

Regional impacts of periodical cicadas on oak radial increment

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Abstract: We investigated the effects of periodical cicadas (*Magicicada* spp.) on growth of their hosts using records of radial tree-ring growth on oaks (*Quercus* spp., a common host genus) and pines (*Pinus* spp., a common nonhost genus) growing within the ranges of 13- and 17-year broods. Growth of oaks was significantly depressed during years of adult emergence by about 4%. Effects in years following emergences or in years prior to emergences were variable or absent. Spectral analyses revealed a significant tendency for periodicity in the growth of oaks, but not pines, matching that of the life cycle of the broods. These results provide some of the first evidence for landscape-level effects of a root-feeding insect and demonstrate that periodical cicadas have a small but detectable effect on growth of their hosts on a geographical scale, considerably larger than previously suspected.

Résumé : Nous avons étudié les effets des cigales dix-sept ans (*Magicicada* spp.) sur la croissance de leurs hôtes en utilisant des données dendrochronologiques pour les chênes (*Quercus* spp., un genre qui sert communément d'hôte) et pour les pins (*Pinus* spp., un genre qui n'est pas un hôte commun) dont la croissance correspond à l'écart de 13 à 17 ans entre les générations. La croissance des chênes a été significativement réduite d'environ 4 % pendant les années d'émergence des adultes. Les effets étaient variables ou absents pendant les années qui suivaient ou précédaient les périodes d'émergence. Des analyses spectrales ont révélé une tendance significative concernant la périodicité de la croissance dans le cas des chênes, mais non dans le cas des pins. Cette périodicité correspond à celle du cycle vital des nouvelles générations. Ces résultats constituent une des premières preuves des effets, à l'échelle du paysage, d'un insecte qui se nourrit à partir du système racinaire et démontrent que les cigales dix-sept ans ont un effet modeste, quoique détectable, sur la croissance de leurs hôtes à une échelle géographique considérablement plus vaste qu'anticipé précédemment.

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Introduction

The life cycle of periodical cicadas (*Magicicada* spp.) in eastern North America (Fig. 1) is one of the most spectacular entomological phenomena in the world. Each generation lasts either 13 or 17 years, and most of their development is spent in the nymphal stage underground, feeding on roots. Following the final nymphal molt, adults emerge from the soil and ascend to the canopy where they mate, oviposit in twigs, and die within the space of 3–4 weeks. A few weeks later, first instar nymphs hatch from the eggs, descend to the forest floor, and once more initiate root feeding.

Periodical cicadas are among the most abundant forest insects in eastern deciduous forests, with densities reaching $2.6 \times 10^6 \text{ ha}^{-1}$ (Lloyd and Dybas 1966a, 1966b; Karban 1980). Currently 15 different "broods" (developmentally synchronized cohorts temporally isolated from other such groups) are known, each composed of three or four sympatric species existing in both a 13- and 17-year form (Williams and Simon 1995; Marshall and Cooley 2000).

Over most of the range of periodical cicadas, brood distributions are allopatric, such that all individuals at a given location emerge synchronously during the same year.

Numerous short-term demographic effects of emergences have been documented on both the avian and mammalian predators on periodical cicadas and the broad-leafed trees that serve as their hosts. Evidence for the latter stems from work by Karban (1980, 1982, 1985) and Hogmire et al. (1990), who performed several studies investigating the relationship between periodical cicada densities and radial growth of trees. The first of these (Karbon 1980) compared growth of small scrub oaks (*Quercus ilicifolia*) as a function of the number of oviposition scars left by cicada females. Trees containing three or more such scars suffered significantly lower radial growth in the year of the emergence and in each of the subsequent 4 years, whereas trees with fewer scars and trees prior to the year of emergence regardless of the number of scars exhibited no decrease in growth relative to trees lacking scars. This effect most likely stems from lower photosynthate availability resulting from a combination of twig mortality caused by high densities of oviposition wounds and the response of trees to wounds, which is to produce a gum that interferes with egg survival. Subsequent work found a significant reduction in radial growth of apple trees (*Malus pumila*) the year following an emergence, but not during the emergence year itself (Karbon 1982). No perceptible effect of the introduction of cicada nymphs was observed on either acorn production or rootlet densities in scrub oaks (Karbon 1985).

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These results suggest that cicadas may have a substantial effect on host trees, decreasing growth by as much as 30% in the year of emergences, as well as the years following emergences (Karban 1980). Such an effect might be expected to result in regional “pulses” in total biomass accumulation, since broad-leafed trees make up the majority of total plant biomass in much of the range of periodical cicadas in eastern North America (Iverson and Prasad 1998).

Here, we investigate the effects of periodical cicada emergence on trees over a much larger geographic scale using maps of the distributions of the various periodical cicada broods combined with data on radial growth of trees from the International Tree-Ring Data Bank (ITRDB), a repository of over 1000 site-standardized chronologies from around the world. While effects of cicadas have been studied on individual trees, nothing is known about the impact of cicadas on tree growth on a regional scale. Our goal is to evaluate the large-scale effects of periodical cicadas on radial growth of their hosts and to investigate the possibility, suggested by Karban (1980), that cicadas may induce a periodical pattern of tree growth in their hosts or otherwise have a long-term effect on radial growth.

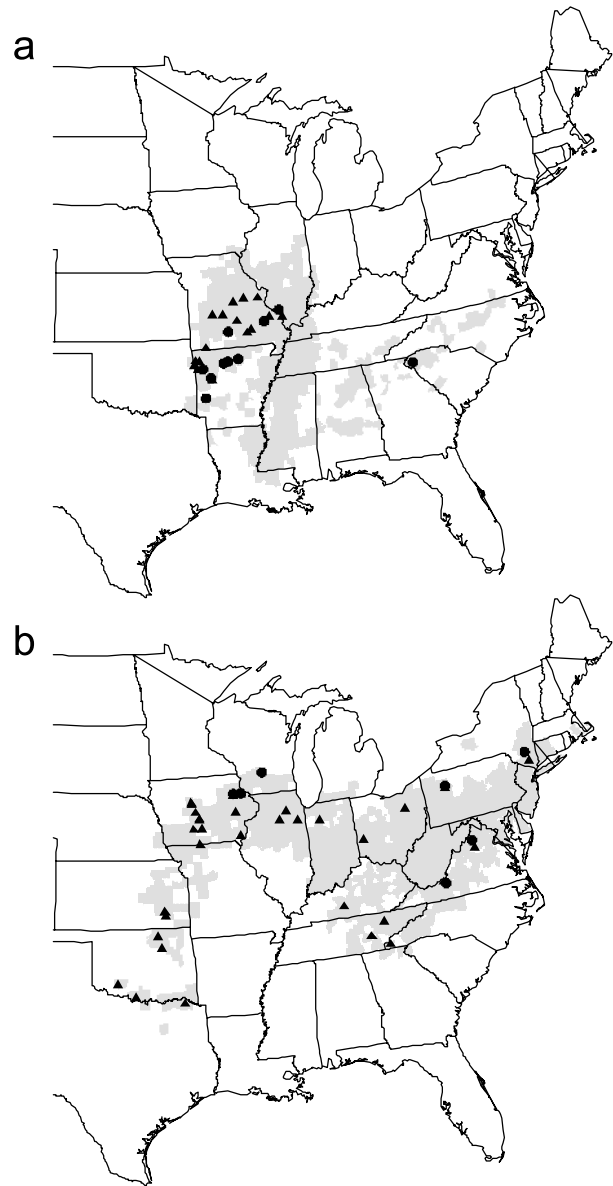
Materials and methods

Normalized average percent mean growth from cross-dated (Fritts 1976) stands of trees was obtained from the ITRDB (<http://www.ngdc.noaa.gov/paleo/treering.html>). Sites were matched to the coincident cicada brood using historical county-level records of brood emergence (Marlatt 1907; Simon 1988) and a geographical information system (Fig. 1). Then, based on known emergence patterns for each brood, the number of years since an emergence (where the year of an emergence = 0) was determined for each site \times year combination. Data from counties with records of two or more broods or with historically low-density emergences were discarded. Brood distributions are largely allopatric, so these situations were rare.

Periodical cicada nymphs feed on a range of broad-leafed, deciduous trees (Butler 1886; Dybas and Lloyd 1974; White 1980). We concentrated on oaks (*Quercus* spp.) as hosts, which were, by far, the most common genus of periodical cicada hosts represented in the tree-ring data. For comparison, we used pines (*Pinus* spp.), which were the most common coniferous (nonhost) genus in the data bank. Although periodical cicadas use pines to a limited extent, they rarely oviposit or feed on the roots of conifers (White et al. 1982) and thus offer an excellent control. Chronologies used in the analyses went back as far as 1552 AD and were, on average, 271 years in length.

Radial growth was analyzed as follows. To ensure the absence of long-term environmental trends, we detrended (using a linear model) and standardized (mean = 0, SD = 1) the normalized yearly mean growth for each stand as given in the ITRDB. Each chronology typically spanned several centuries and thus coincided with multiple periodical cicada generations. Therefore, for each chronology, normalized increment values were averaged across all generations by the number of years since adult emergence in the brood present in the site. Implicit in this procedure is the assumption that brood boundaries have not shifted over the last several hun-

Fig. 1. Eastern U.S.A. showing the geographic range of (a) 13-year and (b) 17-year periodical cicada (*Magicicada* spp.) broods. Plotted are localities where chronologies of oaks (*Quercus* spp.) (triangles) and pines (*Pinus* spp.) (circles) were available for analysis.



dred years, an assumption generally supported by the observation that current brood distributions are largely coincident with those described nearly 100 years ago (Marlatt 1907; Simon 1988). Indices of standardized growth were divided according to brood type (13-year vs. 17-year) and genus (*Quercus* vs. *Pinus*) and analyzed using stand averages as independent samples.

Separate analyses were conducted for the two genera and both brood types. These analyses were performed both on the individual years since emergence and by combining years into four categories: (1) the year of emergence, (2) 1–4 years postemergence, (3) 1–3 years preemergence, and (4) all remaining years (years 5–9 postemergence for those within the range of 13-year broods; years 5–13 post-

emergence for those within the range of 17-year broods). This latter procedure divided years so as to allow clearer determination of effects during the years immediately following emergences (specifically, the 4 years Karban (1980) found to exhibit reduced growth), the years immediately preceding emergences (not found to exhibit reduced growth by Karban (1980)), and the remaining intermediate years.

Because mean growth for different numbers of years since emergence is measured on the same trees, a repeated-measures ANOVA is appropriate. Unfortunately, too few stands of pines were available for this analysis using individual years since emergence. Consequently, we performed repeated-measures ANOVA for the analyses combining years since emergence into four categories and standard ANOVA for the analyses using individual years since emergence. Statistical significance of the two procedures (standard ANOVA and repeated-measures ANOVA) on the combined data were identical, and thus, our conclusions are most likely robust to this statistical difficulty.

To indicate the significance of individual values, we performed binomial tests with the null hypothesis that mean standardized growth would be greater than (or less than) the overall mean in 50% of the chronologies. Results significant at the $P < 0.05$ level are reported. To test for differences between oaks and pines, we performed Mann–Whitney U tests on each of the individual years to determine pairs of values significantly different at the $P < 0.05$ level. Because multiple tests were performed, some of these tests would be expected to yield significant results by chance alone. Thus, we consider the consistency of results between 13- and 17-year species as important as the individual statistical tests.

Periodicity in growth of the trees induced by cicadas was tested by calculating the spectral density functions for periods of 2–25 years for each chronology. The periods corresponding to the maximum spectral density were compared between chronologies within the range of 13- and 17-year broods using a Wilcoxon two-sample test (Sokal and Rohlf 1981); separate comparisons were performed for oak and pine chronologies. Spectral density functions were computed using the SAS software (SAS Institute Inc. 1997).

Results

Mean standardized tree-ring growth differed significantly among years since emergence for oaks growing within the range of both types of broods (Table 1). For pines, growth varied significantly for trees growing within the range of 13-year broods but not for 17-year broods. During the year of emergences, oaks growing within the range of both types of broods grew (1) less than during any subsequent year, (2) significantly less ($P < 0.05$) than average, and (3) significantly less ($P < 0.05$) than pines in emergence years (Fig. 2). Subsequent growth did not vary consistently between trees growing within the range of 13- and 17-year broods.

Results were generally similar when years since emergence was combined into four categories. When stands growing in 13-year broods were compared with those in 17-year broods, ANOVA again showed significance for all but pines growing within the ranges of 17-year broods (Table 1). However, because years since emergence was divided into

Table 1. Effects of years since emergence of standardized tree-ring growth.

Cicada brood	No. of sites	Years since emergence separate ^a		Years since emergence combined into four categories ^b	
		<i>F</i>	df	Wilks' λ	df
Oak (<i>Quercus</i> spp.)					
13-year	24	8.5	12,299***	5.9	3,21**
17-year	36	3.9	16,595***	9.2	3,33***
Both	60	—	—	13.9	3,57***
Pine (<i>Pinus</i> spp.)					
13-year	10	3.5	12,117***	5.3	3,7*
17-year	7	1.6	16,102	0.6	3,4
Both	17	—	—	2.4	3,14

Note: Growth is the mean for all years in a given amount of time since an emergence. Categories for combining years since emergence are (1) emergence years, (2) 1–4 years postemergence, (3) 1–3 years preemergence, and (4) all intervening years. For both genera, analyses were done for sites within the range of 13- and 17-year broods. For the combined data, analyses were also done combining trees within the range of both types of broods. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Values not followed by an asterisk had $P > 0.05$.

^aANOVA.

^bRepeated-measures ANOVA.

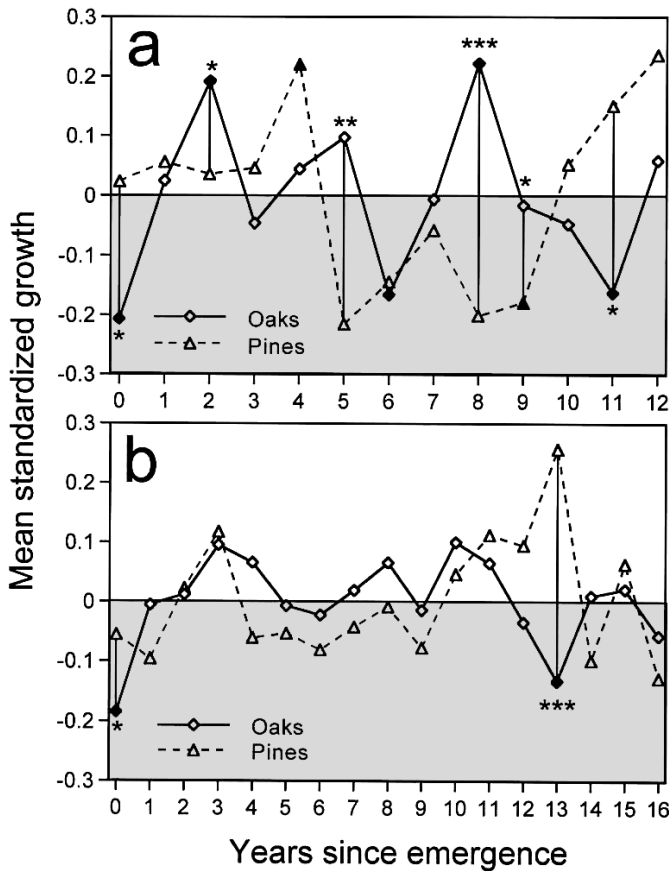
equivalent categories for stands growing within the ranges of the two types of broods, it was also possible to perform a single analysis for each genus of tree by combining all sites. In these combined analyses, growth of oaks, but not pines, varied significantly according to years since emergence (Table 1). Growth of oaks was not significantly different from average in the 4 years following emergences for trees in either category (Fig. 3). Subsequent growth was not significantly different from average for oaks within the range of 17-year broods (Fig. 3b), while oaks within the range of 13-year broods grew significantly less than pines during the 3 years prior to emergences and significantly more than pines during the intermediate years (Fig. 3a).

Spectral analysis of oak chronologies indicated the presence of periodicities of approximately 13 or 17 years, depending on whether trees were growing within the range of 13- or 17-year cicada broods (Table 2). Periods corresponding to the maximum spectral density of chronologies from within the range of 13-year broods were significantly different from those within the range of 17-year broods ($z = -2.20$; $P = 0.03$). In contrast, periods corresponding to the maximum spectral density of pines did not differ among chronologies located within the ranges of 13- and 17-year broods ($z = -0.05$; $P = 0.96$).

Discussion

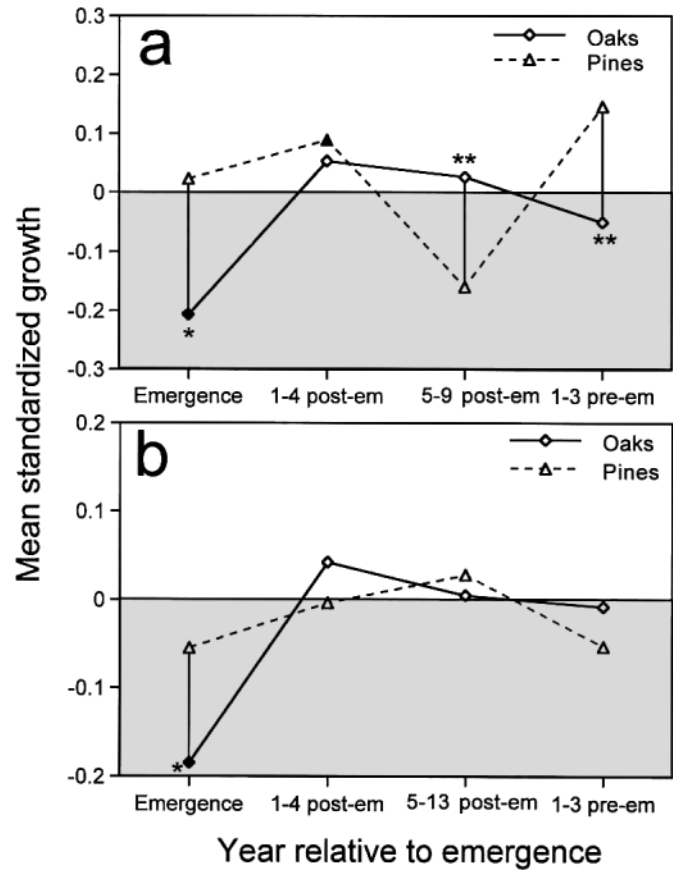
Our results confirm that periodical cicadas decrease radial growth of their host trees during years of emergence compared both with overall mean growth and with growth of nonhost trees. This extends Karban's (1980) finding of an adverse effect of cicadas on radial growth of trees during years of emergence to the landscape encompassed by the entire geographic range of periodical cicadas.

Fig. 2. Mean standardized radial growth of host (oak: *Quercus* spp.) and nonhost (pine: *Pinus* spp.) stands growing within the range of (a) 13-year and (b) 17-year cicada (*Magicicada* spp.) broods for each year starting with adult emergences (year = 0). Values are deviations from the overall mean measured in standard deviations. Solid symbols are significantly different from the mean ($P < 0.05$) based on binomial tests. Pairs of symbols connected by thin vertical lines are significantly different between oaks and pines based on Mann–Whitney U tests, with asterisks reflecting the significance of the difference (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).



The magnitude of the effect was neither as dramatic nor long-lasting as the 30% reduction in growth among scrub oaks containing three or more oviposition sites starting in the year of an emergence and continuing for each of the 4 subsequent years found by Karban (1980). However, in contrast with prior studies, trees in our sample were mature trees, which in general are less susceptible to the effects of cicadas than saplings (Karbon 1982), and were chosen independently of the presence of cicadas. Thus, given that densities of periodical cicadas vary considerably within and between the ranges of different broods (Lukens and Kalisz 1989; Dybas and Davis 1962; Dybas and Lloyd 1974), our results are not directly comparable with those of prior studies. Rather than documenting the maximum effect of cicadas on growth of individual host trees, our results demonstrate that the overall effect of periodical cicadas on radial growth of their hosts is relatively modest but detectable throughout the range of the cicadas. Such landscape-level effects have

Fig. 3. Mean standardized radial growth of host (oak: *Quercus* spp.) and nonhost (pine: *Pinus* spp.) stands growing within the range of (a) 13-year and (b) 17-year cicada (*Magicicada* spp.) broods divided into four categories ((1) year of emergence, (2) 1–4 years postemergence, (3) intervening years (5–9 years postemergence in (a) and 5–13 years postemergence in (b)), and (4) 1–3 years preemergence). Values are deviations from the overall mean measured in standard deviations. Solid symbols are significantly different than the mean ($P < 0.05$) based on binomial tests. Pairs of symbols connected by thin vertical lines are significantly different between oaks and pines based on Mann–Whitney U tests, with the number of asterisks reflecting the significance of the difference (*, $P < 0.05$; **, $P < 0.01$).



not previously been reported at this geographic scale for any insect.

In our analyses, growth of oaks within the range of periodical cicadas grew on average about 0.2 standard deviations less than the overall mean during the year of emergences (Fig. 2) and exhibited slightly, but nonsignificantly, greater growth than average during the 4 years following emergences (Fig. 3). Although it is difficult to directly translate these values into the percent decrease in growth due to cicada emergences, an approximation of this figure can be made using normalized growth values taken directly from the ITRDB. By treating these values similarly to the standardized values, mean growth of oaks was 4.1% below average during the year of emergences and 0.8% above average during the 4 years following emergences for trees growing within the ranges of cicada broods.

Table 2. Mean maximum spectral density values of standardized chronologies for oaks and pines located within the range of 13- and 17-year cicada broods.

Cicada broods	No. of sites	Mean \pm SE maximum spectral density (years)
Oak (<i>Quercus</i> spp.)		
13-year	24	13.8 \pm 1.0
17-year	36	16.5 \pm 0.9
Pine (<i>Pinus</i> spp.)		
13-year	10	16.3 \pm 1.1
17-year	7	15.4 \pm 1.8

To estimate the relative energetic importance of this value, we used data from Brookhaven, New York (within the range of Broods XIII and XIV), studied by Whittaker and Woodwell (1969). Overall average stem production by oaks in the forest was estimated as 128 g·m⁻²·year⁻¹. Assuming that stem production is reduced by 4.1% in an emergence year, this represents a biomass loss of 5.3 g·m⁻²·year⁻¹ and a reduction of 0.6% to the total estimated aboveground net annual productivity. This latter value is comparable with the relative importance of periodical cicadas at fairly low densities in Arkansas (Brood XIX), as indexed by the ratio of sodium, potassium, phosphorus, and nitrogen in the adult cicada population to those in the annual litterfall (Wheeler et al. 1992).

Evidence for an effect of periodical cicadas on oaks beyond the year of emergences was equivocal. Considering oaks growing within the range of 13-year broods, growth was significantly greater than average in years 2 and 8 postemergence and significantly less than average in years 6 and 11 postemergence (Fig. 2a). For oaks within the range of 17-year broods, growth after emergence years was significantly less than average only in year 13 postemergence (Fig. 2b). Combining years into categories eliminated most of this variability and resulted in a lack of significantly different (from average) mean growth for oaks growing in both the ranges of 13- and 17-year broods during all three postemergence year categories (Fig. 3). This suggests that despite the various significant results reported in Figs. 1 and 2, growth of oaks is unrelated to periodical cicadas, except for a reduction during emergence years.

The observation that the impact of cicadas on tree growth is limited to years of adult emergence indicates that nymphs feeding underground have negligible effects on their hosts. This is plausible, since tree root xylem fluids are primarily composed of water (Cheung and Marshall 1973). Consequently, the feeding of nymphs on root fluids by nymphs may have little impact on availability of the photosynthate that affects tree growth. While nymphal feeding might reduce water uptake in trees, the effect is unlikely to be significant. Root feeding by young nymphs may cause some mortality of rootlets (White and Strehl 1978), and if extensive, this could have substantial effects on trees. However, extensive rootlet mortality caused by periodical cicadas has yet to be documented and, therefore, it remains uncertain whether nymphal feeding affects trees in this manner.

In contrast with nymphs, adult periodical cicadas are known to adversely affect trees via oviposition wounds. Females oviposit by cutting longitudinal slits in twigs and in-

serting eggs directly into these wounds. Trees typically respond to this wounding by producing gum that may adversely affect egg survival (Karban 1983). When multiple oviposition wounds are made on the same twig, the entire twig may die and heavily infested trees may exhibit extensive "flagging" caused by numerous dead twigs (White 1981; Hogmire et al. 1990). Subsequent gum production and twig mortality are likely to have negative effects on photosynthate availability. These effects could explain the reduction in tree growth on years of adult emergence observed here and in prior studies (Karban 1980, 1982, 1985; Hogmire et al. 1990).

One unexplained aspect of this effect is that twig mortality usually occurs in midsummer, by which time most radial increment and "earlywood" production in trees is complete. This suggests that oviposition wounding affects "latewood" production but would be unlikely to affect earlywood production in the current year. Few studies of hardwoods have attempted to differentiate effects of insect damage on these two phases of tree growth (Muzika et al. 2000), and more detailed growth measurements would be useful to clarify these effects.

For pines, the relationship between radial growth and emergences was variable between trees growing within the range of 13- and 17-year broods (Figs. 2 and 3). This, along with the nonsignificant overall effect of year since emergence on growth of pines within the range of 17-year broods (Table 1) and the nonsignificant overall effect of year since emergence on growth of pines when years were combined into categories (Table 1), suggest that there is no consistent relationship between emergences and radial growth of pines. This is expected given that pines are rarely used as hosts by either adult or larval cicadas.

Although we detected no significant effects of cicada emergences on growth following emergences, spectral analyses revealed a previously undetected periodicity in radial growth by host trees of lengths matching the life cycle of the cicadas. No such match was detected in chronologies of pines. Thus, as suggested by Karban (1980), cicadas appear to induce a detectable periodicity in growth of their hosts matching their extraordinary life cycles.

In summary, periodical cicadas have a small but detectable effect on the pattern of radial growth of trees on which they lay eggs on a regional scale. Overall, the effect is relatively small, on the order of 4%, and only detectable during emergence years. Thus, periodical cicada are apparently not the serious pests suggested by earlier studies. They are, however, sufficiently important to induce detectable patterns in tree-ring growth, and potentially other components of the community, on a much larger scale than previously suspected.

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