



Plant architecture affects periodical cicada oviposition behavior on native and non-native hosts

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Variation in plant quality provides a basis for oviposition site selection for a variety of insects. Of the plant traits that influence plant–insect interactions, plant architecture has received little attention despite its putative role in modulating oviposition behavior. In a common garden comprised of native and non-native plant species, we assessed how host plant architecture and identity influenced the oviposition behavior of 17-year periodical cicadas (Homoptera: Cicadidae: *Magicicada*). On each host, we quantified the availability of branches suitable for oviposition and compared those measures with the branches used by ovipositing cicadas. Using this approach, we determined how the structural attributes of plants (i.e. branch diameter, length and incline) affected oviposition site selection. We then related cicada oviposition preferences to offspring performance by quantifying egg hatching success. On each host species, cicadas selectively used broader and longer branches for oviposition, suggesting that branch architecture provides a basis for oviposition behavior irrespective of plant identity. Broader and longer branches were more abundant on native than on non-native hosts in our study, contributing to greater oviposition loads among the native species. Egg hatching success was similar among native and non-native hosts. However, it is possible that the use of native plants for oviposition could enhance offspring output because native hosts generally contained more viable eggs per egg nest and more egg nests per plant. While previous accounts of cicada oviposition preferences have focused on differences in oviposition loads among hosts, our evaluation of within-host branch selection by ovipositing cicadas helps to clarify oviposition preferences at a higher resolution and demonstrates that plant architecture provides an important basis for oviposition behavior. Furthermore, because branch structure can differ substantially among host species, our results suggest that periodical cicadas may be sensitive to the changes in plant composition that often result from non-native plant invasions.

Oviposition site selection is often an adaptive response to variation in host plant quality (Jaenike 1990, Mayhew 1997). For a variety of herbivorous insects, adults are more mobile than juveniles, and because plants exhibit fine-scale heterogeneity in a number of traits that affect insect performance (Marquis 1992), offspring fitness can be constrained largely by the parent's choice of an oviposition site (Mayhew 1997, 2001, Gripenberg et al. 2010). In light of the potential fitness consequences of oviposition site selection, understanding the determinants of oviposition behavior can help identify factors that moderate plant–insect interactions and influence insect population dynamics (Thompson 1988, Mayhew 1997).

The manner in which non-native plants modify insect oviposition behavior is of particular concern since plant invasions are occurring at unprecedented rates and impacting ecosystems worldwide (Mack et al. 2000, Pimentel et al. 2000). Non-native plant invasions can reduce native plant diversity and abundance, thereby altering the composition of plants available to herbivores (Yurkonis et al. 2005, Hejda et al. 2009, Flory and Clay 2010, Simao et al. 2010). Invader-induced shifts in plant community structure can influence insect oviposition behavior by constraining the availability of preferred hosts (Gibbs and van Dyck 2009).

For dispersal-limited insects, the increased presence of non-native plants may force females to use less suitable plants for oviposition, perhaps at a cost to reproductive success. Indeed, native and non-native plant species may differ in their suitability as hosts, and this variation in oviposition site quality can vary both within and among individual plants (Karbon 1992). Patterns of native and non-native plant use by herbivorous insects often correlate with a number of plant traits, such as tissue nutrient content and secondary chemistry, plant architecture, and flowering and vegetative phenology (reviewed by Marquis 1992). Of these traits, however, plant architecture is among the least studied despite its putative role in modulating oviposition behavior (Marquis and Whelan 1996, Marquis et al. 2002, Espirito-Santo et al. 2007).

Previous studies have generally quantified plant architecture in terms of overall host stature or growth form and demonstrate that the frequency of oviposition tends to increase with plant size and complexity (Tiritilli and Thompson 1988, Haysom and Coulson 1998, Araujo et al. 2006). More detailed studies of host plant architecture have also examined the effects of leaf density and branch structure on insect behavior (Alonso and Herrera 1996, Marquis et al. 2002). Apart from measures of overall plant stature, branch architecture can vary considerably among host plants, and

the structural attributes of branches may affect the quality of oviposition sites by either imposing physical constraints on the process of oviposition or influencing the environmental conditions surrounding the incubating eggs. A more thorough analysis of host plant architecture that considers the structural attributes of the branch chosen by the ovipositing female would clarify the manner in which branch structure influences oviposition site selection, thereby providing insight into the ecology of plant–insect interactions. In this study, we quantified host plant architecture in terms of three key attributes of branch structure (i.e. branch diameter, length and incline) for an array of native and non-native host plant species and evaluated how branch structure affects the oviposition behavior and hatching success of 17-year periodical cicadas (Homoptera: Cicadidae: *Magicicada*).

During emergence years, periodical cicadas are among the most abundant herbivores in North American deciduous forests where they develop belowground for a period of 13 or 17 years before emerging synchronously at high densities (Dybas and Davis 1962, Dybas and Lloyd 1974, Williams et al. 1993). Adults live briefly aboveground, during which time they must select host plants suitable for the long-term survival of their offspring. Oviposition occurs along the underside of branches of a variety of native and non-native plant species (Dybas and Lloyd 1974, White 1980, Cook et al. 2001, Cook and Holt 2006, Brown and Zuefle 2009, Clay et al. 2009), a process that is likely constrained by branch structure since an ovipositing female must grasp and inject her ovipositor repeatedly along the long axis of the host branch. Upon hatching, cicada nymphs fall from egg nests and burrow underground to feed on root xylem fluids of the host plant (Williams and Simon 1995). Unlike adults, soil-dwelling nymphs are limited in their ability to move among host plants, and thus their success is largely constrained by the adult's choice of an oviposition site (Karbon 1984, Williams and Simon 1995). In light of the long generation time of periodical cicadas, host plant composition and thus the availability of suitable oviposition sites is likely to change between successive emergence years. Periodical cicadas may be particularly vulnerable to shifts in host plant composition because the fragmented habitat in which they most commonly occur is highly susceptible to non-native plant invasions (Meiners et al. 2002, Flory and Clay 2006). To help gauge the vulnerability of periodical cicadas to changes in host plant composition, it is necessary to evaluate whether oviposition site selection is driven by host species identities or other likely determinants of oviposition behavior, such as host plant architecture.

We evaluated periodical cicada oviposition behavior within an experimental common garden comprised of native and non-native host plant species. We quantified the availability of branches suitable for oviposition and compared those measures with the branches used by ovipositing cicadas, an approach that provided an unbiased evaluation of host plant selection. We then related patterns of oviposition behavior to offspring performance by quantifying cicada egg hatching success, a measure of performance that reflects the most immediate and direct fitness consequences of oviposition site selection. Through this design, we sought to determine how host plant architecture affects the oviposition behavior and hatching success of periodical cicadas.

If plant architectural traits influence oviposition site selection and hatching success, and if such traits are related to plant origin (i.e. native vs non-native species), then shifts in plant community composition that result from non-native plant invasions may alter cicada population dynamics.

Methods

Study site and species

We conducted this study within the Indiana Univ. Research and Teaching Preserve at a site characterized by a mosaic of abandoned agricultural fields and bottomland hardwood forest (39°13'10"N, 86°32'10"W; Monroe County, IN, USA). Periodical cicadas of Brood X, a large brood that spans the Midwest and reaches peak densities near Monroe County, Indiana (Young and Kritsky 1988), occur within this habitat. Six weeks prior to the 2004 emergence of Brood X, we established an experimental common garden comprised of six woody plant species: *Acer rubrum* (red maple), *Cornus florida* (dogwood), *Cercis canadensis* (redbud), *Lonicera maackii* (honeysuckle), *Ligustrum obtusifolium* (privet) and *Elaeagnus umbellata* (autumn olive), hereafter referred to by generic names only. These species represent three of the most common woody natives (*Acer*, *Cornus* and *Cercis*) and three of the most invasive woody non-natives (*Lonicera*, *Ligustrum* and *Elaeagnus*) in early successional forests of the region (Braun 1950, Czarapata 2005). No data are available on the relative abundances of these species in the forests immediately adjacent to the study site, but all six species are common in Monroe County (Flory and Clay 2006). Within the adjacent forests, the native species in our study are more common than the non-native species (Mattingly and Flory unpubl.).

This common garden provided an ecologically-relevant setting to experimentally evaluate periodical cicada oviposition behavior because cicadas generally emerge in mature hardwood stands but oviposit in nearby successional habitat (Clay et al. 2009). All native and non-native individuals were transplanted from local natural areas and survived the emergence of Brood X. To minimize biases arising from differences in overall host plant stature, we chose host individuals with similar values of plant height (mean \pm SE): *Acer* (2.78 \pm 0.10 m), *Cornus* (2.00 \pm 0.06 m), *Cercis* (2.22 \pm 0.08 m), *Lonicera* (1.64 \pm 0.04 m), *Ligustrum* (2.13 \pm 0.07 m), and *Elaeagnus* (2.18 \pm 0.08 m).

To establish an experimental set of host plants for evaluating patterns of cicada oviposition preference, we transplanted 144 plants into a 48 \times 3 grid formation, the long axis of which paralleled a mature forest edge. We partitioned this formation into 12 blocks, whereby each block contained two individuals of each of the six host species. For each host species within each block, we netted the canopy of one individual to exclude cicadas and left the other individual unnetted and susceptible to cicada oviposition. In this study, we focused exclusively on patterns of cicada oviposition among the 72 unnetted host plants. The netting treatment pertains to a complementary study that evaluates the response of host plants to cicada oviposition damage (Flory and Mattingly 2008). We randomized the position of host species within each block and positioned host plants with

2.5 m between neighboring individuals. Cicadas emerged locally in mid-May 2004 and occurred throughout the study site for approximately five weeks. Several chorusing centers were established within the adjacent forest habitat, thereby providing a nearby source of mated females. We began our measurements of oviposition preference after the adult cicadas died in late-June 2004.

To evaluate patterns of egg hatching success, we established a second set of host plants that could be destructively harvested. We transplanted an additional four individuals of each of the six host species into the study site. These individuals were transplanted in the previously described manner and arranged in a randomized block design. We positioned this arrangement of 24 host plants adjacent to the larger experimental plantation. Oviposition occurred on each host plant in early-June 2004. Cicada eggs generally hatch within 6–10 weeks following oviposition (Williams and Simon 1995). In late-August 2004, we harvested the 24 host plants and dissected cicada egg nests along the branches to quantify egg hatching success.

Available oviposition sites

Host species that provide a greater number of suitable oviposition sites within a study area may exhibit greater use simply by chance alone. Even if cicadas do not exhibit an active preference for such plants, they could mistakenly be considered preferred hosts in the absence of data describing the relative availability of oviposition sites. Thus, accurate evaluations of oviposition preferences must also consider the availability of suitable oviposition sites, for such an account enables one to distinguish between the active selection and random use of host branches during oviposition. To quantify host branch availability, we measured the diameter (± 1 mm), length (± 1 mm), and incline ($\pm 0.1^\circ$) of every branch that occurred at the widest point in the canopy of each host plant. We defined a branch as the distance between two successive branching points (i.e. the internode distance), the attributes of which were measured as in Mattingly and Jayne (2004). Branches with diameters between 3 and 11 mm are most frequently used as sites for oviposition by periodical cicadas (White 1973, 1980, Lloyd and White 1976). Thus, to provide a more definitive measure of host branch availability, we also measured the total length of all branches with diameters between 3 and 11 mm on each host plant.

Oviposition preference

We measured the diameter (± 1 mm), length (± 1 mm), and incline ($\pm 0.1^\circ$) of every branch that contained at least one egg nest on each host plant. During oviposition, the repeated injection of the ovipositor into a branch of the host plant creates a characteristic scar comprised of a linear arrangement of egg nests. Female cicadas generally deposit 20–30 eggs into each egg nest (White and Lloyd 1981, Williams and Simon 1995). In many cases, however, a female may simply inject her ovipositor once, resulting in a scar with a single egg nest. Here we define an oviposition scar as the discrete scar along a branch of the host plant resulting from either a single ovipositor incision or multiple ovipositor incisions.

For every oviposition scar on each host plant, we measured total scar length (± 1 mm) and counted the number of egg nests per scar.

To evaluate oviposition preferences, we used general linear models (PROC GLM) to assess the effects of host species identity and nativity status on the extent to which available branches were used by ovipositing cicadas (SAS ver. 9.1, SAS Inst.). The individual host plant served as the unit of observation in our analyses. For each host plant, we quantified branch use by dividing the cumulative length of every oviposition scar by the total length of all branches with diameters between 3 and 11 mm. In our models, all variables were fixed, and species identity was nested within nativity status. We inspected residual plots (normal probability plots, histograms, and residual-estimate scatter plots) to confirm that the data were normally distributed with homogeneous variance. We used Tukey-Kramer HSD tests to make pairwise mean comparisons on significant effects. To determine whether cicadas randomly or selectively used branches based on attributes of branch diameter, length, and incline, we used paired t-tests to compare median values for the structure of available branches with those of branches used by ovipositing cicadas for each combination of host species and branch attribute. Median values of available and used branches were paired for each host plant. For each host species, we used correlation analysis to evaluate the extent to which measures of branch diameter, length, and incline were correlated with one another among the branches used by ovipositing cicadas. We used mixed linear models (PROC MIXED) to evaluate the influence of branch structure on the number of egg nests per branch. In order to couple this response with branches of known structure, the host branch served as the unit of observation in these analyses, and we accounted for individual host effects by including host plant identity as a random effect in our model. For each host species, we examined all combinations of predictor variables (branch diameter, length, and incline) and used Akaike's information criteria (AIC) to select the best-fitting model.

Hatching success

For each harvested host plant, we randomly selected 7–10 branches that contained at least one oviposition scar and measured the diameter, length, and incline of each branch and counted the number of egg nests within each oviposition scar. On each selected branch, we dissected all egg nests and counted the hatched and unhatched eggs (White 1973). We defined egg nest density as the average number of eggs (hatched and unhatched alike) per egg nest per oviposition scar. We calculated hatching success as the percentage of hatched eggs per oviposition scar.

We used general linear models (PROC GLM) to assess the effects of host species identity and nativity status on egg nest density and hatching success. For each host plant, we averaged the response variables across the branches that were selected for egg nest dissections, and thus the host plant served as the unit of observation in these analyses. In our models, all variables were fixed, and species identity was nested within nativity status. We inspected residual plots to confirm that the data were normally distributed with homogeneous variance. We used mixed linear models (PROC

MIXED) to evaluate the influence of branch structure on egg nest density and hatching success. In order to couple these responses with branches of known structure, the host branch served as the unit of observation in these analyses, and we accounted for individual host effects by including host plant identity as a random effect in our models. For each host species, we examined all combinations of predictor variables (branch diameter, length, and incline) and used Akaike's information criteria (AIC) to select the best-fitting model.

Results

Oviposition preference

Cicada oviposition occurred on each of the 72 host plants at the study site. For each host species, we measured the following numbers of oviposition scars, egg nests, and branches upon which oviposition occurred, respectively: *Acer* (944, 3871 and 606), *Cornus* (622, 1011 and 148), *Cercis* (989, 1104 and 235), *Lonicera* (1025, 1823 and 439), *Ligustrum* (518, 881 and 371), and *Elaeagnus* (198, 547 and 271). Greater than 97% of oviposition scars occurred on branches with diameters between 3 and 11 mm for all host species. However, the extent to which cicadas oviposited on branches within this diameter range depended on the species identity ($F_{4,55} = 10.4$, $p < 0.0001$) and nativity status ($F_{1,55} = 34.5$, $p < 0.0001$) of host plants. Ovipositing cicadas used branches of native *Acer* more extensively than those of the other five host species, and the branches of non-native *Elaeagnus* received the least amount of oviposition damage (Fig. 1). The cumulative length of oviposition scars comprised a greater percentage of branch length on native ($15.3 \pm 1.8\%$) than non-native ($6.3 \pm 1.0\%$) hosts.

For each host species, cicadas selectively used broader (Fig. 2) and longer (Fig. 3) branches than expected from the availability of branches on each species within the study site (Table 1). Cicadas selectively used steeper branches on *Cornus* and *Cercis* but randomly used branch inclines on the other host species (Fig. 4, Table 1). For each host species, measures of branch diameter, length, and incline were not strongly correlated with one another (Table 2), and values of R^2 ranged between 0.0004 and 0.241 for the relationship between branch diameter and length, the attributes of branch structure for which cicadas exhibited active selection. For each host species, the number of egg nests per branch increased with branch diameter and length but was not affected by incline (Table 3).

Hatching success

For each host species, we measured the following numbers of oviposition scars, egg nests, and eggs, respectively: *Acer* (74, 265 and 4641), *Cornus* (28, 88 and 1517), *Cercis* (31, 93 and 1383), *Lonicera* (65, 183 and 2512), *Ligustrum* (50, 116 and 1619), and *Elaeagnus* (53, 132 and 2181). Hatching success did not differ among host species ($F_{4,18} = 0.3$, $p = 0.87$) or between native and non-native hosts ($F_{1,18} = 0.2$, $p = 0.66$). Percentages of hatched eggs were high both on native ($76.8 \pm 6.9\%$) and non-native ($80.8 \pm 2.2\%$)

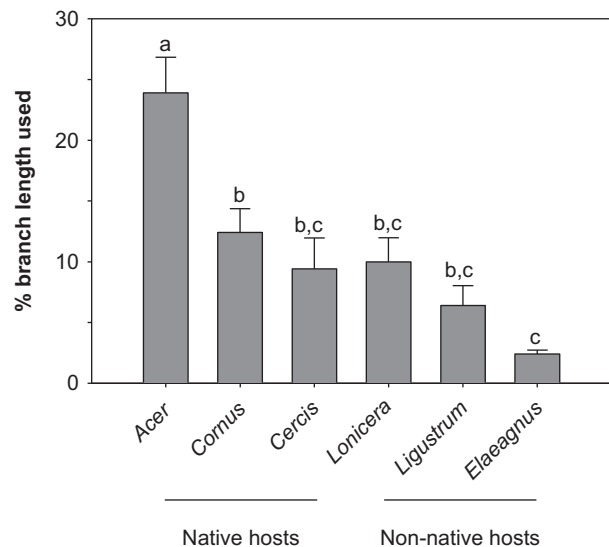


Figure 1. For each host plant species, the percent of branch length bearing oviposition scars on branches with diameters between 3 and 11 mm. Data represent means \pm 1 SE, and different letters indicate significant differences among host plant species.

species. Egg nest density depended on the species identity ($F_{4,18} = 3.6$, $p = 0.026$) and nativity status ($F_{1,18} = 6.0$, $p = 0.025$) of host plants. Egg nests on *Lonicera* contained fewer eggs than those on the other host species, and nests on native hosts generally contained more eggs than those on non-native hosts (17.3 ± 1.4 eggs per nest vs 12.6 ± 1.4 eggs per nest, respectively).

For each host species, branch structure did not affect egg nest density or hatching success (Table 4). The one exception to this otherwise consistent pattern is that hatching success increased significantly with branch diameter for *Cornus*.

Discussion

Oviposition preference

Periodical cicadas selectively used broader and longer branches for oviposition. Moreover, this influence of branch structure on oviposition behavior was apparent for each native and non-native host in our study, demonstrating that plant architecture can provide a basis for oviposition preferences irrespective of host plant identity or nativity status. While previous accounts of periodical cicada oviposition preferences focus exclusively on interspecific differences in oviposition loads among hosts (White 1980, Cook et al. 2001, Clay et al. 2009), our evaluation of within-host branch selection by cicadas helps to clarify oviposition preferences at a higher resolution and provides further insight into important factors influencing oviposition behavior. To our knowledge, only one other study has examined patterns of within-host oviposition site selection by periodical cicadas. Yang (2006) demonstrated that cicadas exhibit preferences for oviposition sites along the western aspect of tree trunks. This orientation positions ovipositing females in direct sunlight in the afternoon during peak daily temperatures, potentially providing an environmental cue for oviposition behavior. As

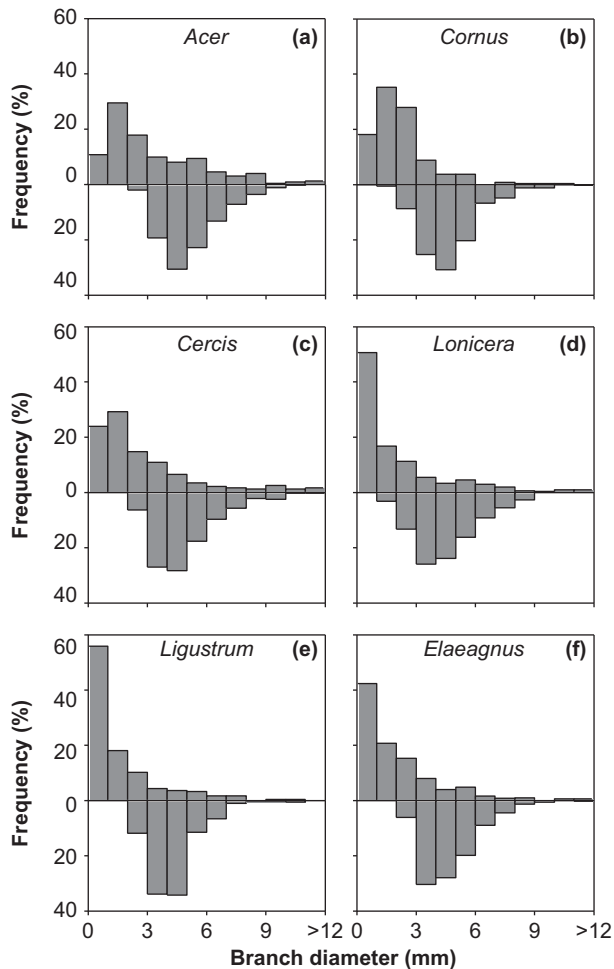


Figure 2. Frequency distributions of available branch diameters (upper panel) and diameters of branches used by ovipositing cicadas (lower panel) on (a) *Acer* (median values, respectively: 3 and 5 mm), (b) *Cornus* (2 and 5 mm), (c) *Cercis* (2 and 5 mm), (d) *Lonicera* (1 and 5 mm), (e) *Ligustrum* (1 and 5 mm) and (f) *Elaeagnus* (2 and 5 mm). Percentages of available branch length with diameters between 3 and 11 mm were lower for *Ligustrum* ($35.0 \pm 2.7\%$) and *Elaeagnus* ($40.2 \pm 3.0\%$) compared with the other host plant species: *Acer* ($74.7 \pm 4.6\%$), *Cornus* ($67.3 \pm 5.1\%$), *Cercis* ($59.4 \pm 4.5\%$) and *Lonicera* ($50.7 \pm 2.1\%$). A greater percentage of branch length within this diameter range occurred on native ($66.9 \pm 2.9\%$) than non-native ($42.0 \pm 7.0\%$) host species.

with the light environment of a given host plant (Yang 2006), we demonstrate that branch structure is also an important predictor of cicada oviposition behavior.

Regardless of host species identity, the selective use of broader and longer branches for oviposition may impart fitness benefits to periodical cicadas. During oviposition, a female cicada must securely grasp a branch to inject her ovipositor into the xylem tissue of the host plant (Williams and Simon 1995). As such, branch structure may affect oviposition behavior by either facilitating the process of oviposition or ensuring favorable conditions for incubating eggs. Although oviposition typically occurs along the long axis of a branch, an ovipositing cicada must negotiate additional branches emanating from the branch selected for oviposition. A female cicada will encounter these lateral branches more frequently when ovipositing on shorter branches.

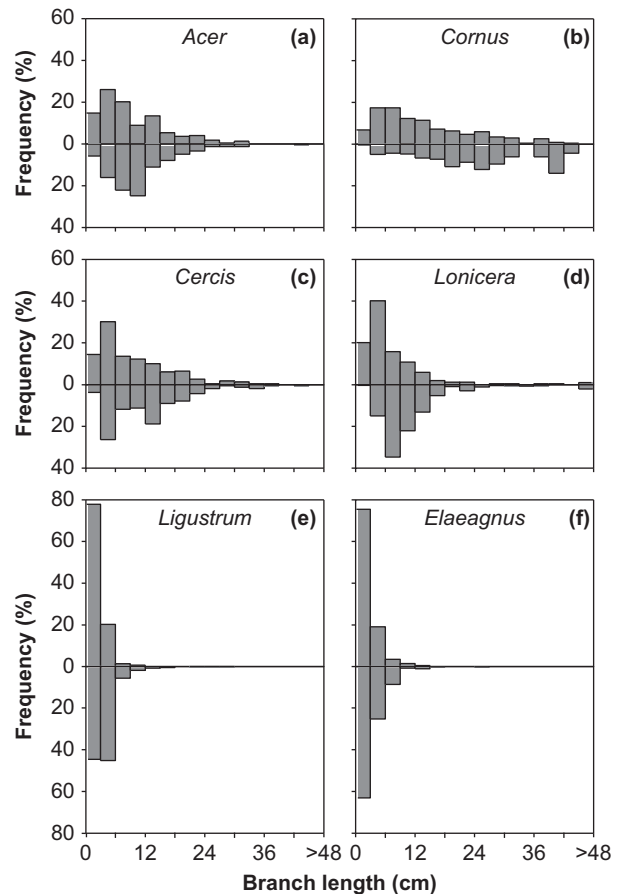


Figure 3. Frequency distributions of available branch lengths (upper panel) and lengths of branches used by ovipositing cicadas (lower panel) on (a) *Acer* (median values, respectively: 7.1 and 9.8 cm), (b) *Cornus* (11.2 and 24.7 cm), (c) *Cercis* (7.7 and 10.8 cm), (d) *Lonicera* (5.0 and 9.0 cm), (e) *Ligustrum* (2.2 and 3.3 cm) and (f) *Elaeagnus* (2.2 and 2.6 cm).

Thus, the selective use of longer branches may facilitate a more efficient bout of oviposition, which could enhance female fecundity since adult cicadas are vulnerable to predation during oviposition due to their poor flying ability and general lack of defenses (Williams and Simon 1995). The selective use of broader branches, on the other hand, could help to minimize the occurrence of flagging (i.e. the death of a branch in response to oviposition damage), one of the leading causes of egg mortality (Williams and Simon 1995). Cicada eggs are vulnerable to desiccation as they develop within host branches, and hatching success is greatly reduced when branches wither and break in response to oviposition damage (White 1981). Flagging is less likely to occur among branches with relatively large diameters, though such occurrences are also a function of egg nest density (White 1981). The selective use of broader and longer branches that we document in our study is consistent with the plant vigor hypothesis (Price 1991), which proposes that insects often respond to within-host variation by selecting relatively large plant modules as oviposition sites. Although there are likely fitness consequences associated with the choice of oviposition sites, the manner in which branch structure affects the mechanics of oviposition and the frequency of flagging requires further evaluation.

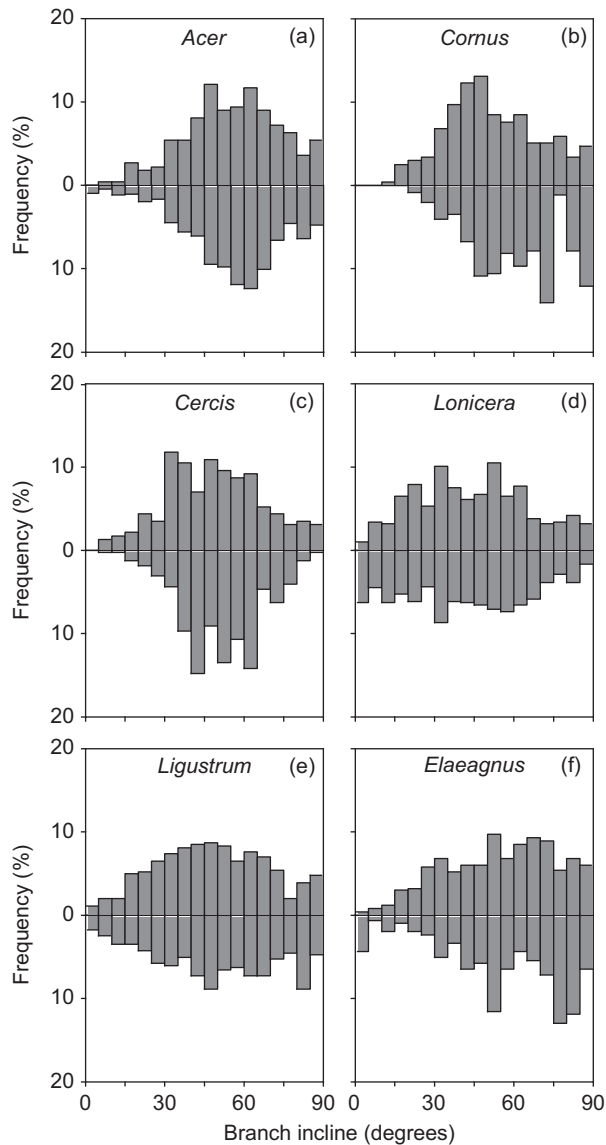


Figure 4. Frequency distributions of available branch inclines (upper panel) and inclines of branches used by ovipositing cicadas (lower panel) on (a) *Acer* (median values, respectively: 55.9° and 58.2°), (b) *Cornus* (49.8° and 61.8°), (c) *Cercis* (47.8° and 51.9°), (d) *Lonicera* (43.9° and 41.6°), (e) *Ligustrum* (47.4° and 50.9°) and (f) *Elaeagnus* (56.0° and 57.6°).

Our study included only three native and three non-native host species, and overall differences in oviposition loads between these native and non-native hosts were driven by the preference of cicadas for native *Acer* and their avoidance of non-native *Elaeagnus*. Although our small native/non-native sample size limits what we can infer about the effects of host nativity status on cicada oviposition behavior, the extent to which cicadas oviposited on the host species in our study agreed largely with the observations of Clay et al. (2009). Among the native species in our study, *Acer* and *Cornus* are often cited as preferred hosts (Forsythe 1976, White 1980, Miller and Crowley 1998, Brown and Zuefle 2009). White (1980) reported that branches with diameters between 3 and 11 mm are preferred by ovipositing cicadas, and for each host plant in our study, nearly all egg nests occurred on

Table 1. For each host species, degrees of freedom (DF) and p values from paired t-tests comparing median values for the structure of available branches with those of branches used by ovipositing cicadas.

| Host species | DF | Branch attribute | | |
|------------------|----|------------------|--------------|-------------|
| | | Diameter | Length | Incline |
| <i>Acer</i> | 10 | <0.001 (9.9) | 0.056 (2.2) | 0.38 (0.9) |
| <i>Cornus</i> | 11 | <0.001 (9.4) | 0.001 (4.5) | 0.051 (2.2) |
| <i>Cercis</i> | 11 | <0.001 (16.6) | 0.045 (2.3) | 0.003 (3.8) |
| <i>Lonicera</i> | 11 | <0.001 (14.8) | 0.004 (3.7) | 0.69 (0.4) |
| <i>Ligustrum</i> | 11 | <0.001 (13.0) | <0.001 (6.9) | 0.32 (1.0) |
| <i>Elaeagnus</i> | 11 | <0.001 (11.7) | 0.047 (2.2) | 0.92 (0.1) |

Notes: median values of available and used branches were paired for each host plant. Values of t are indicated parenthetically after each p-value.

branches within this diameter range. Furthermore, because we accounted for host branch availability, we show that oviposition preferences reflect differences among host species in the proportion of their total branch length comprised of branches with diameters between 3 and 11 mm. As such, preferred hosts had a greater proportion of branches suitable for oviposition. Indeed, for the most and least preferred species in our study, the proportion of total branch length within this diameter range for *Acer* (75%) was nearly double that of *Elaeagnus* (40%) despite similarities in overall plant stature. Our results thus demonstrate that branch structure can be an important predictor of cicada oviposition preferences – and one that is likely independent of host species identity or nativity status – but studies that consider a wider array of host species could be conducted to further evaluate the generality of this response.

Oviposition loads were greater on the native than the non-native hosts in our study. As with oviposition preferences among species, differences in the proportion of total branch length falling within the preferred diameter range (i.e. 3 to 11 mm) also help to explain oviposition patterns on native (67%) and non-native (42%) hosts. Compared with the architecture of the non-native species, the native hosts that we examined had a greater availability of longer and broader branches, the attributes of branch structure subjected to selective use by ovipositing cicadas. Although non-native plants are often prevalent within successional habitats where oviposition occurs, few studies have directly compared the extent to which cicadas use native versus non-native hosts. Brown and Zuefle (2009) recently documented oviposition preferences among an array of native and non-native (or alien, as defined in their study) host species. Although the plants were much smaller in overall stature than those in our study, native hosts generally had longer and broader branches and greater

Table 2. Correlation coefficients describing relationships among attributes of branch structure for each host plant species.

| Host species | Diameter × length | Diameter × incline | Length × incline |
|------------------|-------------------|--------------------|------------------|
| <i>Acer</i> | -0.07 | 0.20 | 0.02 |
| <i>Cornus</i> | -0.14 | 0.46 | -0.02 |
| <i>Cercis</i> | 0.12 | 0.49 | 0.05 |
| <i>Lonicera</i> | 0.36 | 0.36 | 0.29 |
| <i>Ligustrum</i> | 0.15 | 0.29 | 0.09 |
| <i>Elaeagnus</i> | 0.15 | 0.16 | -0.11 |

Table 3. Coefficient estimates and significance of parameters in models predicting the effects of branch structure on the number of egg nests per branch.

| Host species | DF | Diameter | | | Length | | |
|------------------|-----|----------|------|--------|----------|-------|--------|
| | | Estimate | t | p | Estimate | t | p |
| <i>Acer</i> | 592 | 5.74 | 5.38 | <0.001 | 0.48 | 16.70 | <0.001 |
| <i>Cornus</i> | 134 | 10.38 | 3.69 | <0.001 | 0.41 | 8.14 | <0.001 |
| <i>Cercis</i> | 221 | 1.84 | 1.64 | 0.10 | 0.14 | 5.78 | <0.001 |
| <i>Lonicera</i> | 425 | 8.93 | 8.75 | <0.001 | 0.10 | 5.89 | <0.001 |
| <i>Ligustrum</i> | 357 | 1.94 | 3.72 | <0.001 | 0.16 | 7.62 | <0.001 |
| <i>Elaeagnus</i> | 258 | 1.71 | 4.04 | <0.001 | 0.18 | 7.54 | <0.001 |

Note: for each host species, the best-fitting model did not include branch incline as a parameter.

oviposition loads than did non-native hosts. Brown and Zuefle (2009) also suggest that branch diameter is an important predictor of oviposition preferences, a notion that we further support with the results of our study.

For the common successional species examined in our study, we demonstrate that branch structure differs considerably among a select group of native and non-native hosts and is an important predictor of cicada oviposition behavior. Other factors, however, may contribute to the observed differences in oviposition loads between native and non-native hosts. The relatively recent invasion of the non-native species in our study suggests that few generations of periodical cicadas have had an opportunity to encounter and acquire a taste for them. *Elaeagnus*, for example, was introduced to the United States in 1830 for horticultural and wildlife purposes (USDA and NRCS 2010), allowing at most ten generations of periodical cicadas to experience the branch architecture and other attributes of this species. In light of the brief coevolutionary history between periodical cicadas and non-native species, it is likely that cicadas are more adapted to native hosts, a factor that may further influence oviposition preferences.

Table 4. Coefficient estimates and significance of parameters in models predicting the effects of branch structure on egg nest density and hatching success.

| Host species | DF | Diameter | | | Length | | |
|------------------|----|----------|-------|-------|----------|-------|------|
| | | Estimate | t | p | Estimate | t | p |
| Egg nest density | | | | | | | |
| <i>Acer</i> | 35 | 1.06 | 1.19 | 0.24 | | | |
| <i>Cornus</i> | 22 | 0.83 | 0.83 | 0.42 | 0.27 | 1.77 | 0.09 |
| <i>Cercis</i> | 33 | 0.51 | 0.68 | 0.50 | | | |
| <i>Lonicera</i> | 34 | 1.09 | 1.35 | 0.19 | | | |
| <i>Ligustrum</i> | 34 | 1.06 | 1.43 | 0.16 | -0.72 | -0.83 | 0.41 |
| <i>Elaeagnus</i> | 31 | 1.59 | 1.98 | 0.057 | -1.93 | -1.58 | 0.13 |
| Hatching success | | | | | | | |
| <i>Acer</i> | 34 | -4.06 | -1.67 | 0.11 | 0.68 | 0.95 | 0.35 |
| <i>Cornus</i> | 22 | 5.79 | 2.83 | 0.010 | 0.27 | 0.82 | 0.42 |
| <i>Cercis</i> | 32 | 6.61 | 1.55 | 0.13 | -0.03 | -0.07 | 0.95 |
| <i>Lonicera</i> | 33 | 3.17 | 1.40 | 0.17 | -0.76 | -1.20 | 0.24 |
| <i>Ligustrum</i> | 34 | -2.13 | -1.03 | 0.31 | 3.66 | 1.61 | 0.12 |
| <i>Elaeagnus</i> | 31 | -2.13 | -1.47 | 0.15 | 1.10 | 0.51 | 0.61 |

Notes: for each host species, the best-fitting model did not include branch incline as a parameter. Additionally, a blank cell indicates that branch length was not selected as a parameter in the best-fitting model.

Hatching success

Hatching success was similar among the six host plant species in our study. Despite observed preferences for oviposition sites, it is possible that these host species provided equally favorable conditions for egg incubation, as suggested by the relatively low levels of mortality during the egg hatching stage. Although periodical cicadas frequently oviposit on an array of non-native species (Smith and Linderman 1974, Miller and Crowley 1998, Brown and Zuefle 2009), differences in hatching success between native and non-native hosts have not been evaluated previously. As in our study, White (1980, 1981) documented high percentages of hatched eggs (>75%) in egg nests on a diverse group of host species. In light of similarities in hatching success among native and non-native species in our study, and because branch structure did not affect hatching success (with the exception of a diameter effect on *Cornus*), oviposition preferences may merely reflect the physical constraints of branch structure on the process of oviposition, whereby cicadas exhibit preferences for hosts with greater proportions of longer and broader branches that are more tractable for an ovipositing female. In support of this notion, oviposition site selection has been shown to optimize adult rather than offspring performance for other herbivorous insects (Scheirs et al. 2004). For the common successional plant species selected for our study, native hosts had greater proportions of broader and longer branches – branch attributes that were positively associated with egg nest density – and thus generally contained more viable eggs per egg nest and more egg nests per plant. Despite similarities in the percentages of eggs hatched among native and non-native plant species, preferences for native hosts could yield a greater number of newly-hatched nymphs, representing an absolute increase in reproductive success associated with oviposition site selection.

Offspring performance can be quantified through measures of growth, fecundity, or survival (Thompson 1988, Mayhew 1997). In this study, we used egg hatching success to quantify offspring survival because this measure reflects the most immediate and direct fitness consequences of oviposition site selection. As demonstrated here and documented previously (Cory and Knight 1937, White 1980, 1981), cicada mortality during the egg hatching stage is relatively low across a wide array of host plant species. During the 6- to 10-week egg incubation period, flagging and the production of compounds that occlude egg nests (e.g. resin or callous tissue) are the main causes of egg mortality (White 1981, Williams and Simon 1995). It is unlikely that these factors influenced patterns of hatching success in our study since gum-producing species were not included in our sample of host plants, the formation of callous tissue was not observed, and flagging infrequently occurred on each host species. This suggests that the physical constraints on egg development were comparable among the six plant species in our study. In contrast to this brief period aboveground in which eggs are vulnerable to these host plant responses, periodical cicada nymphs develop belowground for an exceptionally prolonged period of time (approx. 13 or 17 years), and it is likely that the fitness consequences of oviposition site selection are manifested in later stages of nymphal development. Karban (1984), for example, documented

extremely high levels of mortality within the first two years of nymphal development. Mortality during the early stage of nymphal development is often attributed to predation and the failure of newly-hatched nymphs to locate suitable host roots rather than inherent differences among host plant species. Although periodical cicadas spend the vast majority of their life cycle belowground as nymphs, little is known about the ecological interactions that occur during this phase of development, and thus studies are needed to evaluate the longer-term consequences of oviposition site selection on offspring performance.

Conclusions

This study provides one of the first analyses of within-host branch selection by ovipositing cicadas, an approach that complements recent efforts in evaluating cicada oviposition preferences among hosts (Brown and Zuefle 2009, Clay et al. 2009) and offers additional insight into important factors influencing oviposition behavior. Moreover, this study is the first to directly relate fine-scale oviposition preferences to egg hatching success across an array of native and non-native plants common to the successional forests in which cicadas occur. Our results show that periodical cicadas generally preferred the native hosts in our study but selectively used broader and longer branches on each of the native and non-native species, indicating that plant architecture strongly affected oviposition behavior regardless of species identity. Oviposition preferences likely reflect the physical constraints of branch structure on the process of oviposition rather than differences among hosts in providing suitable conditions for egg development since hatching success was similar among native and non-native hosts in our study. However, it is possible that the selective use of native plants for oviposition could enhance the absolute output of offspring because the native hosts in our study generally contained more viable eggs per egg nest and more egg nests per plant. In summary, plant architecture is an important predictor of oviposition behavior, and because branch structure can differ substantially among hosts, periodical cicadas may be sensitive to the changes in host plant composition that can result from non-native plant invasions. The widespread distribution of both periodical cicadas and non-native plant invaders across eastern deciduous forests in the US warrants additional studies that evaluate the ecological impacts of plant invasions on oviposition behavior.

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