Effects of oviposition by periodical cicadas on tree growth

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Abstract: Periodical cicadas (*Magicicada* spp.) occur at very high densities and synchronously emerge from underground every 13 or 17 years. During the emergence, adults lay eggs in tree branches, causing significant damage; however, the long-term impact of this damage is unknown. We conducted two large-scale field studies during the 2004 emergence of one brood (Brood X) to measure the growth of trees in relation to oviposition damage by periodical cicadas. In the first experiment, we netted areas to exclude cicadas from plots in 15 early successional forests and then measured trunk circumference for 3 years on more than 4000 trees of 52 species. In this experiment, oviposition had no detectable effect on the growth rates of trees. In the second study, we measured oviposition on 12 common tree species across six sites. We then measured the annual growth rings of these trees for 3 years after the emergence. In this experiment, oviposition was correlated with a slightly reduced growth in the emergence year and following year when the data were analyzed together, but when tree species were examined individually there were no clear effects of oviposition on tree growth. These data suggest cicada oviposition has little effect on the radial growth of trees, particularly in comparison to other factors.

Résumé : Les cigales 17 ans (*Magicicada* spp.) atteignent de très fortes densités lorsqu'elles émergent du sol simultanément à tous les 13 ou 17 ans. Durant l'émergence, les adultes pondent leurs œufs dans les branches des arbres causant ainsi des dommages importants dont l'impact à long terme est inconnu. Nous avons réalisé des études de terrain à grande échelle durant l'émergence de 2004 de la nouvelle génération X pour mesurer la croissance des arbres en relation avec les dommages causés par l'oviposition des cigales 17 ans. Dans la première expérience, nous avons utilisé des filets pour exclure les cigales des parcelles dans 15 forêts aux premiers stades de succession et, pendant 3 ans, nous avons mesuré la circonférence du tronc de plus de 4000 arbres représentant 52 espèces. Nous n'avons décelé aucun effet de l'oviposition sur le taux de croissance des arbres. Dans une deuxième étude, nous avons mesuré l'oviposition sur 12 espèces communes d'arbres dans six stations. Nous avons ensuite mesuré les cernes annuels de ces arbres pendant les 3 années qui ont suivi l'émergence. L'oviposition était corrélée avec une légère réduction de croissance l'année de l'émergence et l'année suivante lorsque les données étaient analysées globalement. Par contre, l'oviposition n'avait aucun effet évident sur la croissance des arbres lorsque les espèces étaient examinées individuellement. Ces données indiquent que l'oviposition des cigales a peu d'effet sur la croissance radiale des arbres, particulièrement si l'on compare à d'autres facteurs.

[Traduit par la Rédaction]

Introduction

Insect herbivores can be important in structuring plant communities. Herbivores can alter plant growth rate, reproduction, disease risk, and lifetime fitness, and can affect community density, diversity, and successional rate (e.g., Brown and Gange 1992; Davidson 1993). Periodical cicadas (*Magicicada* spp.) spend the majority of their life underground feeding on xylem from tree roots. They synchronously emerge in enormous densities every 13 or 17 years (depending on the brood) and, while they feed little as adults, their oviposition causes severe damage to small branches on trees, which wither and die over the following weeks, and is similar to the effects of tissue loss to direct herbivory. The impacts of these oviposition events on trees are unknown. The massive and predictable emergences of periodical cicadas have parallels with other outbreaking forest insects, like gypsy moths and tent caterpillars. However, periodical cicadas may differ in their effects on tree growth given their lack of host specificity and their multiple impacts on trees, such as oviposition damage, nutrient pulses from dead adults (Yang 2004), and release from extended root feeding prior to emergence.

Several studies, and much anecdotal evidence, have reported a detrimental effect of cicada damage on ornamental and fruit trees (e.g., Smith and Linderman 1974; Hogmire et al. 1990; Williams and Simon 1995), but only a few previous studies have examined the impact of oviposition damage or root feeding by periodical cicadas on the growth and fitness of trees in natural ecosystems. The results of three previous studies in natural systems are equivocal, ranging from a strong detrimental effect to a small but measurable negative effect to no effect. Cook and Holt (2002) and Karban (1980) only examined oaks (*Quercus* spp.), and Karban (1980) and Koenig and Liebhold (2003) were restricted to a single site. Karban (1980) compared differences in annual growth rings of scrub oaks (*Quercus ilicifolia*)

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with and without naturally occurring cicada oviposition damage. He found that the growth of damaged trees was significantly reduced during the emergence year and for 4 years after the emergence. In addition, the growth rate of these trees was lower after the emergence event than before. In another study, Koenig and Liebhold (2003) used the International Tree-Ring Data Bank to look for effects of periodical cicadas over a long time horizon and a wide geographic range. Within the range of periodical cicadas, they compared the growth of oaks with that of pines (*Pinus* spp.), which generally do not host cicadas, and found a 4% average reduction in the growth of oaks during the emergence years, but no reduction in pines. They also found a periodicity in the growth of oaks that corresponded significantly to the periodicity of periodical cicadas but found no periodicity of pines corresponding to the cycling of cicadas. In the only previous to examine the impact of oviposition of periodical cicadas across a range of species, Cook and Holt (2002) found no significant impacts of cicadas on the growth of seven tree species or the fitness of the dominant tree, *Cornus drummondii*, at a single site in eastern Kansas. *Cornus* species tend to be heavily attacked by periodical cicadas (Cook et al. 2001; Clay et al. 2009) and, therefore, should have a high potential for impacts from oviposition damage. Because of their massive numbers, periodical cicadas have a high potential to reduce the growth of tree species, but there is little evidence either for or against significant effects on tree growth as a result of oviposition by periodical cicadas.

In this paper we report the results of two large field studies in natural forest communities that address the following questions: (1) Does oviposition damage by periodical cicadas reduce tree growth? and (2) Do the effects of oviposition damage vary among tree species or among sites? In the first study (netting experiment), we manipulated cicada densities by covering large plots with insect exclusion netting and then measured the circumference of trees annually for three growing seasons after the cicada emergence. Few previous studies have experimentally manipulated periodical cicada densities (but see Karban 1982; Ahern et al. 2005; Flory and Mattingly 2008). In a second study (growth ring study), we measured oviposition on individuals of the most common tree species at replicate sites and then harvested trees after three growing seasons to measure the annual growth ring increments before and after the cicada emergence. In total, we measured oviposition and growth for 4048 trees in the netting experiment and an additional 518 trees in the growth ring study, including a total of 52 species at 15 sites. This is by far the largest data set on the impacts of periodical cicada oviposition on tree growth, and it focuses on the impacts of one of the largest broods (Brood X), allowing us to more definitively address the effect of periodical cicadas on forest communities.

Methods

Cicada broods are identified by their year of emergence and are numbered based on the scheme of Marlatt (1907). Brood X, like all 17-year broods, is a combination of three species: *Magicicada septendecim*, *Magicicada septendecula*, and *Magicicada cassini*. We examined the impact of oviposition after the 2004 emergence of Brood X, which is one of the most widespread and densest broods of periodical cicadas, covering Indiana, Kentucky, and Tennessee, and continuing east to the Atlantic coast. Southern Indiana is near the geographical center of the brood and is among the areas with the highest Brood X densities (Kritsky et al. 2005; Simon 1988), making this an ideal location to measure the impacts of periodical cicada oviposition.

Female periodical cicadas oviposit by making longitudinal incisions on the underside of branches having a diameter between 3 and 11 mm (White 1980) and deposit a cluster of eggs in the interior wood (Marlatt 1907). Multiple egg nests typically are deposited in rows of 4–12 nests, leading to a zipper-like appearance on the underside of the branches. This leaves a persistent scar that is easy to identify and measure and that can often lead to branch death. Periodical cicadas prefer to oviposit on young trees in open, sunlit sites (e.g., Williams and Simon 1995; Cook et al. 2001; Yang 2006), but nymphs emerge from the ground in greater densities in mature forests (Clay et al. 2009). Because of their limited belowground movement, cicada nymphs are usually only present in soils of forest communities old enough to have experienced a prior emergence. To separate the effects of oviposition damage by adult cicadas from the effects of feeding by nymphal cicadas, we selected study sites that had been abandoned from agriculture (crops or pasture) or cleared within 10–15 years prior to the 2004 Brood X emergence (for more details of sites see Clay et al. 2009). Although the root systems of cut trees may survive enough to support cicada nymphs in cleared sites, the cleared sites had significantly less cicada emergence than more mature forests (Clay et al. 2009). No cicada nymphs would be expected in abandoned agricultural lands. These early successional sites also provide a stronger test of the impacts of cicada oviposition on trees. Young trees should be more susceptible to deleterious effects from oviposition because a higher proportion of their branches are of suitable size for cicada oviposition and because cicadas prefer to oviposit in open, sunlit areas.

Netting experiment

We selected 15 early successional sites in southern Indiana, with an average canopy height of approximately 2 m. The sites represented regenerating forest in clearcuts, abandoned agricultural land, and tree farms established on former agricultural land. In April 2004, prior to the cicada emergence, we established 6–12 plots of 5.2 m × 15.2 m at each site. We covered half of each plot (5.2 m × 7.6 m) with cicada exclusion netting (1.9 cm (3/4 in.) mesh, 5.2 m (17 ft.) wide, Orchard Valley Supply, Inc.) to reduce cicada oviposition on the trees. The other half of each plot was left unnetted. Nets were laid over the tops of the trees, draped over the sides of the plots, and secured with wire twists. The nets did not extend all the way to the ground, so some cicadas were able to enter the plots from beneath the nets. Since these sites lacked woody vegetation during the previous cicada emergence or had been cleared since then, few cicadas emerged from the soil in these areas (1.1 ± 1.4 emergence holes/0.25 m^2 quadrat compared with 5.0 ± 0.26 holes/0.25 m^2 quadrat in mature forests). The nets were removed soon after the adult cicadas died.

After removing the nets, we permanently marked a sam-

Table 1. Species, sample sizes, and average oviposition rates for the two studies.

	Netting experiment		Growth ring study		
Species	No. of trees	No. of sites	No. of trees	No. of sites	Mean oviposition (±SE)*
Acer negundo	23	3	28	1	0.27±0.03
Acer rubrum	64	5	61	2	0.39±0.02
Acer saccharum	98	4			0.30±0.03
Alnus rugosa	3	1			0.04±0.04
Asimina triloba	43	2			0.08±0.03
Betula nigra	23	1			0.28±0.13
Carpinus caroliniana	7	3			0.47±0.15
Carya spp.	93	9			0.14±0.03
Celtis occidentalis	7	2			0.18±0.07
Cephalanthus occidentalis	18	1			0.05±0.02
Cercis canadensis	69	5			0.05±0.02
Cornus florida	84	8	85	3	0.47±0.02
Cornus stolonifera	28	2			0.18±0.06
Crataegus spp.	6	3			0.23±0.21
Diospyros virginiana	50	5	38	2	0.24±0.02
Fagus grandifolia	39	5			0.34±0.10
Fraxinus americana	664	12	53	2	0.28±0.01
Fraxinus pennsylvanica	33	1			0.36±0.03
Hypericum prolificum	63	1			0.23±0.04
Juglans nigra	111	3			0.21±0.03
Juniperus virginiana			25	1	0.21±0.03
Lindera benzoin	67	3			0.23±0.04
Liquidambar styraciflua	28	2	27	1	0.15±0.03
Liriodendron tulipifera	591	8			0.08±0.01
Nyssa sylvatica	23	3			0.18±0.06
Ostrya virginiana	20	3			0.16±0.05
Platanus occidentalis	333	9	104	2	0.28±0.02
Populus deltoides	41	4	26	1	0.14±0.02
Prunus serotina	143	6	29	1	0.18±0.02
Pyrus calleryana	9	1			0.12±0.00
Quercus alba	117	4	8	1	0.40±0.04
Quercus bicolor	45	1			0.36±0.034
Quercus imbricaria	37	1			0.39±0.04
Quercus macrocarpa	18	1			0.39±0.0
Quercus michauxii	123	1			0.56±0.03
Quercus palustris	41	2			0.35±0.05
Quercus rubra	156	9	34	1	0.23±0.02
Rhus copallinum	397	7			0.11±0.01
Rhus glabra	6	2			0.00±0.00
Robinia pseudoacacia	9	3			0.37±0.14
Salix nigra	63	3			0.22±0.03
Sassafras albidum	173	6			0.12±0.02
Tilia americana	2	1			0.00±0.00
Ulmus rubra	74	6			0.20±0.05
Vaccinium stamineum	8	1			0.41±0.22

*Trees in the netted plots were not included in the calculation of mean oviposition.

ple of trees in each plot, reflecting the composition of species and sizes present (average 15 trees/plot, 2026 netted trees, 2016 unnetted trees, Table 1). For each tree, we recorded the species, initial trunk circumference, and oviposition damage. To estimate oviposition damage, we randomly selected three branches per tree and measured the length of oviposition scars over a 30 cm segment per branch (90 cm total branch length/tree). We recorded percent oviposition as

$$[1]\qquad \%\ \text{oviposition} = \frac{\text{length of sampled branches with oviposition scars}}{\text{total length of sampled branches } (= 90\ \text{cm})}$$

Periodical cicadas have been reported to oviposit almost exclusively on branches 3–11 mm in diameter (White 1980), but we observed substantial oviposition on slightly larger branches, so we sampled branches 3–13 mm in diameter.

We measured trunk circumference at breast height unless trees forked at a lower level, in which case we measured below the fork. We marked the location of the measurement with a permanent marker, so we could measure the same location on the trunk in subsequent years. We measured circumference at four time periods: summer 2004 immediately after the cicada emergence, and each subsequent winter from 2005–2007. We used these four circumference measures (c) to define four measures of relative growth:

$$[2]\qquad \mathrm{smr1} = \frac{(c_{2005} - c_{2004})}{c_{2004}}$$

$$[3]\qquad \mathrm{year2} = \frac{(c_{2006} - c_{2005})}{c_{2005}}$$

$$[4]\qquad \mathrm{year3} = \frac{(c_{2007} - c_{2006})}{c_{2006}}$$

$$[5]\qquad \mathrm{tot} = \frac{(c_{2007} - c_{2005})}{c_{2005}}$$

The smr1 term includes only late-season growth for 2004, because the first measurement was taken in midsummer 2004 and does not include early-season growth. We used the winter 2005 measurement to estimate total growth (tot) because midsummer circumference measurements are highly variable because of fluctuations in the moisture content of trees. We used relative growth rather than absolute growth to account for differences in growth increments of trees of different sizes and because initial circumference was slightly smaller in netted plots than in unnetted plots (5.7 ± 0.07 cm in netted plots and 6.3 ± 0.08 cm in unnetted plots; $P < 0.0001$). This was a result of the practical restrictions of stretching nets over the tops of the trees and the correlation between tree height and circumference.

We analyzed differences among sites, species, and netting treatment, using PROC MIXED in SAS version 9.1 (SAS Institute 2003). We also ran a similar model by replacing the categorical variable of netting treatment with the individual oviposition measures for each tree. In both models, plot was nested within site; site was treated as a random effect; and species, treatment, and oviposition were treated as fixed effects. This resulted in a model of growth = treatment (or oviposition), species, site, plot(site), and all interactions.

Growth ring study

For the growth ring study, we focused on the three or four most common tree species at each site and utilized variation in natural levels of oviposition to compare differences among trees with different levels of oviposition damage and to compare longer-term growth rates of trees before and after the oviposition event. At each of six sites (four sites were also used in the netting experiment), we selected all the tree species that were common enough to easily locate 50 individuals (1–4 species/site, Table 1). This resulted in a total of 12 species across all sites. We measured oviposition on each tree, as described above, except that we sampled ten 30 cm branch lengths per tree for a total of 300 cm of total branch length per tree. Oviposition was again expressed as the percentage of measured branch area with oviposition scarring, as in eq. 1.

In the winter of 2007, after 2.5 years of growth following the cicada emergence, we harvested at least 25 trees of each species at each site by cutting with a chainsaw approximately 10 cm above the soil. We collected samples of the full cross-section of the trunk, allowed them to dry, and then sanded them to improve visualization of the cell structure in the wood. We measured the width of each ring to the nearest 0.01 mm with an electronic microcaliper linked to a computer (Speer et al. 2001). To adjust for differences in intrinsic growth rates among species and among individuals, we calculated the relative ring width by dividing the width of each ring from 2002 to 2006 by the mean ring width in the 3 years prior to the cicada emergence (2001–2003). We analyzed the effect of oviposition on relative ring width by using an analysis of covariance (ANCOVA) on species, site, year, and oviposition, with site treated as a random factor and all other factors fixed. We then also used regression analyses for each species sampled at each site to further explore if there were effects at particular sites that may have been missed when averaging across sites and species. We included years prior to the emergence in these analyses as a control for spurious statistical correlations between oviposition and growth. All tests were performed using PROC MIXED and PROC REG of SAS version 9.1 for Windows.

Results

Netting experiment

Oviposition damage by periodical cicadas was quite high at all of our sites (Fig. 1), permitting a strong test of the effects of oviposition by periodical cicadas. The netting treatment reduced oviposition across all sites by 38% (df = 1, $F = 126.2$, $P < 0.0001$; Fig. 1). Mean (± SE) oviposition in netted plots was 13.3% ± 0.4% compared with 21.3% ± 0.6% in unnetted plots. Netted plots had significantly lower oviposition than unnetted plots at all sites except one, where the netting was partially blown off in a storm. We excluded this site from all analyses that tested the effect of the netting treatment on growth. It is possible that the nets themselves had some detrimental effects on trees. For example, tulip poplar (*Liriodendron tulipifera* L.), a fast-growing species, grew through the nets, resulting in some deformed growth and damage to the trees when the nets were removed. However, there were no statistically significant differences in the effect of the netting treatment for tulip poplar compared with other, slower-growing species.

The mean growth rates of the netted and unnetted trees were identical (Fig. 2, Table 2). The netting treatment had significant interactions with both site and species, indicating that the netting treatment differentially affected the growth of different species at different sites (Table 2, Fig. 1) and that some species may have been affected by the netting treatment itself. Because the netting treatment did not completely exclude oviposition, we used an ANCOVA to analyze the effect of oviposition on growth directly.

Fig. 1. Proportion of oviposition at each site as determined by the proportion of branch length with oviposition scars from periodical cicadas. Proportion of oviposition is shown separately for the netting experiment and the growth ring study. Error bars represent one standard error of the mean.

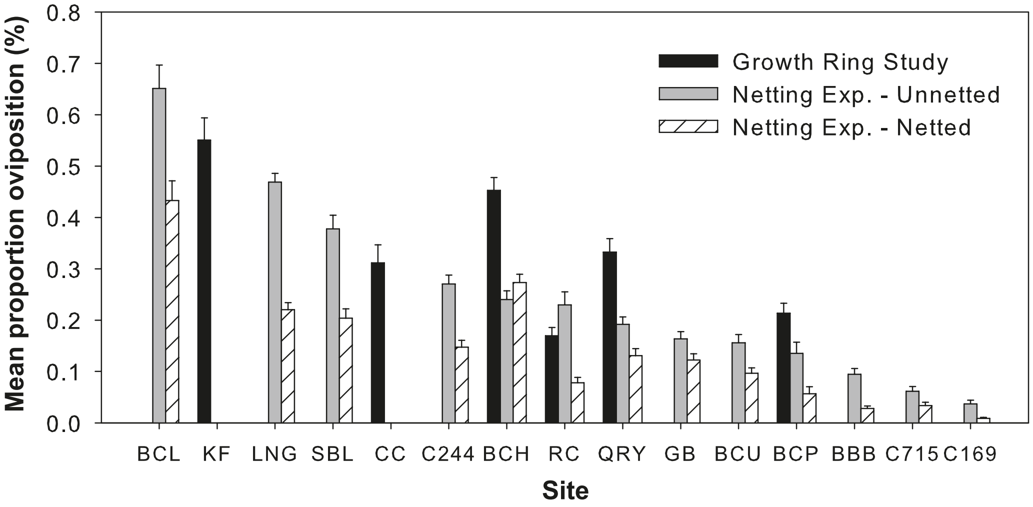
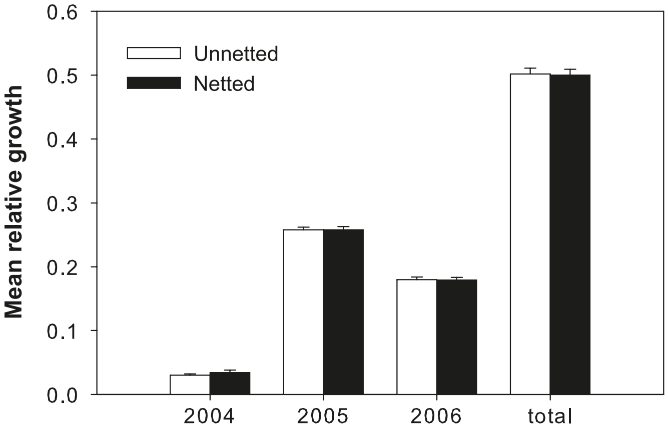


Fig. 2. Mean (±SE) growth rate of trees in netted and unnetted plots. The growth rates were not statistically different.



Oviposition had no effect on growth rates over any time period, but growth was strongly affected by both site and species (Table 2). None of the interactions with oviposition were significant, suggesting the interactions with the treatment effect were a result of the netting itself rather than an effect of cicada oviposition. The results for all of the growth variables except summer 2004 growth gave the same qualitative results. No significant effects were found for summer 2004, but these measurements include only late-season growth because the initial measurement was made after the nets were removed in the early summer. We ran the model with initial circumference included to test if initial tree size affected growth, but this had no effect on any of the growth measures, and was excluded from later analyses.

There was no effect of cicada oviposition damage on tree mortality. Of the 4049 trees we marked and followed for 2.5 years after the periodical cicada emergence, we confirmed dead, or were unable to locate, 120 trees — less than 3% of the total. The majority of these (83) were damaged by ice at a single site where flooding followed by freezing sheared many trees. Of the marked trees at this site 34% were severely damaged or killed. There was no difference in oviposition between trees that were damaged by ice (15.5% ± 2.3% oviposition) and those that were not (14.2% ± 1.8%; $P = 0.659$). After excluding trees that were lost as a result of ice damage at this site, there was still no effect of oviposition on the mortality of trees ($P = 0.592$).

Growth ring study

We analyzed annual growth rings of trees, which can be more precisely measured than can changes in circumference. This also allowed us to measure past years' growth prior to the periodical cicada emergence. An ANCOVA of site, species, year, and oviposition on relative ring width revealed significant effects of year and the interaction of year by oviposition, but the overall main effect of oviposition was not significant (Table 3). These effects reflect that saplings grow faster as they age and that oviposition did not occur until 2004.

As an additional examination of the effects of oviposition, we regressed relative ring width against oviposition for each year from 2003 to 2006. We included 1 year prior to the 2004 emergence as a control for significant effects that were not due to the effect of oviposition by periodical cicadas. There was a slight negative slope between relative ring width and oviposition in 2003, but this slope was small and not statistically significant (Fig. 3). In the year of and the year following the cicada emergence (2004 and 2005) there was a significantly negative relationship between relative ring width and oviposition, with a steeper negative slope than prior to the emergence (Fig. 3). This effect disappeared by 2006. These correlations were highly significant but explained only a limited portion of the variation ($R^2 = 0.07$ for both 2004 and 2005).

When we examined this relationship more closely by looking at each species independently, we found little evidence of a negative effect of oviposition on tree growth (Table 4). We regressed relative ring width on oviposition for each species at each site independently (18 combinations) to exclude interactions. In the emergence year (2004) three species, *Acer negundo*, *Cornus florida*, and *Platanus*

Table 2. Results of (A) an analysis of variance (ANOVA) on total relative growth for the netting experiment including the netting treatment as a factor and (B) an analysis of covariance (ANCOVA) using oviposition.

Source*	df	F/Z†	P‡	$\eta_P{}^{2}$§
(A) ANOVA				
Treatment^{F}	1	0.09	0.771	0.000
Species^{F}	48	3.84	**<0.001**	0.215
Site^{R}	14	1.84	**0.033**	0.077
Plot(site)^{R}	117	3.41	**<0.001**	0.146
Treatment × species^{F}	37	1.26	0.201	0.024
Treatment × site^{R}	14	1.11	0.133	0.009
Treatment × species × site^{R}	48	0.01	0.494	0.017
Treatment × plot(site)^{R}	110	1.75	**0.040**	0.070
Species × plot(site)^{R}	419	3.66	**<0.001**	0.209
Treatment × species × plot(site)^{R}	135	3.53	**<0.001**	0.069
Residual^{R}	2844	38.25		
(B) ANCOVA				
Oviposition^{F}	1	0.00	1.000	0.000
Species^{F}	48	2.93	**<0.001**	0.063
Site^{R}	14	1.76	**0.039**	0.030
Plot(site)^{R}	117	3.60	**<0.001**	0.102
Oviposition × species^{F}	45	0.41	0.999	0.013
Oviposition × site^{F}	14	0.06	1.000	0.002
Oviposition × species × site^{F}	63	0.68	0.980	0.030
Oviposition × plot(site)^{F}	117	0.78	0.939	0.044
Species × plot(site)^{R}	333	6.01	**<0.001**	0.187
Oviposition × species × plot(site)^{F}	193	0.81	0.979	0.069
Residual^{R}	2755	37.42		

*Superscipt after factor name denotes whether it was treated as a fixed (F) or random (R) effect. In (B) interactions including oviposition were treated as fixed effects because PROC MIXED could not calculate interaction terms as random. None of these interactions was statistically significant as a fixed effect and would be even less significant if properly treated as a random effect because of the larger denominator term.

†F values are reported for fixed effects, and Z values are reported for random effects.

‡P values less than 0.05 are highlighted in bold.

§Partial eta-squared values, $\eta_P{}^2$, indicate the effect size of each factor and are calculated as SS_{effect} / (SS_{effect} + SS_{error}).

Table 3. Results of an analysis of covariance for the growth ring study.

Source*	df	F/Z†	P‡	$\eta_P{}^{2}$§
Site^{R}	4	1.20	0.115	0.047
Species^{F}	10	8.86	0.106	0.049
Site × species^{R}	2	—	—	0.002
Year^{F}	4	3.96	**0.047**	0.014
Site × year^{R}	16	1.52	0.065	0.023
Species × year^{F}	40	2.26	0.112	0.041
Site × species × year^{R}	8	0.49	0.312	0.002
Oviposition^{F}	1	1.27	0.377	0.000
Oviposition × site^{R}	4	0.28	0.388	0.007
Oviposition × species^{F}	10	3.35	0.252	0.023
Oviposition × site × species^{R}	2	0.46	0.324	0.003
Oviposition × year^{F}	4	4.72	**0.030**	0.007
Oviposition × site × year^{R}	16	—	—	0.008
Oviposition × species × year^{F}	40	1.79	0.195	0.025
Oviposition × site × species × year^{R}	8	—	—	0.000
Error	2399	—	—	—

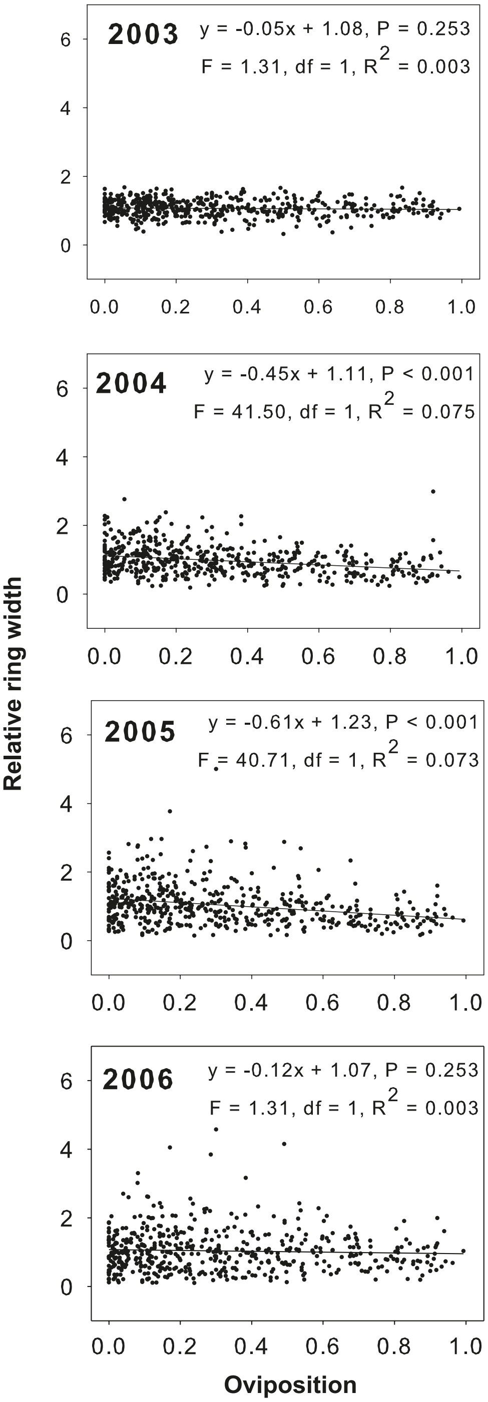
*Superscipt after factor name denotes whether it was treated as a fixed (F) or random (R) effect.

†F values are reported for fixed effects, and Z values are reported for random effects. Values marked with dashes had insufficient degrees of freedom to be calculated by PROC MIXED.

‡P values less than 0.05 are highlighted in bold.

§Partial eta squared values, $\eta_P{}^2$, indicate the effect size of each factor and are calculated as SS_{effect} / (SS_{effect} + SS_{error}) using the type III SS reported by PROC GLM in SAS version 9.1.

Fig. 3. Correlation between ring width and oviposition for 2003–2006 in the growth ring study. Data for 2003 are presented as a control for any spurious correlations.



occidentalis had significant negative correlations between oviposition and relative ring width. Of these, *P. occidentalis* also had a negative correlation with oviposition prior to the cicada emergence. In 2005, one species, *Juniperus virginiana*, had a significant positive correlation between oviposition and growth, and *P. occidentalis* still had a negative correlation. In 2006, four of the eighteen species by site combinations were significantly positively associated with oviposition, and there were no negative correlations. These positive correlations after the oviposition event suggest that oviposition by periodical cicadas may positively affect the growth of some species in the long run. For a further comparison of the effect size of each factor, we also calculated the partial eta squared (η_P^2) values for each factor in the model. This measure of effect size is the proportion of effect and error variance that is attributable to each factor, and it provides a comparable measure of the effects between the different factors examined (Olejnik and Algina 2003). η_P^2 values indicate that the effects of site and species and the interaction of species by year have the most explanatory power in the model (Table 3).

In a previous paper (Clay et al. 2009), we documented preferences of periodical cicadas towards different tree species for oviposition. To determine if trees that were differently preferred by periodical cicadas had different responses to oviposition damage, we defined each species as preferred, neutral, or avoided (Clay et al. 2009). There was no correlation between the preference category of a species and the positive or negative relationship between growth and oviposition in this study.

Discussion

These results indicate that oviposition by periodical cicadas has no significant detrimental effect on the long-term growth rate or survival of trees. Neither the circumference measurements of tree trunks in the netting experiment nor the annual growth rings in the growth ring study showed any significant negative effects of oviposition by periodical cicadas on the growth of trees when all tree species are analyzed together. When species were examined individually in the growth ring study most showed no effect of oviposition, but of those that had a statistically significant relationship, more were positive than negative. In addition to the analyses presented here, we also ran analyses excluding site and species, and analyses for each site and species individually. In only a few cases for individual species and sites did we find a significant treatment or oviposition effect, but given the number of multiple tests, the number of significant results was equal to the number expected by random chance. In total, the large number of statistical tests and the power of the study (given the large number of trees, species and sites examined) provide no evidence of an effect of oviposition by periodical cicadas on tree growth.

Why doesn't cicada oviposition harm trees?

Several characteristics of cicada oviposition may contribute to a tree's ability to compensate for this damage. It has been suggested that plants may be better able to compensate for herbivory when it happens early in the season (Maschinski and Whitham 1989), occurs in a single bout (Cartwright and Kok 1990; Mauricio et al. 1993), or is evenly distributed rather than clumped (Honkanen and Haukioja 1994; Mauricio et al. 1993). All of these factors apply to periodical cicadas. They oviposit in a single 3–4 week period in late spring once every 13 or 17 years. Periodical cicadas tend to disperse their damage; females often avoid ovipositing directly adjacent to a pre-existing cicada nest (Simon 1981; White 1981), which results in a more evenly distributed pattern of damage, and our field surveys indi-

Table 4. Regression slopes of relative annual ring widths on oviposition for each species at each site in the growth ring study.

Species	Site	*N*	2003	2004*	2005	2006
Acer negundo	BCP	28	–0.235	**–1.336**	–1.507	–1.679
Acer rubrum	BCP	28	–0.552	–0.646	–0.169	–0.250
Acer rubrum	KF	33	–0.815	–0.591	–0.085	–0.239
Cornus florida	BCH	38	–0.002	**–0.431**	–0.136	0.036
Cornus florida	CC	26	0.181	–0.275	–0.248	–0.056
Cornus florida	QRY	21	0.313	0.388	0.240	**1.085**
Diospyros virginiana	BCH	27	0.034	–0.001	0.389	0.422
Diospyros virginiana	CC	11	0.177	–0.135	–0.304	–0.152
Fraxinus americana	BCH	24	0.282	–0.224	–0.249	–0.145
Fraxinus americana	QRY	28	–0.757	–0.741	–0.982	0.064
Juniperus virginiana	CC	25	–0.111	0.021	**0.658**	**0.704**
Liquidambar styracifolia	BCP	27	–0.035	–0.392	–0.289	1.090
Platanus occidentalis	BCP	33	0.158	–0.019	0.721	**0.744**
Platanus occidentalis	RC	69	**–0.791**	**–1.939**	**–1.508**	–0.023
Populus deltoides	RC	26	–1.191	–1.184	0.410	–1.015
Prunus serotina	QRY	29	0.344	–0.026	0.380	0.874
Quercus alba	BCH	8	–0.833	–0.946	0.896	1.305
Quercus rubra	BCH	34	–0.581	–0.026	0.985	**2.393**

Note: Results with a *P* value <0.05 are highlighted in bold.

*Emergence year of periodical cicadas.

cated that virtually all trees received some oviposition damage (Clay et al. 2009).

Oviposition by periodical cicadas also has several characteristics that may help a tree's ability to compensate for damage. While oviposition weakens branches, they typically do not die right away but instead continue photosynthesizing for a month or more following the oviposition event. The loss of apical tips of small branches, as is typical with flagging from cicada oviposition, often results in increased growth of the remaining branch (Lehtila et al. 2000). Moreover, when adult cicadas die, their carcasses tend to cluster around the base of trees and can provide a significant nutrient pulse (Yang 2004), which may help trees compensate for the oviposition damage (Maschinski and Whitham 1989) or otherwise stimulate growth. All of these characteristics of periodical cicadas may moderate the impacts of their oviposition on trees. In addition, because trees have very high apparency to herbivores due to their long lives and large growth forms, they have often evolved the ability to tolerate damage rather than actively prevent it (Feeny 1976; Haukioja and Koricheva 2000; Rhoades and Cates 1976).

The branch death that results from oviposition by periodical cicadas may be similar to a pruning effect, which can invigorate some trees (Crawley 1983). Plants with many crowded leaves may be above the optimal leaf area index for photosynthesis, and the removal of some leaves can bring plants closer to this optimum and increase the overall photosynthetic capacity of the plant (Black 1964; Mooney and Gulmon 1982). Pruning is a recommended horticultural practice to improve tree health, increase structural strength, and stimulate fruit production (Trumble et al. 1993). In addition, trees often self-prune small older branches as they mature to increase light availability and air movement within the canopy (Haukioja and Koricheva 2000). The branch death that results from periodical cicada oviposition could potentially have positive effects on trees. This could be tested by comparing photosynthetic rates before and after the emergence of periodical cicadas or by comparing fruit production on trees with and without oviposition in the year of and years following the emergence.

Impacts on lifetime fitness of trees

Most trees are long-lived and the annual reproductive output of smaller, younger trees is typically small compared with the reproductive output in later years when the tree is mature. We predict that even if there were a reduction in reproductive effort for a single year as a result of oviposition by periodical cicadas, it would have only minor effects on the lifetime fitness of trees. While we did not measure the reproductive effort of trees in this study, Flory and Mattingly (2008) found no effect of oviposition by periodical cicadas on flower or fruit production in three native species and three introduced species. Another study found no effect on fruit production in *Cornus drummondii*, the most common tree at an early successional site in Kansas (Cook and Holt 2002). Growth to maintain competitive ability is likely to be more important to saplings than reproductive effort. Our data demonstrate that oviposition damage by periodical cicadas does not reduce the growth rate or the competitive ability of trees, as indicated by the equal growth of damaged and undamaged trees in crowded early successional forests.

Most trees in early successional forests do not survive to become mature canopy trees. Young trees have a very high natural mortality as a result of competition, thinning, and other biotic and abiotic stresses. For example, a flood followed by a hard freeze killed approximately one-third of the trees at one site. At other sites, we observed many trees damaged or killed by larger treefalls, vines, insect damage, and disease. These factors are clearly important to the growth and survival of trees relative to the effect of oviposition by periodical cicadas.

Aboveground versus belowground effects of cicadas

This study focused on the impact of aboveground oviposition, but it is important to consider the relative impact of periodical cicadas in both the aboveground and belowground portions of their life cycle. Periodical cicadas spend the majority of their lives underground as nymphs feeding on xylem fluids from roots. They are aboveground for only 4–6 weeks every 13 or 17 years. Their numbers and the immediate effects of their oviposition are extremely impressive during these emergences, resulting in extensive branch scarring and many dead branches on trees and on the ground. However, these impacts may be minor compared with the prolonged underground feeding of nymphs. Our results do not incorporate the effects beyond the first 3 years of nymphal feeding on tree growth. This potentially important effect of periodical cicadas remains unexamined.

Previous results on effects of periodical cicadas on trees

Previous studies on the effects of oviposition by periodical cicadas on trees have found varying results. Our results agree most closely with those of Cook and Holt (2002) who found no effect of cicada damage on tree growth. They examined seven species in a descriptive study conducted at a single site in eastern Kansas that was dominated by a single species (93% *Cornus drummondii*). Miller (1997) found no effect of cicada oviposition on a suite of urban and horticultural tree species, other than natural pruning. Several studies have documented damage during the oviposition year in terms of branch loss, alteration of growth form, and reduced flower or fruit production, particularly in horticultural trees (Hamilton 1962; Williams 1987), but these effects may be short-lived and have little effect on the overall competitive ability, health, or fitness of trees. Karban (1980) and Koenig and Liebhold (2003) both reported negative effects of oviposition by periodical cicadas on radial growth of trees in natural systems, but these effects on growth could have been due to nymphal feeding by periodical cicadas rather than direct effects of oviposition. The trees in our study were growing at high densities in naturally occurring early successional forests where root systems of adjacent trees may overlap, therefore, there may not be a clear correlation between aboveground oviposition damage and belowground nymphal feeding on the same individual.

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