and TIE + CAT treatments compared with controls, respectively (Fig. 1). There was a significant tree effect ($Z = 2.00$, $P = 0.023$) for hatching density. The densities of caterpillars hatching in the three treatments followed a similar pattern (Fig. 3a). This pattern was driven in large part by species in the leaf-tying guild (Table 1) that preferred to oviposit in pre-existing leaf ties (Fig. 3b). The apparent preference of leaf-ties for previously occupied ties was driven entirely by the oviposition pattern of *Pococera expandens* (Wlk.), which showed a strong preference for occupied ties; when *P. expandens* was excluded from the analysis, the densities of the remaining leaf-tier species was not different (Fig. 3b). There were three instances of leaf-tiers ovipositing on leaves in the control treatment; these eggs (*P. reflexella*) were placed in the interstice between the leaf and the clip. The density of psocids hatching in leaf ties was three times greater than

Table 1. Leaf-chewing arthropods colonizing and ovipositing on leaves in the three treatments (C = non-tied control leaves, T = initially unoccupied ties, T + C = ties with a *Psilocorsis* caterpillar added initially). Asterisks indicate species found in low abundance in the study (< 5 individuals)

| Taxon† | Colonized | Oviposited | Leaf shelter builder |
|--|-------------|-------------|----------------------|
| Coleoptera | | | |
| Chrysomelidae | | | |
| <i>Pachybrachis</i> sp. | T, T + C | C, T, T + C | |
| Curculionidae | | | |
| <i>Cyrtopistomes castaneus</i> (Roelofs) | C, T, T + C | – | |
| Hymenoptera | | | |
| Tenthredinidae | | | |
| <i>Caliroa</i> sp. | T, T + C | T, T + C | |
| Lepidoptera | | | |
| Arctiidae | | | |
| <i>Halysidota tessellaris</i> (JE Smith)* | C, T | – | |
| Bucculatricidae | | | |
| <i>Bucculatrix</i> spp.* | T, T + C | T | |
| Gelechiidae | | | |
| <i>Arogalea cristifasciella</i> (Cham.) | T, T + C | – | x |
| <i>Chionodes fuscomaculella</i> (Cham.) | C, T, T + C | T, T + C | x |
| <i>Coleotechnites quercivorella</i> (Cham.)* | – | T, T + C | x |
| <i>Pseudotelphusa</i> sp. nov. | T, T + C | T + C | x |
| <i>Trypanisma prudens</i> (Clem.) | C, T, T + C | T, T + C | |
| escape hole gelechiid* | C, T, T + C | C | |
| Gracillariidae | | | |
| <i>Pyllonorycter tcheua</i> (?)* | T | C | |
| Hesperiidae | | | |
| <i>Erynnis juvenalis</i> (F)* | T, T + C | – | x |
| Limacodidae | | | |
| <i>Acharia (Sabine) stimulea</i> (Clem.)* | – | T + C | |
| <i>Euclea delphinii</i> (Boisduval)* | T + C | T + C | |
| <i>Natada nasoni</i> (Grt.) | – | C, T | |
| Megalopygidae | | | |
| <i>Lagoa crispata</i> (Pack.)* | T + C | – | |
| Noctuidae | | | |
| <i>Acronicta increta</i> (Morr.) | C | C, T + C | |
| <i>Hyperstrotia secta</i> (Grt.)* | T | – | |
| <i>Morrisonia confusa</i> (Hbn.)* | T | – | x |
| Notodontidae | | | |
| <i>Nadata gibbosa</i> (JE Smith)* | T | T | |
| Oecophoridae | | | |
| <i>Machimia tentoriferella</i> (Clem.) | T, T + C | – | |
| <i>Psilocorsis quercicella</i> (Clem.) | T, T + C | T, T + C | x |
| <i>Psilocorsis reflexella</i> (Clem.)‡ | C, T, T + C | C, T, T + C | x |
| Pyrilidae | | | |
| <i>Oneida lunalis</i> (Hulst)* | T + C | – | x |
| <i>Pococera expandens</i> (Wlk.) | – | T, T + C | x |
| basket-maker pyralid* | T | T | x |
| Tischeriidae | | | |
| <i>Tischeria citrinipennella</i> (Clem.) | C, T + C | T, T + C | |
| <i>Stigmella</i> sp. | T, T + C | T, T + C | |
| Tortricidae | | | |
| <i>Pandemis limitata</i> (Rob.)* | T + C | – | x |
| frass-tube tortricid | T, T + C | T, T + C | |
| Phasmida | | | |
| Phasmatidae | | | |
| <i>Diapheromera femorata</i> (Say)* | T | – | |

†Nomenclature for Lepidoptera follows Hodges (1983).

‡In early instars, a third *Psilocorsis* species, *P. cryptolechiella*, is indistinguishable from *P. reflexella*.

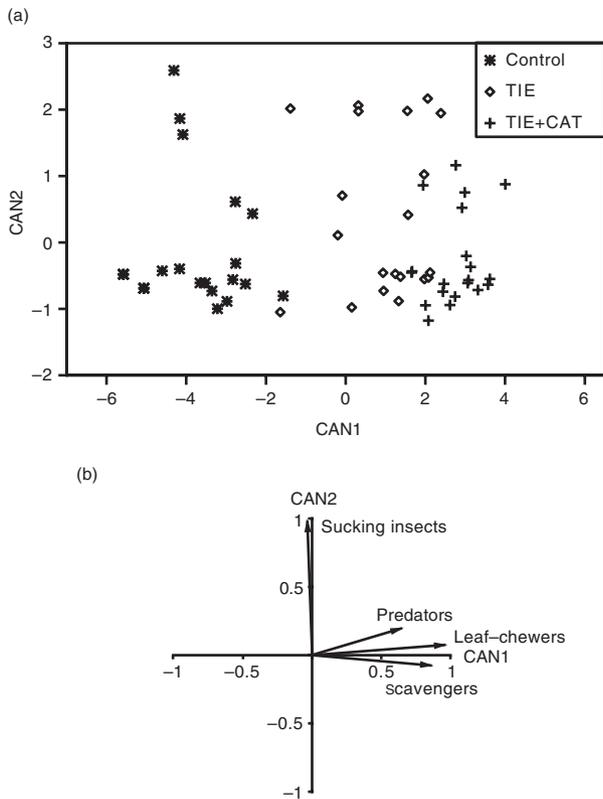


Fig. 2. (a) Scatter plot of two canonical variables (CAN1 and CAN2) illustrating the joint response of four guilds of early colonizing arthropods to three experimental treatments (C, control; TIE, artificial leaf ties added; TIE+CAT, caterpillars added to artificial ties). (b) Total canonical structure indicating relative contributions of each of the four arthropod guilds to the canonical coefficients. The arthropod communities present in each of the three treatments separate along the first axis (CAN1), based on the densities of leaf-chewers, scavengers, and predators, with higher values of CAN1 corresponding to higher densities of these three arthropod guilds.

the density hatching on non-tied leaves (Fig. 3c); however, psocids did not show a preference for occupied vs. unoccupied ties. The single species of psocid was the dominant species hatching from the leaves, accounting for 68% of all hatching arthropods. The other major scavenger, thrips, showed a strong oviposition preference for leaf ties over non-tied leaves, but in contrast to psocids, preferred occupied to unoccupied ties (Fig. 3c). Sucking insects and predators were in low densities, but had a significant oviposition preference for tied leaves [$G_{adj.} = 14.8$, d.f. = 2, $P < 0.001$ (sucking insects); $G_{adj.} = 8.5$, d.f. = 2 $P = 0.02$ (predators)].

Combined colonization and oviposition

On average, a non-tied leaf pair was host to less than two arthropods (summing across both early colonists and those

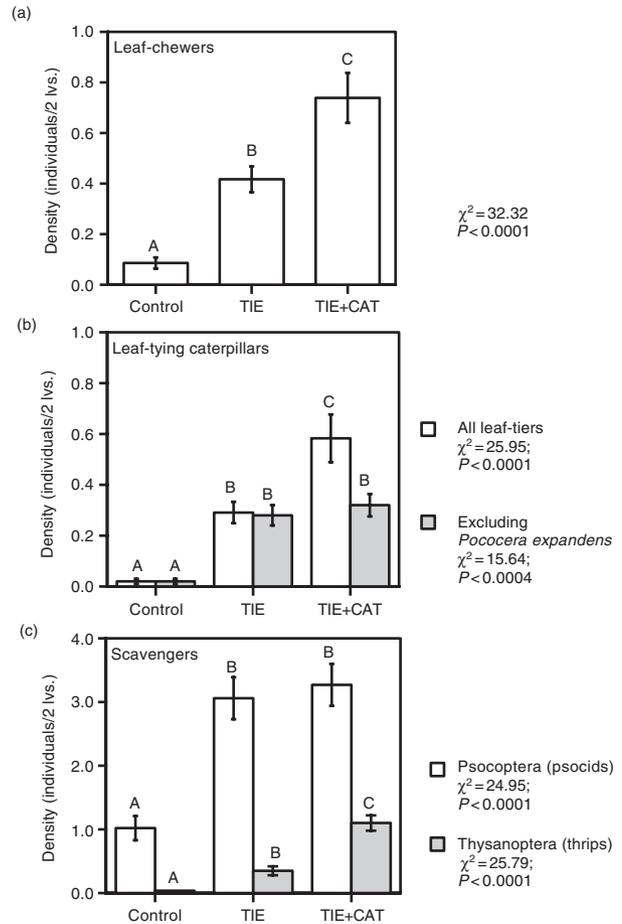


Fig. 3. Mean (\pm SE) densities of all leaf-chewing insects (a), leaf-tying caterpillars (b), and scavengers (c) hatching from treatment leaves. Means with the same letter are not significantly different based on Friedman's Test of ranked data and the associated means separation procedure (Zar, 1999).

hatching from eggs), whereas leaf pairs in the TIE and TIE+CAT treatments hosted approximately six and nine arthropods respectively (Fig. 1).

Discussion

Leaf shelters had a dramatic effect on both the abundance and composition of forest arthropods on *Quercus alba*. Within 14 days, most of the artificial leaf shelters had been located and colonized, suggesting that the habitat provided by oak leaf shelters is a high quality resource for oak arthropods representing a variety of feeding guilds and at least three trophic levels (herbivores, scavengers, and predators). In contrast, there were no major groups of arthropods that preferred to occupy non-tied leaves, suggesting that these exposed leaves are either avoided or not preferred by most oak arthropods searching for colonization and/or feeding sites during the course of the study.

It is possible that different results would have been obtained had the experiment been run at a different time of the season. For example, one common species of leaf-tier, *Arogalea cristifasciella* (Cham.), was not recorded colonizing the artificial ties, probably because the experiment was run just prior to emergence of first generation adults; had it been run a week or two later, oviposition events by this species would probably have been recorded. In addition, generalist predators and sucking insects, which were scarce in June, typically increase in abundance in the late summer and early fall at the study site (R. J. Marquis & J. T. Lill, unpubl. data), suggesting that treatment effects on those groups may be more evident at other times of the season. Future studies are needed in order to generalize these effects across the season and probe for possible time \times treatment interactions.

The arthropods colonizing the experimental leaf pairs arrived by various routes. Of the 32 species of leaf-chewing insects found colonizing and/or ovipositing, slightly more than one-third (12 species) build leaf shelters, reinforcing previous findings that pre-existing shelters are actively sought out by other species (or subsequent generations) of shelter-builders (Lill & Marquis, 2003; Lill, 2004). More than half of these shelter-building caterpillar species also oviposited in the artificial leaf shelters, suggesting that oviposition is an important (or perhaps the primary) route of colonization. Only one species of leaf-tier, *P. expandens*, however, showed a strong preference for previously occupied shelters, suggesting that most of these moth species do not use occupancy-related cues in selecting oviposition sites but perhaps search for *tight spaces* on foliage in which to insert their ovipositors, that is leaves that are overlapping or touching in some way (Marquis *et al.*, 2002). These results are in agreement with those of a previous experiment in which no difference in the seasonal accumulation of leaf-chewing species between trees with occupied vs. non-occupied artificial ties was found (Lill & Marquis, 2003). Early instar leaf-tying caterpillars have been observed constructing ties between oak leaves and fallen dead leaves, between leaves and flagging tape, between the clips and the leaf surface, and in the tight crevices between leaf galls and laminae, supporting this interpretation. Similarly, Cappuccino and Martin (1994) reported that oviposition by secondary colonists did not differ between damaged and undamaged birch leaf ties, suggesting little or no role for occupancy-related cues.

There were also many non-shelter building herbivores that frequently oviposited into experimental leaf ties, including casebearing beetles in the genus *Pachybrachis*, *Caliroa* sp. sawfly larvae, leaf miners, and even a limacodid caterpillar, *Natada nasoni* (see Table 1), all of which tend to be somewhat gregarious. All of the scavenging species, especially the psocids and thrips, preferred leaf ties for oviposition; of these two groups, however, only the thrips showed a preference for occupied leaf shelters, which may reflect differences in their respective diets (with the thrips utilizing more animal-based detritus than the psocids). Both predators and sucking insects (primarily leaf hoppers and aphids) also preferentially

oviposited in or on leaf shelters, but were relatively uncommon at the time this experiment was run.

Two species, the Asiatic oak weevil, *Cyrtopistomes castaneus* (Roelofs), and the common acorn weevil, *Curculio* sp., colonized the shelters as adults, probably using them as a hideout during the day (i.e. they typically were found resting rather than feeding). A third species, *Machimia tentoriferella* (Clem.), constructs sheet webs on the lower surfaces of oak leaves, and moves frequently; during these moves, it may move into leaf ties for additional shelter.

It is apparent from these results that forest arthropods occupy leaf shelters for different reasons and with different degrees of fidelity. The leaf-tying caterpillars, which will not feed outside of leaf shelters, spend considerable time and energy constructing and maintaining their shelters (Fitzgerald & Clark, 1994; Berenbaum, 1999). Placing eggs directly in existing shelters or at points of contact between leaves would minimize the amount of time and energy neonate larvae expend searching for a construction site, during which time the larvae may be prone to desiccation (Willmer, 1982; Larsson *et al.*, 1997) and the adults and larvae may be prone to attack by natural enemies (Bergelson & Lawton, 1988; Bernays, 1997). The scavengers (psocids, thrips, and a common rove beetle), are all very small and likely seek out shelters for a hospitable microclimate and because shelters represent a likely source of food, given the high occupancy rate by other arthropods. Although it was apparent that the thrips and rove beetles occupying these leaf ties were not feeding on caterpillars, it is possible that they feed on eggs or smaller arthropods, such as mites. Since natural enemies were relatively scarce inside these shelters, it is quite possible that all of the primary and secondary occupants of these leaf shelters seek them out for protection. Various studies have indicated that insects occupying leaf shelters gain protection against generalist predators, including birds (Atlegim, 1989; R. J. Marquis & C. J. Whelan, unpubl. data), ants (Fowler & MacGarvin, 1985; Heads & Lawton, 1985; Damman, 1987; Vasconcelos, 1991; Loeffler, 1996), ladybird beetles (Messina *et al.*, 1997), hemipterans (Morris, 1972), social wasps (Damman, 1987), spiders (Morris, 1972; Damman, 1987), and fish (Mueller & Dearing, 1994).

One potential negative consequence of using shelters as colonization/oviposition sites, however, is that they are frequently already occupied and thus are likely to result in competition (both intra- and inter-specific). There have been several studies that have shown that ovipositing females avoid plants or plant parts occupied (or perceived as occupied) by conspecifics or heterospecifics (reviewed in Thompson & Pellmyr, 1991). Very high levels of damage by sequential occupation of leaf shelters on white oak have been observed previously at the study site, so it is quite possible that larvae could become food-limited. A previous study on this system, however, found no effect of the age of the leaf tie on the likelihood of secondary occupation by other leaf-tiers (Lill, 2004). This suggests that moths may lack the ability to discriminate among shelters with differing numbers of occupants or variable amounts of remaining edible tissues when selecting oviposition sites.

In summary, the strong effects of leaf shelters on patterns of arthropod colonization and oviposition demonstrated in this study suggest that leaf shelters (and the engineering arthropods that construct them) are an important organizing force influencing the spatial patterning of oak arthropods both within and among trees. As such, they are likely to influence the local population dynamics of the affected species. Moreover, because many of the affected herbivore species were found to recruit to leaf shelters through oviposition, plants containing leaf shelters may incur increased herbivore loads, resulting in increased amounts and/or altered distributions of leaf damage, both of which may have implications for plant fitness (Marquis, 1992a,b). Because shelter-building caterpillars are a prominent feature of the herbivore faunas associated with broad-leaved trees throughout eastern North America and Europe (Lill & Marquis, 2003), it is predicted that they will have similar ecological impacts in these forest ecosystems.

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References

- Anderson, C. & McShea, D.W. (2001) Intermediate-level parts in insect societies: adaptive structures that ants build away from the nest. *Insectes Sociaux*, **48**, 291–301.
- Atlegrim, O. (1989) Exclusion of birds from bilberry stands: impact on insect larval density and damage to bilberry. *Oecologia*, **79**, 136–139.
- Berenbaum, M. (1999) Shelter-making caterpillars: rolling their own. *Wings*, **22**, 7–10.
- Bergelson, J.M. & Lawton, J.H. (1988) Does foliage damage influence predation on the insect herbivores of birch? *Ecology*, **69**, 434–445.
- Bernays, E.A. (1997) Feeding by caterpillars is dangerous. *Ecological Entomology*, **22**, 121–123.
- Brody, A.K. & Waser, N.M. (1995) Oviposition patterns and larval success of a pre-dispersal seed predator attacking two con-familial host plants. *Oikos*, **74**, 447–452.
- Cain, M.L., Eccleston, J. & Karieva, P.M. (1985) The influence of food plant dispersion on caterpillar searching success. *Ecological Entomology*, **10**, 1–7.
- Cappuccino, N. (1993) Mutual use of leaf-shelters by lepidopteran larvae on paper birch. *Ecological Entomology*, **18**, 287–292.
- Cappuccino, N. & Martin, M.-A. (1994) Eliminating early-season leaf-tiers of paper birch reduces abundance of mid-summer species. *Ecological Entomology*, **19**, 399–401.
- Carroll, M.R. & Kearby, W.H. (1978) Microlepidopterous oak leaf tiers (Lepidoptera: Gelechioidea) in central Missouri. *Journal of the Kansas Entomological Society*, **51**, 457–471.
- Damman, H. (1987) Leaf quality and enemy avoidance by the larvae of a pyralid moth. *Ecology*, **68**, 88–97.
- Dethier, V.G. (1959) Food plant distribution and density and larval dispersal as factors affecting insect populations. *Canadian Entomologist*, **91**, 581–596.
- Dwyer, G. (1995) Simple models and complex interactions. *Population Dynamics: New Approaches and Synthesis* (ed. by N. Cappuccino and P. W. Price), pp. 209–228. Academic Press, San Diego, U.S.A.
- Evans, E.W. & Dixon, A.F.G. (1986) Cues for oviposition by ladybird beetles (Coccinellidae): response to aphids. *Journal of Animal Ecology*, **55**, 1027–1034.
- Fitzgerald, T.D. & Clark, K.L. (1994) Analysis of leaf-rolling behavior of *Caloptilia serotinxella*. (Lepidoptera: Gracillariidae). *Journal of Insect Behavior*, **7**, 859–872.
- Fowler, S.V. & MacGarvin, M. (1985) The impact of hairy wood ants, *Formica lugubris*, on the guild structure of herbivorous insects on birch, *Betula pubescens*. *Journal of Animal Ecology*, **54**, 847–855.
- Fukui, A. (2001) Indirect interactions mediated by leaf shelters in animal-plant communities. *Population Ecology*, **43**, 31–40.
- Gross, P. (1993) Insect behavioral and morphological defenses against parasitoids. *Annual Review Of Entomology*, **38**, 251–273.
- Heads, P.A. & Lawton, J.H. (1985) Bracken, ants and extrafloral nectaries. III. How insect herbivores avoid ant predation. *Ecological Entomology*, **10**, 29–42.
- Hodges, R. (1983) *Checklist of the Lepidoptera of America north of Mexico*. Wedge Entomological Foundation, London, U.K.
- Holmes, R.T. & Schultz, J.C. (1988) Food availability for forest birds: effects of prey distribution and abundance on bird foraging. *Canadian Journal of Zoology*, **66**, 720–728.
- Hunter, A.F. & Elkinton, J.S. (2000) Effects of synchrony with host plant on populations of a spring-feeding lepidopteran. *Ecology*, **81**, 1248–1261.
- Ives, A.R. (1992) Density-dependent and density-independent parasitoid aggregation in model host-parasitoid systems. *American Naturalist*, **140**, 912–937.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as ecosystem engineers. *Ecology*, **78**, 1946–1957.
- Larsson, S., Häggström, H.E. & Denno, R.F. (1997) Preference for protected feeding sites by larvae of the willow-feeding leaf beetle *Galerucella lineola*. *Ecological Entomology*, **22**, 445–452.
- Lill, J.T. (2004) Seasonal dynamics of leaf-tying caterpillars on white oak. *Journal of the Lepidopterists' Society*, **58**, 1–6.
- Lill, J.T. & Marquis, R.J. (2003) Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology*, **84**, 682–690.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute, Cary, North Carolina, U.S.A.
- Loeffler, C.C. (1996) Caterpillar leaf folding as a defense against predation and dislodgement: staged encounters using *Dichomeris* (Gelechioidea) larvae on goldenrods. *Journal of the Lepidopterists' Society*, **50**, 245–260.
- Marquis, R.J. (1992a) Selective impact of herbivores. *Ecology and Plant Resistance to Herbivores and Pathogens* (ed. by R. S. Fritz and E. W. Simms), pp. 301–325. University of Chicago Press, Chicago, Illinois, U.S.A.
- Marquis, R.J. (1992b) A bite is a bite is a bite? Constraints on response to folivory in *Piper arieianum* (Piperaceae). *Ecology*, **73**, 143–152.

- Marquis, R.J. & Whelan, C.J. (1994) Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology*, **75**, 2007–2014.
- Marquis, R.J., Lill, J.T. & Piccinni, A. (2002) Effect of plant architecture on colonization and damage by leaf-tying caterpillars of *Quercus alba*. *Oikos*, **99**, 531–537.
- Martinsen, G.D., Floate, K.D., Waltz, A.M., Wimp, G.M. & Whitham, T.G. (2000) Positive interactions between leafrollers and other arthropods enhances biodiversity on hybrid cottonwoods. *Oecologia*, **123**, 82–89.
- Messina, F.J., Jones, T.A. & Nielson, D.C. (1997) Host-plant effects on the efficacy of two predators attacking Russian wheat aphids (Homoptera: Aphididae). *Environmental Entomology*, **26**, 1398–1404.
- Morris, R.F. (1972) Predation by insects and spiders inhabiting colonial webs of *Hyphantria cunea*. *Canadian Entomologist*, **104**, 1197–1207.
- Mueller, U.G. & Dearing, M.D. (1994) Predation and avoidance of tough leaves by aquatic larvae of the moth *Paraponyx rugosalis* (Lepidoptera: Pyralidae). *Ecological Entomology*, **19**, 155–158.
- Myers, J.H. (1976) Distribution and dispersal in populations capable of resource depletion. A simulation model. *Oecologia*, **23**, 255–269.
- Price, P.W., Craig, T.P. & Roininen, H. (1995) Working toward theory on galling sawfly population dynamics. *Population Dynamics: New Approaches and Synthesis* (ed. by N. Cappuccino and P. W. Price), pp. 321–338. Academic Press, San Diego, U.S.A.
- Renwick, J.A.A. & Chew, F.S. (1994) Oviposition behavior in Lepidoptera. *Annual Review Of Entomology*, **39**, 377–400.
- SAS Institute (1989) *SAS/STAT User's Guide, Version 6*, 4th edn, Vol. 1. SAS Institute, Cary, North Carolina, U.S.A.
- Singer, M.C., Ng, D. & Thomas, C.D. (1988) Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution*, **42**, 977–985.
- Thompson, J.N. (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata*, **47**, 4–14.
- Thompson, J.N. & Pellmyr, O. (1991) Evolution of oviposition behavior. *Annual Review Of Entomology*, **36**, 65–89.
- Vasconcelos, H.L. (1991) Mutualism between *Maieta guianensis* Aubl., a myrmecophytic melastome, and one of its ant inhabitants: ant protection against insect herbivores. *Oecologia*, **87**, 295–298.
- Wagner, M.R. & Raffa, K.F. (1993) *Sawfly Life History Adaptation to Woody Plants*. Academic Press, San Diego, U.S.A.
- Willmer, P.G. (1982) Microclimate and the environmental physiology of insects. *Advances in Insect Physiology*, **16**, 1–57.
- Zar, J.H. (1999) *Biostatistical Analysis*. Prentice Hall, Upper Saddle River, New Jersey, U.S.A.

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