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Response of host plants to periodical cicada oviposition damage

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Abstract Insect oviposition on plants is widespread across many systems, but studies on the response of host plants to oviposition damage are lacking. Although patterns of oviposition vary spatially and temporally, ovipositing insects that exhibit outbreak characteristics may have strong effects on host plants during peak abundance. Periodical cicadas (*Magicicada* spp.), in particular, may reduce the performance of host plants when they synchronously emerge in massive numbers to mate and oviposit on host plants. Here we provide the first experimental manipulation of host plant use by periodical cicadas to evaluate the impact of cicada oviposition on plant performance across a diversity of host species within an ecologically relevant setting. Using a randomized block design, we established a plantation of three native and three exotic host plant species common to the successional forests in which cicadas occur. During the emergence of Brood X in 2004, we employed a highly effective cicada exclusion treatment by netting half of the host plants within each block. We assessed multiple measures of host plant performance, including overall plant growth and the growth and reproduction of individual branches, across three growing seasons. Despite our thorough assessment of potential host plant responses to oviposition damage, cicada oviposition did not generally inhibit host plant performance. Oviposition densities on unnetted host plants were comparable to levels documented in other studies, reinforcing the ecological relevance of our results, which indicate that cicada oviposition damage did not generally reduce the performance of native or exotic host plants.

Keywords Native/exotic · *Magicicada* · Branch death · Plant growth · Insect–plant interactions

Introduction

Insect–plant interactions strongly influence the dynamics and composition of plant communities in many ecosystems (Strong et al. 1984), and most often these interactions take the form of insect herbivory and oviposition. Insect herbivory can reduce the growth and reproduction of host plants (Kauffman and Maron 2006; Marquis 1984; Root 1996), resulting in altered competitive interactions among plant species and shifts in the composition of plant communities (Carson and Root 2000; Maron and Crone 2006). The effects of insect herbivory have been well-documented across many systems (Huntly 1991). In contrast, the effects of insect oviposition on plants have received much less attention, even though a broad diversity of insect species oviposit on plants across a variety of habitats (Jaenike 1990). Similar to herbivory, insect oviposition can have negative effects on host plants by damaging vascular tissue (Weissling et al. 2003; White 1981) and providing openings for pathogens to infect host plants (Biere and Honders 1996; Kanzaki and Futai 2006; van der Zwet et al. 1997). Patterns of insect oviposition differ on spatial and temporal scales (Cook and Holt 2006; Powell and Logan 2005), but the severity of the negative effects of oviposition on host plants likely increases with the degree of oviposition damage.

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Although insect–plant interactions vary temporally in natural systems, insects that exhibit outbreak characteristics are particularly important drivers of community dynamics in forested systems (Bouchard et al. 2006; Kneeshaw and Bergeron 1998; Naidoo and Lechowicz 2001). As a consequence of insect outbreaks, forest stand compositions can be altered if insects exhibit preferences for host plants and if preferred host species suffer reductions in growth or reproduction (Bouchard et al. 2005; Kaitaniemi et al. 1999; Naidoo and Lechowicz 2001). During spruce budworm outbreaks, for example, balsam fir and spruce species are highly preferred by budworms but intolerant of budworm damage, which reduces fir and spruce dominance and allows non-host species to proliferate (Bouchard et al. 2005; Kneeshaw and Bergeron 1998). Insect oviposition may similarly alter plant communities if damage due to oviposition reduces the performance of host plants, and the effects of insect oviposition may be substantially heightened if ovipositing insects exhibit outbreak characteristics. Periodical cicadas (*Magicicada* spp.), for example, are a widespread group of insects in North America that synchronously emerge in enormous numbers and oviposit extensively on a diversity of host plant species (Dybas and Lloyd 1974; White 1980; Williams et al. 1993). Although emergences are infrequent within a given habitat, when they occur cicadas are the single most abundant forest animal in biomass per unit area (Dybas and Davis 1962), suggesting that damage due to cicada oviposition may have considerable effects on plant communities. Cicadas often occur within early-successional forests, and within these habitats, the impact of cicadas may change competitive dominance among plant species, which in turn can have substantial effects on forest species composition and successional trajectories (Bishop 2002; Davidson 1993).

Previous studies assessing host plant responses to cicada oviposition have been restricted to observational studies (Cook and Holt 2002; Miller and Crowley 1998), ornamental and agricultural plants (Hogmire et al. 1990; Smith and Linderman 1974), and individual host species (Karban 1980) and genera (Koenig and Liebhold 2003). Studies focusing on the response of host plants to cicada oviposition generally indicate that oviposition causes visible damage to host plant branches (White 1981; Williams and Simon 1995), but there have been variable reports on the effects of cicada oviposition on host plant growth and reproduction (Cook and Holt 2002; Crawley 1989; Hogmire et al. 1990; Koenig and Liebhold 2003). In cultivated fruit trees and ornamentals, for example, cicada oviposition was correlated with wilting and branch breakage (Crawley 1989) as well as reduced tree growth (Hogmire et al. 1990). In addition, cicada emergences have been negatively correlated with the growth of oak trees (Karban 1980; Koenig and Liebhold 2003). However, Cook and Holt (2002) observed that cicada oviposition often resulted in dead branch tips but was not clearly correlated with plant growth or fruit production for the host species in their study. The varied results of such observational studies combined with the general lack of studies involving multiple host plant species within a natural context indicates that comprehensive experimental studies are needed to accurately evaluate the response of host plants to periodical cicada oviposition.

During the emergence of Brood X in 2004, we conducted a common garden field study using six native and exotic host plant species planted in a randomized experimental array. We experimentally manipulated cicada oviposition damage by excluding cicadas from half of the plants and quantified host plant performance using multiple measures of host plant growth and reproduction. In this study, we evaluated the effects of cicada oviposition on host plant performance across a diversity of plant species within an ecologically relevant setting, which represents the first experimental assessment of host plant responses to periodical cicada oviposition damage.

Methods

Study system

Periodical cicadas occur throughout the forests of eastern North America and are classified into broods by their periodicity and year of synchronous emergence (Dybas and Lloyd 1974; Marlatt 1907). Cicadas live as nymphs belowground for 13 or 17 years while feeding on the root xylem of host plants (White and Strehl 1978). Adult cicadas emerge at densities that are often greater than 3,000,000 individuals per hectare (Dybas and Davis 1962) and live aboveground for 2–6 weeks, during which time mating occurs when male cicadas form chorusing centers in the forest canopy to attract females (Williams and Simon 1995). After mating, a female cicada uses an ovipositor to create a series of slits on the underside of host plant branches, and up to 30 eggs are inserted into each oviposition slit (Karban 1980). Oviposition slits result in conspicuous and persistent scars on host plants that often cause branch tips to wilt or break and die (White 1981). After 6–10 weeks, cicada nymphs hatch from the eggs, fall from the branches, and burrow into the ground, where they remain until the next emergence year (Karban 1984).

Experimental design

We conducted this experiment at the Bayles Road site of the Indiana University Research and Teaching Preserve, which is a mosaic of old fields, drainage canals, and bottomland hardwood forest (39°13′10″N, 86°32′24″W). In early May 2004, we established a plantation comprising three of the most common native woody species in young eastern deciduous forests (Braun 1950): *Acer rubra* (red maple), *Cornus florida* (flowering dogwood), and *Cercis canadensis* (redbud), and three of the most problematic woody exotic invaders in such forests (Czarapata 2005): *Lonicera maackii* (bush honeysuckle), *Ligustrum obtusifolium* (Eurasian privet), and *Elaeagnus umbellata* (autumn olive); hereafter referred to only by genus. The native species were obtained from Beech Creek Tree Farm (Greene County, IN, USA), and the exotic species were transplanted from various natural areas within 50 km of Bloomington, IN, USA. The overall height at the time of planting was similar among species (mean ± SE): *Acer*: 2.78 ± 0.10 m, *Cercis*: 2.22 ± 0.08 m, *Cornus*: 2.02 ± 0.06 m, *Elaeagnus*: 2.18 ± 0.08 m, *Ligustrum*: 2.10 ± 0.07 m, and *Lonicera*: 1.64 ± 0.04 m.

We transplanted 24 individuals of each species (144 plants total) into a 48 × 3 grid formation with 2.5 m spacing between adjacent host plants. The long axis of the grid was parallel to and approximately 5 m from trees lining a wooded creek. We divided the grid into 12 blocks and planted two individuals from each of the six host species within each block at random positions. Individuals that had died within two weeks of transplanting were replaced.

In late May 2004, immediately prior to the cicada emergence, we enclosed the canopy of one individual per species per block with lightweight netting specifically designed to exclude cicadas (Gardenplus Cicada Netting, 4 × 4 mm mesh, Dupont, Wilmington, DE, USA). Cicadas emerged soon after the netting was applied and established numerous chorusing centers near our study site. We removed the netting in July 2004 after all adult cicadas had died. The netting was in place for only six weeks, and we observed no adverse effects of the netting on host plant growth.

To assess the effectiveness of the netting treatment at excluding cicadas, we counted and measured the lengths of all oviposition scars on each host plant. Cicada oviposition occurs almost exclusively on host branches with diameters of between 3 and 11 mm (Lloyd and White 1976; White 1980), so we evaluated oviposition damage relative to the availability of branches within this range of branch diameters. We divided the total length of oviposition scars by the total length of branches between 3 and 11 mm for each individual host plant to calculate the percent of suitably sized branch length used for oviposition.

Response of host plants to cicada oviposition

To evaluate the response of host plants to cicada oviposition, we quantified various growth and reproductive characteristics of each host plant. All dead branches from each plant were removed in June 2005, dried at 60 °C for 96 hr, and weighed (±0.1 g). To quantify overall plant growth, we measured the basal diameter (±1 mm) of all stems on each plant at 5 cm above the soil surface in July 2004. We repeated this measure for surviving plants in August 2006 and calculated the average yearly basal diameter growth for each plant. To quantify vegetative productivity at a finer scale, we arbitrarily tagged ten branches on each individual in spring 2005 and measured the diameter (±1 mm) at 5 cm from the nearest proximal node as well as the total length (±1 mm) of each tagged branch. In spring 2006, we repeated these measurements on all tagged branches and calculated the average relative growth in branch diameter and length for each host plant. We quantified the effects of oviposition on host plant reproduction by counting the number of flowers produced per tagged branch in the spring of 2005. In the fall of 2005, all fruit on each of the ten tagged branches per individual was collected, counted, dried at 60 °C to constant mass, and weighed (±0.01 g).

Statistical analysis

We analyzed dead branch biomass and relative basal diameter growth separately with ANOVAs using the GLM procedure of SAS (Version 9.1, SAS Institute Inc. 2002), which considered netting treatment, native/exotic status, and species nested within status as fixed effects and block as a random effect. Post hoc Tukey tests were used to test for differences among species and between treatments within responses.

Relative branch diameter and branch length growth were combined into a multivariate analysis of variance (MANOVA) with netting treatment, native/exotic status, and species nested within status as fixed effects and block as a random effect. In 2005, only *Cornus*, *Elaeagnus*, *Lonicera*, and *Ligustrum* produced notable numbers of flowers and fruit. We analyzed the reproductive measures (flowers per centimeter of branch, fruit biomass per branch, and fruit number per branch) for these four species using MANOVA with netting treatment and species as fixed effects and block as a random effect. We present Pillai's trace statistic for results of multivariate analysis (Scheiner 2001).

Host plant species and individuals within species received a wide range of oviposition damage. Thus, the response of the host plants may have depended on the amount of oviposition they received. We used simple linear regression (Proc REG, SAS Institute Inc. 2002) to evaluate the effect of percent branch length used for oviposition on each measure of plant growth and reproduction.

Results

Overall, there were 2,805 scars on unnetted host plants and 18 scars on netted plants, which represents a 99.4% reduction in cicada oviposition under the netting treatment. The degree of oviposition damage differed among host plant species ($F_{(4,55)} = 10.4$, $P < 0.0001$). The mean and range of percent branch length used for oviposition for each native species was *Acer*: 22.9 (12.5–48.5)%, *Cercis*: 5.7 (3.0–9.2)%, and *Cornus*: 12.4 (3.9–25.6)%, and for each exotic species was *Elaeagnus*: 2.4 (0.9–4.0)%, *Ligustrum*: 6.4 (1.1–19.1)%, and *Lonicera*: 10.0 (0.2–23.3)%.

Dead branch mass was greater for unnetted (mean ± SE; 32.6 ± 5.0 g) than netted (21.7 ± 5.50 g) host plants ($F_{(1,97)} = 5.03$, $P = 0.027$), but there was no overall difference between native and exotic species ($F_{(1,97)} = 0.91$, $P = 0.34$, Fig. 1a). Testing the species individually revealed that the treatment effect on dead branch mass was only significant for *Acer* ($F_{(1,15)} = 4.53$, $P = 0.05$), although *Cercis* ($F_{(1,7)} = 2.63$, $P = 0.15$) and *Elaeagnus* ($F_{(1,22)} = 1.29$, $P = 0.27$) showed trends of less dead branch mass under the netting treatment (Fig. 1a).

In general, the netting treatment to exclude cicadas did not affect the relative basal diameter growth of the host plants ($F_{(1,89)} = 1.14$, $P = 0.29$, Fig. 1b). There was a marginally significant interaction between treatment and host species identity ($F_{(4,89)} = 1.98$, $P = 0.10$), but individual tests of the species revealed that only *Elaeagnus* ($F_{(1,22)} = 4.20$, $P = 0.05$; Fig. 1b) had a significant positive trend in basal diameter growth under the netted treatment. Independent of the netting treatment, relative basal diameter growth was more than five times greater for exotic (mean ± SE; 0.71 ± 0.07) than native (0.14 ± 0.01) species ($F_{(1,89)} = 44.22$, $P < 0.0001$) and differed among species within native/exotic status ($F_{(4,89)} = 16.19$, $P < 0.0001$).

The netting treatment did not affect the relative branch growth of host plants when the effect was averaged across all species or when each species was tested individually (Table 1, Fig. 2). In addition, there were no differences in branch growth due to the netting treatment among native and exotic host species (Pillai's trace = 0.018; $F_{(2,89)} = 0.83$; $P = 0.44$) or among species within status (Pillai's trace = 0.056; $F_{(8,180)} = 0.65$; $P = 0.73$). However, relative branch growth was greater for exotic than native species (Pillai's trace = 0.324, $F_{(2,89)} = 21.36$, $P < 0.0001$). The netting treatment did not affect the reproductive output of the host plants (Table 1, Fig. 2; species × treatment: Pillai's trace = 0.116, $F_{(9,144)} = 0.64$, $P = 0.76$).

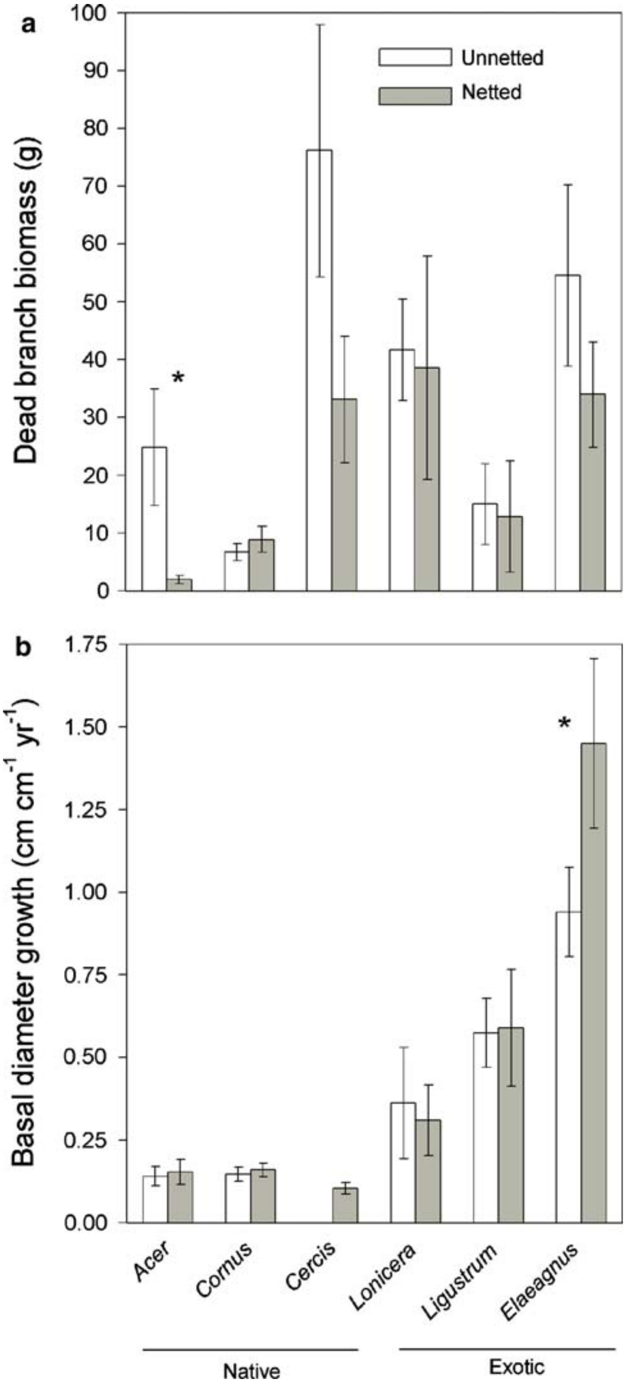

Fig. 1a–b Effects of the netting treatment on the amount of dead branch biomass (**a**) and relative growth in basal diameter (**b**) of the native (*Acer, Cornus*, and *Cercis*), and exotic (*Lonicera*, *Ligustrum*, and *Elaeagnus*) host plant species. The asterisks indicate significant differences at $P \leq 0.05$

Regression analysis revealed three significant relationships between the responses of host plant species and the percentage of branch length used for oviposition. There was a positive relationship between percent use and basal diameter growth for *Elaeagnus* (slope = 0.3, $r^2 = 0.49$, $P = 0.03$), a negative relationship between percent use and branch length growth for *Cornus* (slope = −0.0068, $r^2 = 0.89$, $P = 0.02$), and a negative relationship between percent use and the average number of fruit per branch for

Table 1 MANOVA results for the effects of the cicada exclusion treatment on host plant growth and reproductive output

	Branch growth				Reproductive output			
	df	Pillai's trace	*F*	*P*	df	Pillai's trace	*F*	*P*
All species	2, 89	0.009	0.42	0.66	3, 46	0.034	0.55	0.65
Acer	2, 12	0.067	0.43	0.66				
Cornus	2, 19	0.176	2.03	0.16	3, 5	0.005	0.01	0.99
Cercis	2, 4	0.367	1.16	0.40				
Lonicera	2, 20	0.063	0.67	0.52	3, 16	0.177	1.15	0.36
Ligustrum	2, 20	0.059	0.62	0.55	3, 19	0.137	1.01	0.41
Elaeagnus	2, 20	0.109	1.22	0.32	3, 11	0.071	0.28	0.84

Branch growth includes branch diameter and branch length. Reproductive output includes flower number, fruit number, and fruit biomass. *Acer* and *Cercis* produced very few flowers during the experiment and are not included in the analysis of reproductive output

Cornus (slope = −0.19, $r^2 = 0.80$, $P = 0.04$). No other regression analysis was statistically significant (all values of $P > 0.05$).

Discussion

The extent of cicada oviposition in our experiment was comparable to previously documented levels (Cook and Holt 2002). For the recent emergence of Brood X, Clay et al. (*Differential susceptibility of tree species to oviposition by periodical cicadas*, submitted to Oikos) evaluated cicada oviposition at 44 sites in southern Indiana and found that the average percent of branch length used for oviposition at each site varied from 0.3 to 55%. The percent branch length used for host plants in our study (0.2–48.5%) falls well within this range. In addition, previous studies have correlated cicada oviposition damage with species-specific reductions in host plant performance (Hogmire et al. 1990; Miller and Crowley 1998; Smith and Linderman 1974). Therefore, we hypothesized that we would observe considerable reductions in the growth and reproduction of host plants in our experiment. However, despite the rigor of our experiment, we generally found that cicada oviposition damage did not reduce the performance of host plants, indicating that there are few immediate ecological consequences of cicada oviposition damage for the host plant species we examined.

Cicada oviposition damage increased dead branch mass for *Acer*, the host plant species receiving the greatest degree of oviposition damage, but did not affect dead branch mass in the other host species. These results are consistent with previous studies reporting that cicada oviposition damage often kills host plant branches (Hogmire et al. 1990; Smith and Linderman 1974; van der Zwet et al. 1997; White 1981) but that the proportion of damaged branches that

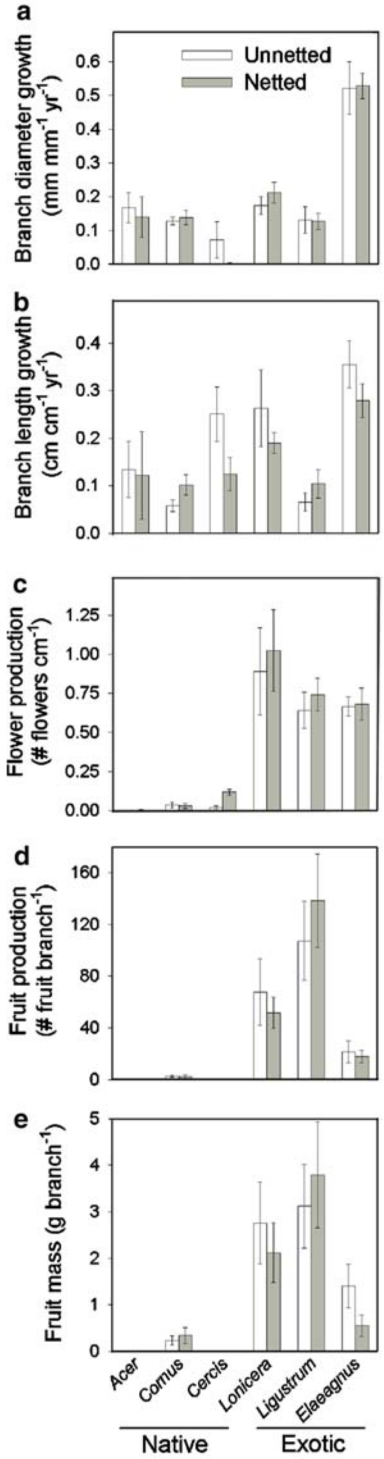

Fig. 2a–e Effects of the netting treatment on branch diameter growth (**a**), branch length growth (**b**), flower production (**c**), fruit production (**d**), and fruit mass (**e**) of the native (*Acer*, *Cornus*, and *Cercis*), and exotic (*Lonicera*, *Ligustrum*, and *Elaeagnus*) host plant species

break and die differs among host plant species (Cook et al. 2001; Miller and Crowley 1998; Oberdorster and Grant 2006). In particular, Smith and Linderman (1974) found that *Acer* and *Cornus* species were especially susceptible to branch death and breakage following oviposition damage, and that branches continued to die through the winter following oviposition. In our study, differences among host species in the extent of branch death resulting from oviposition damage may reflect patterns of host species use by ovipositing cicadas as well as differences in the physiological responses of host species to oviposition damage. For example, species with branches that are less tolerant to disruptions in vascular tissue may be more vulnerable to branch death and breakage (White 1981). Additional studies are needed to clarify the physiological differences among species that may help explain the variation in branch death rates among host plant species in response to cicada oviposition.

In our study, we measured multiple growth and reproductive characteristics of six host plant species, but there were few growth or reproductive effects of cicada oviposition on host plants. *Elaeagnus* plants protected from oviposition damage had significantly greater basal diameter growth than *Elaeagnus* exposed to cicadas. *Elaeagnus* received the lowest amount of oviposition damage, which suggests that *Elaeagnus* may be particularly sensitive to the damage caused by cicada oviposition. However, *Elaeagnus* did not exhibit reduced branch growth, so the mechanism underlying the reduction in basal diameter growth is unclear. Regression analysis indicated a significant positive relationship between the extent of oviposition damage and basal diameter growth for *Elaeagnus*, but because *Elaeagnus* never received more than 4% use, we do not believe that this result is ecologically meaningful. *Acer* had the greatest amount of oviposition damage and the only significant increase in dead branch mass when exposed to cicadas, but *Acer* host plants did not suffer a reduction in basal diameter growth or branch growth with oviposition damage. There was no overall difference between the native and exotic species in their response to oviposition, suggesting that the slower growth rate of the native species did not prevent them from tolerating oviposition damage.

Although there were no differences in growth or reproduction between *Cornus* plants exposed to cicada oviposition and those that were protected, there were significant negative relationships between the degree of oviposition and branch growth, and between oviposition and *Cornus* fruit production. The reduction in branch growth with increased oviposition did not, however, impact the overall growth of *Cornus* plants, suggesting that the plants may have compensated for the reduced growth on highly damaged branches by increasing growth in other branches (Nozawa and Ohgushi 2002). Alternatively, the reduced growth of a few branches may not have significantly reduced whole-plant productivity and therefore did not reduce overall plant growth. Cook and Holt (2002) found no relationship between cicada oviposition damage and the growth of *Cornus* plants in overall height or basal diameter, and no relationship between oviposition and *Cornus* fruit production as evaluated across entire tree crowns. Although we found that growth and fruit production are reduced on individual branches, our results and those of Cook and Holt (2002) indicate that cicada oviposition damage does not reduce the overall performance of *Cornus* plants.

Previously, Karban (1980) documented that oviposition damage was correlated with decreased tree ring growth during emergence years for *Quercus ilicifolia*, and Koenig and Liebhold (2003) observed that *Quercus* spp. had 4% less growth during emergence years. However, neither study could distinguish between the impact of nymphal feeding immediately prior to or following emergences and the effect of oviposition damage. In our study, we experimentally planted host plants where cicada nymphs were not present in the soil and we used trees that were not alive during the last local emergence of periodical cicadas. Thus, feeding by late-instar nymphs immediately prior to the emergence would not have affected the results of our experiment. In addition, young nymphs feeding on the unnetted trees after oviposition would have exaggerated the impacts of cicada oviposition, but this effect was not detected. Additional studies are needed that manipulate cicada oviposition and early- and late-instar nymphs in a factorial design to separate the effects that each cicada life history stage has on the performance of host plants.

In contrast to our results, the majority of previous studies examining the response of host plants to cicada oviposition have reported that the immediate effects of oviposition damage (Smith and Linderman 1974) and the combination of oviposition and feeding by cicada nymphs (Hogmire et al. 1990; Karban 1980; Koenig and Liebhold 2003; Smith and Linderman 1974) reduced host plant growth and reproductive output (van der Zwet et al. 1997). Of these studies, only Hogmire et al. (1990) correlated the extent of oviposition with growth characteristics of host plants, but their study was restricted to apple trees in a managed setting. Of the other studies examining host plant response to oviposition, Smith and Linderman (1974) made observations of ornamental plants, and Miller and Crowley (1998) did not directly measure the impact of oviposition on plant growth. In our study, we experimentally manipulated host plant exposure to cicadas in an ecologically relevant setting and quantified host plant responses using several measures of host plant growth and reproduction across three growing seasons. However, we found few effects of cicada oviposition on the performance of host plants.

In summary, our study demonstrates that periodical cicada oviposition damage does not generally reduce the performance of six common native and exotic host plant species. Although we used a limited number of host plant species in this experiment, and cicadas are known to oviposit on dozens of woody plant species, the species we used are among the most common woody plant species in the early-successional, fragmented habitats where cicadas are most abundant. Our study provides evidence that although the damage caused by cicada oviposition can cause branch death and breakage, host plants may suffer few reductions in growth or reproduction.

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