Differential susceptibility of tree species to oviposition by periodical cicadas

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Abstract. 1. Periodical cicadas occur widely in deciduous forests of eastern North America and represent the largest insect emergences in the world. Their effects on forest community dynamics, via oviposition damage and root feeding, are potentially great but not well understood. If tree species vary in their susceptibility to cicada oviposition and root colonization, then periodical cicadas may affect ecological interactions among tree species and forest composition.

2. We measured oviposition damage on 63 tree species at 52 sites in southern Indiana, U.S.A. for two broods of periodical cicadas. We compared oviposition damage among different sites, habitats, and tree species. We also measured cicada emergence rates in mature and successional forest habitats and from beneath different tree species.

3. Certain tree species received significantly more oviposition damage than others, and the most and least damaged species were consistent between the two broods. For some species, oviposition damage varied between mature and successional sites. Despite the differences in oviposition rates among species, there was no difference in emergence rates from beneath different tree species, suggesting that initial differences in cicada density among tree species are not maintained through the nymphal life cycle.

4. Cicadas oviposited more at successional sites, but emerged more in mature forest stands, suggesting that successive generations of cicadas represent a *shifting mosaic* between forests of different ages. As tree species consistently vary in their susceptibility to oviposition damage, periodical cicadas could alter local competitive interactions and therefore affect forest dynamics.

Key words. Deciduous forests, forest dynamics, host preference, *Magicicada,* oviposition preference, shifting mosaic.

Introduction

Plant–insect interactions are among the most important interactions structuring ecological communities. Approximately one-quarter of all known higher species (excluding microbes and fungi) are plants and another quarter are plant-eating insects (Strong *et al.*, 1984). Herbivorous insects can have dramatic effects on plants, at times affecting the population dynamics of their host plants. Outbreaking species such as gypsy moths, spruce budworms, and autumnal moths have been most heavily studied for their impacts on forest communities, but non-outbreaking insect species can also affect regulation of plant populations (Crawley, 1983). Periodical cicadas are an interesting case of forest herbivores, because they exist at very high densities, have very broad host ranges, and their cyclical emergences have parallels with outbreaking species.

Periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.) are unique to deciduous forests in eastern North America (Williams & Simon, 1995). They spend most of their life underground as nymphs and then emerge on a regular schedule every 13 or 17 years, depending on the brood. They are the largest insect emergence known, with standing biomass and productivity exceeding that of any terrestrial animal in nature (Dybas & Davis, 1962). During the emergence, periodical cicadas create innumerable egg nests on the twigs and small branches of trees and shrubs. Oviposition frequently kills the ends of branches, leading to a phenomenon called *flagging* (White, 1981) where the tips of branches wither and die, and this can increase their susceptibility to disease (Zwet *et al.*, 1997). After 6–8

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weeks, the eggs hatch, nymphs drop to the ground below the tree, burrow into the soil, and attach to small roots where they feed on xylem for the remainder of their 13- or 17-year life cycle (White & Strehl, 1978). This long-term feeding may reduce tree growth (White & Strehl, 1978), and decrease the productivity of woody crops (Banta, 1960; Hamilton, 1962; Hogmire *et al.*, 1990) and the value of horticultural specimens (Smith & Linderman, 1974). The pulsed aboveground damage to branches from oviposition and the prolonged underground feeding by nymphs, may have important effects on the growth and competitive ability of trees. As hatching nymphs drop passively to the ground, we expect a high concordance between levels of oviposition damage and root colonization by nymphs. If certain tree species are subject to greater oviposition than others, periodical cicadas could significantly affect the competitive interactions among tree species and potentially alter forest community dynamics.

The effects of periodical cicadas on tree growth and forest dynamics are not well understood and previous studies report conflicting results. Karban (1980) found significantly reduced radial growth in *Quercus ilicifolia* trees in the year of, and 3 years following, an emergence of periodical cicadas. In two additional experiments, Karban (1982) found increased radial growth when he experimentally excluded cicada nymphs from three trees, but found no reduction in seed production when he added nymphs to trees (Karban, 1985). Koenig and Liebhold (2003), using a large data base of tree ring records, also found evidence of reduced growth in *Quercus* spp. during emergence years compared with *Pinus* spp., which are not a host for cicadas. They also found evidence for periodicity, equal to the periodicity of cicada emergences, in the growth of oaks, but not pines. In contrast, Cook and Holt (2002) found no biologically significant effects of cicada emergences on growth of several tree species or on reproduction of *Cornus drummondii* at a successional site near the western range limit of cicadas.

There has been a substantial amount of previous work on the oviposition preference of periodical cicadas (Skeels, 1907; Dybas & Lloyd, 1974; White, 1980; Cook *et al.*, 2001). However, previous studies on oviposition preference of periodical cicadas have been limited to a single or a few sites, and there have been no large-scale studies that examine oviposition damage and its potential impacts on forest communities across the landscape. The distribution of periodical cicadas is patchy (Oberdorster & Grant, 2006), so damage to trees in a single area may not accurately represent oviposition damage by a brood as a whole. A landscape-level study is needed to compare the degree of oviposition damage and its distribution among tree species.

In this paper we evaluate three competing hypotheses about the relative susceptibility of different tree species to oviposition damage by periodical cicadas: (1) all tree species are equally susceptible and relative damage is a function of cicada density among sites, (2) susceptibility is frequency dependent, such that more common species at a site are more heavily damaged than rare species, and (3) tree species exhibit consistent differences in susceptibility in a predictable rank order. We use the term *susceptibility* to refer to the actual incidence of oviposition damage on a tree. By this definition, susceptibility integrates the density of periodical cicadas in a specific area, oviposition

preference by periodical cicadas for certain tree species, and host resistance characteristics of trees, such as thorns or sap, that reduce oviposition on trees.

Methods

Natural history of periodical cicadas

Seven species of periodical cicadas are recognized: the 17-year cicadas *Magicicada septendecim*, *M. cassini*, and *M. septendecula* and the 13-year cicadas *M. tredecim*, *M. tredecassini*, *M. tredecula*, and *M. neotredecim,* which is largely allopatric with *M. tredecim* (Marshall & Cooley, 2000). Cicada broods are distinguished by their year of emergence, identified with Roman numerals (Marlatt, 1907), and generally include all species of 13- or 17-year cicadas. Within a brood, the three species are partially separated by habitat, but all three species prefer successional habitats (Heath, 1967; Dybas & Lloyd, 1974; Williams & Smith, 1991; Williams & Simon, 1995; Rodenhouse *et al.*, 1997; Yang, 2006) where sympatry is 'about as complete as it could possibly be' (Alexander & Moore, 1962).

After emerging from underground after 13 or 17 years, periodical cicadas shed their nymphal exoskeleton and males form chorusing centres in sunlit areas where mating occurs (Lloyd & White, 1976; Yang, 2006). Females then fly usually less than 50 m away (Karban, 1981) to lay eggs on 3–11-mm-diameter branches and twigs of deciduous trees (White, 1980). Females use their ovipositor to make longitudinal incisions on the underside of branches and deposit 12–20 eggs in clusters (egg nests) in the interior wood (Marlatt, 1907; Lloyd & White, 1976). Multiple egg nests are typically deposited in rows of 4–12 nests, leading to a zipper-like appearance on the underside of branches. This leaves a persistent scar that is easy to identify and measure.

Study sites

We measured emergence and oviposition for two broods in southern Indiana, U.S.A.: Brood XXIII in 2002 (13-year cycle) and Brood X in 2004 (17-year cycle; Fig. 1). Brood X is among the largest of all cicada broods, covering much of the upper Midwest (Kritsky, 1987; Marshall & Cooley, 2000; Sadof, 2000) and reaches some of its greatest densities near Monroe County, Indiana (Young & Kritsky, 1988, Fig. 1). Brood XXIII is centred over the central Mississippi River Valley and includes southwestern Indiana. Thirteen sites with successional forest adjacent to mature forests, were sampled for Brood XXIII, including several reclaimed coal strip mines from the 1960s. We sampled 135 trees in mature forest habitat and 378 trees in successional forest habitat. For the more extensive Brood X, 43 sites were sampled across a range of habitats, including mature forests ($n = 20$ sites, 1163 trees), successional sites ($n = 20$ sites, 5132 trees), and young (<15 years old) tree plantations established in former pastures ($n = 3$ sites, 487 trees). At each site, we sampled trees in proportion to their frequency at a site, rather than sampling a fixed number of trees of each species. This design represents the availability of oviposition sites to
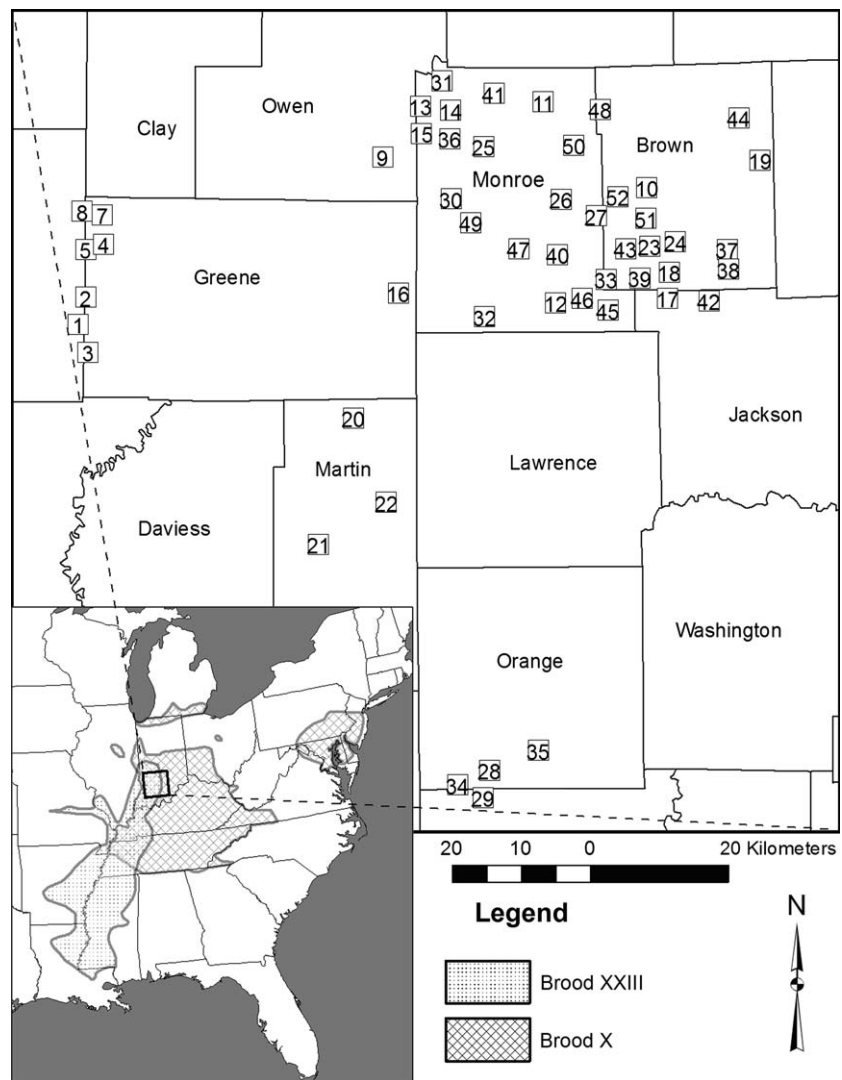
Fig. 1. Location of study sites in southern Indiana and the geographic distribution of Brood XXIII and Brood X. For Brood XXIII, we sampled sites 1–8 and we sampled Brood X at all other sites. Multiple locations were sampled for some sites in Brood XXIII.

cidadas, and allowed us to test for a relationship between the relative abundance of each tree species and their use by ovipositing cicadas.

Mature forests were defined as those with a closed canopy greater than 10 m high dominated by large, mature trees (mean diameter $\pm$ SE = 21.7 $\pm$ 0.65 cm), whereas successional forests had an open canopy of young trees (<17 years old) invading into old fields or clear cut areas (mean diameter 1.9 $\pm$ 0.05 cm). Thus, mature forests were old enough to have experienced multiple generations of cicada emergences, but successional forests had established after the last emergence of periodical cicadas, and therefore should not be colonized by cicada nymphs. In total, oviposition data were collected from 513 trees of 35 species for Brood XXIII, and from 6782 trees of 59 species for Brood X (Table 1). We focused more heavily on successional sites, because they are preferred by all *Magicicada* species, tend to have high densities of cicadas, and the young trees have a higher proportion of biomass in branches of suitable size for oviposition.

Oviposition measurement

Several methods were used to quantify oviposition in each brood. At successional sites, oviposition was measured on three subsamples of 30-cm lengths of branches on randomly selected trees to represent the distribution and frequency of tree species at a site, and on selected trees of the most common species at a site (10 subsamples in 30 cm segments). Oviposition was measured *in situ* on trees that were to have future growth measured (data not shown). Oviposition was measured on clipped branches of other trees. Only branches between 3 and 13 mm in diameter were sampled. This is a slightly larger range than previously reported (White, 1980), because we noticed substantial oviposition on branches at the upper end of this size class.

In mature forests for Brood X, we used pole pruners to randomly sample branches within 6 m of the forest floor. We also measured oviposition in the canopy opportunistically on fallen branches, limbs, and downed trees after a series of strong storms in early summer 2004. Most of these fallen branches were from

Table 1. List of species examined for emergence and oviposition in Brood XXIII and Brood X.

Latin name	Common name	Brood XXIII no. trees (no. sites)	Brood X no. trees (no. sites)
Acer negundo	Box elder	14 (6)	120 (10)
Acer platanoides	Norway maple	—	1 (1)
Acer rubrum	Red maple	79 (13)	404 (24)
Acer saccharinum	Silver maple	2 (1)	75 (6)
Acer saccharum	Sugar maple	—	238 (19)
Alnus rugosa	Alder	10 (2)	1 (1)
Asimina triloba	Pawpaw	—	31 (5)
Betula nigra	River birch	3 (2)	33 (2)
Carpinus caroliniana	Ironwood	—	28 (10)
Carya illinoensis	Pecan	—	3 (1)
Carya spp.	Hickory	16 (3)	114 (19)
Celtis occidentalis	Hackberry	1 (1)	6 (3)
Cephalanthus occidentalis	Buttonbush	—	4 (1)
Cercis canadensis	Redbud	2 (2)	100 (15)
Cornus florida	Flowering dogwood	21 (8)	585 (28)
Cornus stolonifera	Osier dogwood	—	46 (3)
Corylus americana	Hazelnut	2 (1)	19 (2)
Crataegus spp.	Hawthorn	6 (4)	4 (3)
Diospyros virginiana	Persimmon	24 (5)	254 (9)
Elaeagnus umbellata	Autumn olive	41 (7)	113 (5)
Fagus grandifolia	Beech	—	113 (17)
Fraxinus americana	White ash	42 (8)	513 (16)
Fraxinus pennsylvanica	Green ash	—	224 (16)
Fraxinus spp.	Unidentified ash	17 (6)	—
Hypericum prolificum	Shrubby St. John's wort	2 (1)	119 (4)
Juglans nigra	Black walnut	11 (1)	79 (7)
Juniperus virginiana	Red cedar	—	168 (6)
Lindera benzoin	Spicebush	—	84 (5)
Liquidambar styraciflua	Sweetgum	13 (2)	66 (2)
Liriodendron tulipifera	Tulip poplar	4 (2)	484 (24)
Nyssa sylvatica	Black gum	—	32 (5)
Ostrya virginiana	Hop hornbeam	—	26 (7)
Platanus occidentalis	Sycamore	29 (6)	453 (19)
Populus deltoides	Cottonwood	14 (5)	97 (3)
Populus grandidentata	Bigtooth aspen	—	4 (2)
Prunus serotina	Black cherry	19 (8)	235 (15)
Ptelea trifoliata	Common hop-tree	—	3 (1)
Pyrus calleryana	Callery pear	—	17 (1)
Quercus alba	White oak	3 (1)	165 (16)
Quercus bicolor	Swamp white oak	—	37 (1)
Quercus imbricaria	Shingle oak	20 (6)	4 (1)
Quercus macrocarpa	Bur oak	—	1 (1)
Quercus michauxii	Swamp chestnut oak	—	51 (1)
Quercus palustris	Pin oak	—	72 (5)
Quercus rubra	Red oak	19 (8)	335 (22)
Quercus spp.	Unidentified oak	1 (1)	5 (3)
Rhus copallinum	Winged sumac	—	455 (17)
Rhus glabra	Smooth sumac	—	4 (2)
Rhus spp.	Unidentified sumac	9 (5)	—
Rhus typhina	Staghorn sumac	—	29 (2)
Robinia hispida	Spiny locust	—	31 (2)
Robinia pseudoacacia	Black locust	28 (5)	52 (5)
Salix nigra	Black willow	10 (5)	81 (4)
Sambucus canadensis	Elderberry	2 (1)	—
Sassafras albidum	Sassafras	11 (8)	316 (21)
Taxodium distichum	Bald cypress	1 (1)	—
Tilia americana	Basswood	1 (1)	1 (1)
Ulmus alata	Winged elm	—	15 (1)
Ulmus americana	American elm	11 (5)	89 (4)

Table 1. *Continued*

Latin name	Common name	Brood XXIII no. trees (no. sites)	Brood X no. trees (no. sites)
Ulmus rubra	Red elm	—	56 (8)
Ulmus spp.	Unidentified elm	25 (5)	53 (12)
Vaccinium stamineum	Deerberry	—	23 (1)
Viburnum spp.	Viburnum	—	11 (1)
Total		513 (13)	6782 (43)

large branches or entire trees, so cicada damage was not likely to have increased their chance of falling, although some tree species may have been more likely to be damaged by wind than others (Everham & Brokaw, 1996). For Brood XXIII (2002), a 50-m transect was established at each site, running from 40 m into the forest to 10 m outside the edge. Oviposition was measured every 2 m by hand or pole pruners, and each location was classified as successional or mature. Trees within 5 m of the forest dripline were considered edge habitat and excluded from the analyses.

All analyses were calculated on the proportion of sampled branch length that had oviposition scarring. While there are slight differences in the size of egg nests among periodical cicada species (White, 1980), the impact of egg nests on trees is more likely a result of the length of damaged branches than the number of egg nests. Therefore, the proportion of branch length damaged best reflects the impact on trees.

Emergence density

Emergence density was measured by counting the emergence holes of cicadas within 0.5×0.5 m quadrats. When cicada nymphs emerge from underground, they burrow to the surface and leave a hole surrounded by hard-packed soil that is distinctive and long lasting. For Brood XXIII, we counted emergence holes every 2 m along the same transects used to measure oviposition. For Brood X, we counted emergence holes with three different methodologies. In mature forest, we estimated emergence associated with particular tree species, by counting emergence holes in a quadrat 1 m from the base of selected trees ($n = 25$ per site, 21 sites). For a second measure of overall emergence density independent of individual trees, emergence holes were counted in 0.5×0.5-m quadrats located 5 m apart in a 20×20-m grid. At successional sites, emergence was measured in quadrats randomly located across sites. The high density of overlapping small trees at these sites made it impossible to assign quadrats to individual trees.

Data analysis

Since oviposition and emergence varied greatly among sites, and tree species were associated with particular sites, the effects of site and tree species were confounded. To separate these effects, we created two new variables, *oviposition index* and *emergence index*, which we used for all analyses of tree species susceptibility. We calculated these as the proportion of oviposition on an individual tree, the experimental unit used in this study (or the number of holes in the quadrat beneath a tree), minus the mean oviposition (or emergence) rate for that site. This standardizes differences in oviposition and emergence rates among sites as a result of different densities of cicadas, and is a more accurate measure of tree species susceptibility to cicada oviposition. These new variables also have the statistically useful properties of being normally-distributed zero-mean variables with less heterogeneity of variance.

Differences among the three forest types (mature, successional, or plantation) were compared using the arcsine square root-transformed proportion of oviposition and the log-transformed number of emergence holes. These transformations improved the normality of the variables. Some heterogeneity of variances remained according to Levene's test, but no single group had larger variation. ANOVA is also quite robust to general differences in variance (Underwood, 1997). All statistical analyses were performed using PROC GLM in SAS version 9.1 for Windows and significance values were determined by Type III SS. All of the variables were treated as fixed effects.

Results

Oviposition susceptibility among tree species

Tree species differed significantly in their susceptibility to oviposition by periodical cicadas ($P < 0.0001$, Table 2). The most susceptible species in Brood X were *Cornus florida*, *Robinia pseudoacacia*, *Acer rubrum*, *Quercus alba*, *Acer negundo*, *Carpinus caroliniana*, and *Ulmus americana* (Fig. 2). *Platanus occidentalis* was also preferred by Brood XXIII. *Rhus* spp., *Juniperus virginiana*, *Asimina triloba*, *Quercus palustris*, *Diospyros virginiana*, *Rhus hispida*, *Liriodendron tulipifera*, and *Juglans nigra* experienced little oviposition. *Carya* spp. and *Populus deltoides* experienced very little oviposition by Brood XXIII, but an average amount of oviposition by Brood X. There was a significant interaction between brood and species with some species being differently preferred by Brood XXIII than by Brood X (Table 2). Separate ANOVAs run for each species reveals that this effect was as a result of only four species: *C. florida*, *P. deltoides*, *Carya* spp., and *D. virginiana*. Of these four species, only *C. florida* differed in the direction of preference, being highly preferred by Brood X, but avoided by Brood XXIII. However, this result may not be robust, because only five individuals of *C. florida* were sampled from successional forests for Brood XXIII. *C. florida* was also much more strongly preferred by Brood X in successional forests than in mature forests. There was also a significant effect of the three-way interaction between

Table 2. Results of ANOVA for the effects of tree species, cicada brood, and forest age (mature or successional) on the oviposition index.

	Effect on oviposition index*			
Source	d.f.†	MS	F	P
Species	59	0.1765	3.49	<0.0001
Brood	1	0.0026	0.05	0.8203
Brood × Species	27	0.0849	1.68	0.0152
Forest age	2	0.1720	3.40	0.0333
Species × Forest age	54	0.1629	3.22	<0.0001
Brood × Forest age	1	0.0023	0.05	0.8295
Species × Brood × Forest age	6	0.1375	2.72	0.0121
Error	7142	0.0505	—	—

*Oviposition Index = Proportional length of sampled branches with oviposition scars/average proportion of oviposition for all trees at a site.
†Not all species were sampled for both broods and tree plantations were sampled only in Brood X, so the d.f.'s of the interaction terms are determined only by factors that occurred in both broods.

brood, forest age, and tree species (Table 2). This is likely to be a result of the same differences that gave rise to the interactions between species and forest age, and between species and brood.

The interaction between oviposition preference for tree species and forest successional age was highly significant ($P < 0.0001$, Table 2, Fig. 3). Certain species, particularly *Elaeagnus umbellata*, *Diospyros virginiana*, and *Rhus copallinum*, were much more susceptible to oviposition when growing in mature forests than in successional forests. These higher rates of oviposition on *D. virginiana* and *R. copallinum* are particularly striking, because they were among the least susceptible species in successional forests. The main effect of forest age was also significant (Table 2), indicating that there was more oviposition in successional forests than in mature forests.

Interestingly, congeneric species were not similarly susceptible to oviposition by periodical cicadas. Six genera had multiple species sampled for Brood X: *Quercus*, *Acer*, *Cornus*, *Ulmus*, *Fraxinus*, and *Rhus*. Of these genera, only *Rhus* species were consistent and all received little oviposition. Species in the other genera varied widely in their susceptibility to cicada oviposition (Fig. 2). Differences in susceptibility to oviposition among congeners were also found when oviposition was examined directly rather than standardized by site, but the variation in oviposition rates and cicada densities among sites makes those patterns more difficult to interpret.

Oviposition preference and tree species frequency

Oviposition by periodical cicadas was not a function of the frequency of occurrence of the tree species. For each tree species that occurred at three or more sites, we regressed the frequency of a tree species at a site versus the mean oviposition on that species at that site. For Brood XXIII, there were 18 species and only one (*Crataegus* sp.) had a slope significantly different from zero ($P = 0.028$, $r^2 = 0.998$, $\beta = 42.3$, $n = 3$ sites), but the maximum oviposition rate measured on this species was

0.038%, much lower than on other species. Of 34 species for Brood X, only one (*Quercus rubra*) had a significant slope ($P = 0.025$, $r^2 = 0.228$, $\beta = 1.7$, $n = 22$ sites). The binomial probability of observing this many or fewer significant outcomes for this number of species is 77% for Brood XXIII and 49% for Brood X. The significant results for these species are more likely to be a result of random chance from multiple tests rather than a true biological effect. Thus, relative abundance of a tree species had no effect on oviposition rate.

Differences in emergence among tree species

Despite the differences in susceptibility to oviposition among tree species, there was no difference in the density of emergence holes counted beneath different tree species ($F_{18,483} = 0.72$, $P = 0.7879$). In addition, the ordering of species by the emergence index did not correlate with the ordering of species by the oviposition index. *Ulmus rubra*, *Acer negundo*, and *Cercis canadensis* had the highest emergence index, but only *A. negundo* had high oviposition rates. Similarly, *Q. rubra* and *A. saccharinum* had the lowest emergence index, but *Q. rubra* was moderately susceptible to oviposition. This suggests that susceptibility of a host species to oviposition by periodical cicadas does not translate to differential emergence at the end of the 13- or 17-year nymphal period.

Differences in cicada activity by habitat

Cicada activity varied greatly among sites, and was the greatest difference observed in this study. The average proportion of oviposition at a site varied from 0.03 to 55%, with a mean of 22%. Average oviposition rates across all sites were similar for both broods, but emergence rates were higher in Brood XXIII ($P < 0.0001$). Casual observation indicated that Brood X was nearly continuously distributed across suitable habitat within its range, whereas Brood XXIII was much more patchy, with some sites having very high densities and other apparently suitable sites not occupied by cicadas. As we did not sample sites without cicadas, our estimates of density are higher than the average density for Brood XXIII across the environment.

Mature forests had significantly lower oviposition rates and significantly higher emergence rates than successional forests (Fig. 4, Table 2). Tree plantations were similar to successional sites with low emergence and high oviposition. In mature forests, oviposition on fallen branches (many of which were from the upper canopy) was higher than on the lower branches sampled with pole pruners (fallen branches mean ± SE: 0.074 ± 0.004, pole pruners: 0.044 ± 0.006). This difference was not statistically significant, but comparisons are limited as a result of the smaller sample size of fallen branches, and the fact that fallen branches were from only a subset of species. The majority (86%) of fallen branches were from eight species: *A. saccharum*, *Q. alba*, *S. albidum*, *L. tulipifera*, *Q. rubra*, *A. rubrum*, *F. grandifolia*, and *A. saccharinum*. These species tend to be dominant in southern Indiana forests, but they are not necessarily less resistant to wind damage (Everham & Brokaw, 1996).
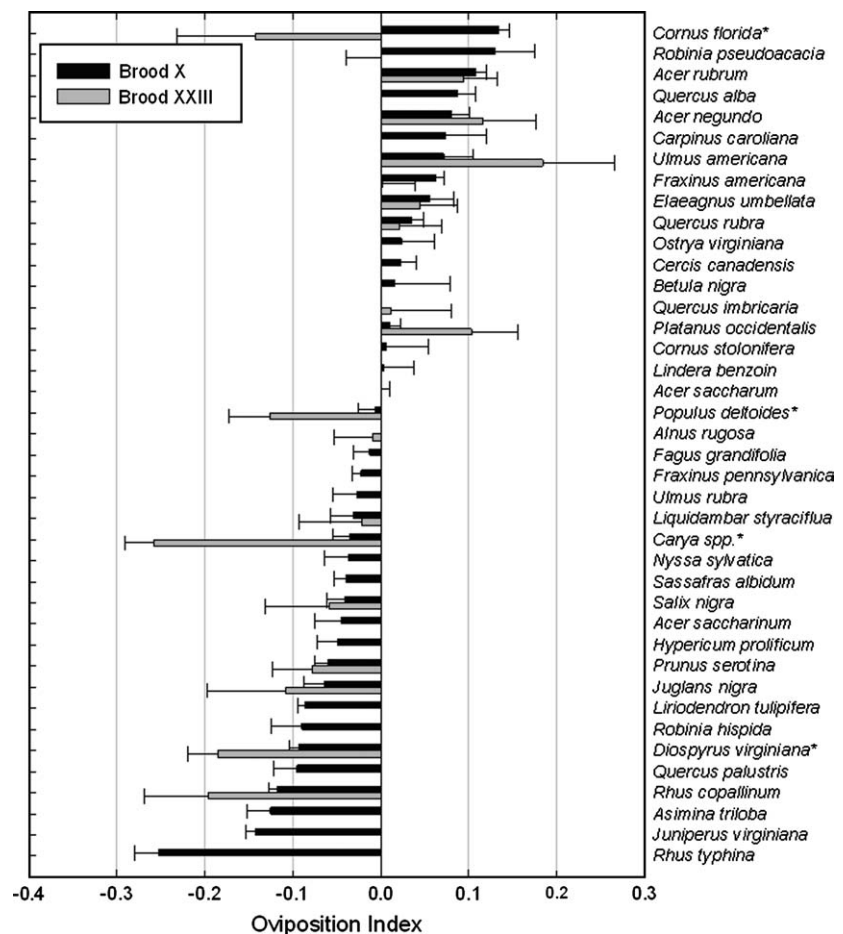
Fig. 2. Mean (± SE) oviposition index for each tree species separated by the two broods. Species are arranged from most to least susceptible by Brood X. For simplicity, species with fewer than 30 individuals across all sites and those that occurred at only a single site are not shown, although they were included in statistical analyses. Not all species were sampled for both broods. Species that differed significantly ($P < 0.05$) in susceptibility to oviposition by the two broods are marked with an asterisk. Scientific names of the tree species are listed in Table 1.

Discussion

Oviposition damage among tree species

Tree species varied markedly in the amount of oviposition damage they received by periodical cicadas. Several species differed in how preferred they were for oviposition in mature versus successional forests, and a few species also differed in oviposition preference between the two broods. Oviposition preference was not frequency dependent; more common tree species did not receive more oviposition than less common species.

We do not know the mechanisms by which certain tree species are preferred or avoided by periodical cicadas, but there are several possible hypotheses. Most species that received little oviposition damage by periodical cicadas have resins, saps, or physical defences that could interfere with egg-hatching success or directly harm adults. Coniferous species were generally avoided, which is consistent with previous studies that have implicated sap production (White *et al.*, 1982). *Rhus* species were also rarely attacked and members of the Anacardiaceae family typically produce sap with a vesicant or blistering effect (Simpson, 2006). *Juglans nigra* and *S. albidum* are known to produce defensive compounds that could affect cicada preference.

The branches of *R. hispida* have very dense spines that may make it difficult for cicadas to oviposit. Hypotheses for why certain species received heavy oviposition damage are less clear. Cicadas may select hosts based on structural characteristics of branches, such as bark thickness or wood toughness (W. B. Mattingly & S. L. Flory, unpubl. data; White, 1980). Several of the most susceptible species, notably *Carpinus caroliniana* and *Cornus florida*, have very hard, dense wood that may be particularly good for the protection of cicada eggs.

For several tree species, oviposition damage differed between mature and successional sites, or between Brood X and Brood XXIII. The most susceptible tree species in mature forests – *E. umbellata*, *D. virginiana*, and *R. copallinum* – were relatively resistant to oviposition when growing in successional sites. These species are more common in successional sites, and their increased preference in mature forests could be a result of microhabitat differences if they occurred more often in light gaps where periodical cicadas prefer to oviposit (Williams & Smith, 1991; Yang, 2006). In addition, *E. umbellata* and *R. copallinum* tend to be understory species in mature forests, so they may have a higher proportion of branches of suitable size within the range of our sampling efforts (≤6 m from forest floor). *Elaeagnus umbellata* was the only non-native species in our study. The lack of
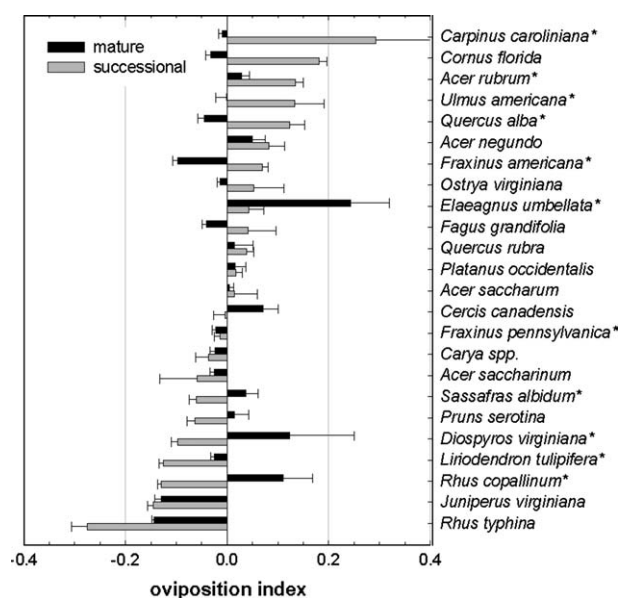
Fig. 3. Mean (± SE) oviposition index for tree species in mature and successional sites (Brood X only). Species for which oviposition index was significantly different between habitats ($P < 0.05$) are marked with an asterisk. Species with fewer than five individuals at both mature and successional sites are not shown, but were included in statistical analyses.

Fig. 4. Mean (± SE) emergence and oviposition among forest successional ages for both cicada broods combined. Emergence holes were measured as the number per 0.25 m². Oviposition was the proportion of sampled branch length that had oviposition scarring. Mature forests had significantly more emergence ($P < 0.0001$) and significantly less oviposition ($P < 0.0001$) than mature forest edges or successional forests.

coevolutionary history with periodical cicadas could affect its preference, but a larger sample size of non-native species would be necessary to test this. Fewer species were differentially preferred by the two broods and for all but one of these (*C. florida*), the direction of preference was the same for both broods.

Our data do not support the hypothesis that tree species that receive more oviposition damage are more suitable hosts for nymphs. There was no difference in emergence rates among tree species, and the most susceptible species for oviposition did not have higher numbers of emergence holes. This is surprising, because nymphs are likely to feed on the roots of the plant on which they were originally oviposited, as they drop directly to the ground after eggs hatch. White (1980) also found that hatching success of eggs on different host species was not well correlated with oviposition preference for those species. Density-dependent mortality may reduce the number of surviving nymphs to such a degree, that there is no correlation between the number of egg nests on a tree and the number of nymphs that survive to emerge from beneath that tree 13 or 17 years later (Karban, 1984). Alternatively, cicadas may select host trees for reasons unrelated to offspring success, such as a preference for their natal species (Hopkins Host Selection Principle; Barron, 2001) or to maximize their egg-laying success rather than offspring fitness (Scheirs *et al.*, 2004).

Cicada activity among sites

Emergence rates of periodical cicadas were highest in the interior of mature forests, but oviposition was highest in successional sites. This corresponds with previous results that have
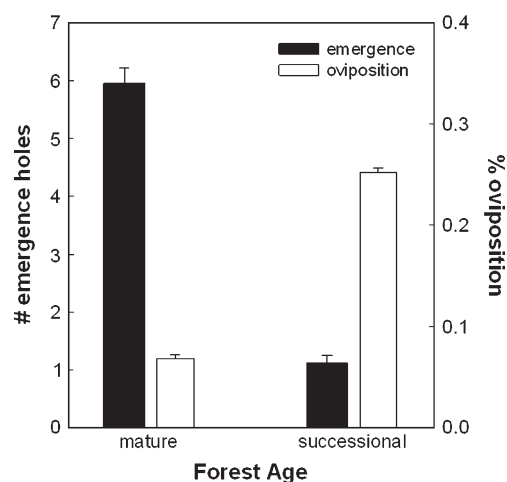
found female cicadas prefer to oviposit on young branches of trees in sunny areas (Marlatt, 1907; Lloyd & White, 1976; Yang, 2006). Successional sites were defined for this study as areas that were essentially devoid of trees during the last periodical cicada emergence, and therefore should be free of cicada nymphs. However, since cicadas prefer open, sunny sites, they may preferentially disperse to successional sites adjacent to mature forests where they emerged. Our results support the hypothesis that cicadas represent a shifting mosaic from older forests to younger successional habitats.

Oviposition rates on fallen branches, many of which were from the upper canopy, were higher than on lower branches. It is unlikely that branches with high oviposition were more likely to fall, because most of the branches we sampled were from large broken branches (>10 cm diameter) or treefalls. To our knowledge, there are no data on cicada oviposition activity in the upper canopy of mature forests, so the data reported here for oviposition damage on fallen branches are the first published estimates of oviposition rates by periodical cicadas in the upper canopy.

Comparison with previous studies on oviposition preference

The differences in susceptibility we found for tree species agree with those reported by Cook *et al.* (2001) for fewer tree species at a single experimental forest. They found high oviposition rates on *Cornus drummondii*, *Ulmus rubra*, and *Acer negundo* and low oviposition on *Rhus* spp. and *Juniperus virginiana*. However, their study site was composed primarily (93%) of *C. drummondii* and included only one of the three 17-year periodical cicada species (*M. cassini*). Our study included many more tree species and was conducted over a wide range of natural habitats, and identified a number of other preferred species including *A. rubrum*, *R. pseudoacacia*, and *Q. alba*.

In an early observational study on tree susceptibility to ovipostition by periodical cicadas, Skeels (1907) observed that *Asimina triloba*, *Lindera benzoin*, *Robinia pseudoacacia*, *Rhus* species, and conifers were very resistant to cicada oviposition while *Carya*, *Quercus*, *Ulmus*, *Acer*, *Cornus*, and *Fraxinus* species were very susceptible. These results correspond with ours, except that we found *R. pseduoacacia* to be highly susceptible and *Carya* spp. somewhat resistant.

Our results do not correspond quite as well with two papers published by Lloyd and colleagues (Dybas & Lloyd, 1974; White & Lloyd, 1979), which indicated an oviposition preference for *Carya, Quercus*, and *Ulmus* species, and to a somewhat lesser extent *P. deltoides* and *C. florida*. The 1974 paper is the most geographically widespread study of periodical cicada behaviour, covering seven different broods across the eastern United States. The present study has much greater site replication within a brood, and thus a greater ability to test for differences in preference. Dybas & Lloyd found that two of the three species in a brood, *M. cassini* and *M. septendecula*, had a very strong preference for *Carya* species. In our study, *Carya* was neutral to slightly avoided, but we did not quantify oviposition damage by specific cicada species.

Our sites encompassed all species of periodical cicadas in both Broods X and Brood XXIII (seven species total) and should accurately represent the preference of an entire brood on trees. Like previous reports (e.g. Dybas & Lloyd, 1962, 1974), we noted that *M. cassini* was most abundant in lowland habitats and *M. septendecim* in upland habitats. *Magicicada septendecula* appeared to be most abundant in suburban habitats, and many of these suburban areas, such as the Indiana University campus, had all three species occurring together. Given the large number of sites and trees sampled and the short time period of the emergence, we were not able to rigorously estimate densities of each species at each site. It would be useful in the future to determine if the impact on trees per unit length of oviposition scarring varies by cicada species, but we have no evidence that impact of oviposition does not correspond to amount of oviposition.

Conclusions

This study represents the most extensive survey of cicada oviposition and emergence yet undertaken. Variation among sites was the strongest effect on oviposition in our data, suggesting that comparison across multiple sites is essential to accurately gauge the impacts and preferences of cicadas across the landscape. We found that certain tree species are highly and consistently susceptible to oviposition by periodical cicadas, whereas other species are largely resistant to oviposition. However, these differences do not persist throughout the nymphal period as evidenced by the similarity of emergence rates beneath different tree species. We also found that successive generations of cicadas are dispersing from older to younger successional sites. While emergence occurs at high densities in mature forests, more oviposition occurs in nearby successional sites. There are conflicting results on whether cicadas affect tree fitness (Karban, 1980; Cook & Holt, 2002), but if cicadas do affect tree growth and fitness, the differential susceptibility of tree species could have significant impacts on the structure and dynamics of forest communities.

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