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The Effect of Periodical Cicadas on Growth of Five Tree Species in Midwestern Deciduous Forests

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Abstract.—Periodical cicada emergences in the eastern United States are one of the largest biomass fluctuations in the world, providing a unique opportunity to study if a root parasite can affect broad-scale patterns of forest growth and succession. We used dendrochronology to examine the direct effect of Brood X (17 y cicada) and Brood XXIII (13 y cicada) periodical cicadas on 89 individual trees from five species (*Acer saccharum, Fraxinus americana, Quercus palustris, Q. velutina and Sassafras albidum*) in Indiana. Standard dendrochronological techniques were used to date the tree-ring samples and our chronologies ranged from 63–98 y in age, spanning from four to eight cicada emergences. We removed the main climate variable from each species chronology by conducting a regression analysis and using the residuals for the remainder of the analysis. Significant climate models were developed for all five species. *Acer saccharum* growth correlated highest with Jun. temperature ($r = -0.392$), *Fraxinus americana* growth correlated with summer Palmer Drought Severity Index (PDSI) ($r = 0.338$), *Quercus palustris* growth correlated with summer precipitation ($r = 0.366$), *Q. velutina* growth correlated with Jul. PDSI ($r = 0.527$) and *Sassafras albidum* growth correlated the highest with Jun. precipitation ($r = 0.406$). A superposed epoch analysis was used to examine the effect of periodical cicadas on each tree species before, during and after multiple emergences on the stand level. No effect from root parasitism prior to emergence was evident in any of the species, but three of the species chronologies showed a significant reduction in growth the year of or the year after the emergence year. Three chronologies showed an increase in growth 5 y following the cicada emergence event.

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INTRODUCTION

Insects are influential in determining the overall physiological health, form and performance of woody plants (Ayres and Lombardero, 2000; Coupe and Cahill, 2003). Insect damage may affect the successional rate and competitive abilities of particular tree species in a forested stand through host preference (Mattson and Addy, 1975; Morrow and LaMarche, 1978; Schowalter, 1996; Parish *et al.*, 1999; Carson and Root, 2000; Carson *et al.*, 2004). Periodical cicadas (*Magicicada* spp.) are root parasites that feed on the xylem fluids of various hardwood trees for 13 or 17 y (depending upon the cicada species) and then emerge from the soil to use the tree canopies for mating,oviposition, and also additional feeding (Marlatt, 1907; White and Strehl, 1978; Williams and Simon, 1995). Eastern United States woodlands have become fragmented due to agriculture, logging and urbanization. The high abundance of forest edges, which are highly preferred by periodical cicadas (Karban, 1981; Clay *et al.*, 2009a), can produce a high concentration of periodical cicadas within relatively small areas of forested land and increase parasite pressure on fragmented and urban forest communities (Medley *et al.*, 2003).

Most literature has focused on the behavior, morphology and reproductive success of periodical cicadas (Karban, 1984, 1997; Young and Kritsky, 1987; Williams and Simon, 1995). Fewer studies have examined the effects that these insects have on the growth of individual trees and forest communities (Karban, 1980; Cook *et al.*, 2001; Cook and Holt, 2002; Koenig and Liebhold, 2003). In particular, we are aware of only one study (Cook and Holt, 2002) that examined the role of periodical cicadas in the succession of forest stands and they found no strong signal of such an effect. Similarly, Clay *et al.* (2009a) found no effect of cicada exclusion on growth of early successional stands. Our approach uses tree-ring width to examine the effect of periodical cicadas on long term patterns of tree growth during (1) the insects' extended nymphal stage prior to emergence when they act as a root parasite, (2) the emergence year when adult cicadas mate, lay eggs in tree branches, die and decompose, and recolonize roots as newly hatched nymphs and (3) following the emergence year when dense populations of early instar nymphs feed from tree roots.

Periodical cicada lifecycle.—Periodical cicadas are only found in the eastern United States in geographically distinct broods (Johnson and Lyon, 1991). They inhabit several different deciduous forest types (Dybas and Lloyd, 1962). In contrast, annual cicadas occur worldwide but generally do not emerge in synchronous broods (Buckley *et al.*, 2001). Historical emergences of periodical cicadas have been traced through the use of written records and various ecological studies. For example, Europeans colonists noted a periodical cicada emergence near the Plymouth Colony in Massachusetts around A.D. 1633 (Young and Kritsky, 1987).

Periodical cicadas are root parasites that spend long periods of time (13 or 17 y) below ground where nymphs feed on xylem fluids (99.9% water and 0.1% minerals, amino acids and nutrients) of various hardwood trees (White and Strehl, 1978). After nymphs emerge in late spring when soil temperatures warm sufficiently and molt to adults, they disperse along woodland edges and sunlit canopies of mature deciduous trees in order to mate and reproduce (Forsythe, 1977; Johnson and Lyon, 1991). After copulation, female cicadas oviposit eggs (up to 20 eggs per puncture) into small diameter tree branches (Reed *et al.*, 1963). The adults die 5 to 6 wk after emergence before the next generation of juveniles hatch, beginning the 13 or 17 y life-cycle anew (White and Strehl, 1978; Johnson and Lyon, 1991; Williams and Simon, 1995).

Periodical cicadas have been grouped into individual broods, 15 of which are active today, with some emerging every 17 y (Broods I–XVII) and some every 13 y (Broods XVIII–XXX) (Williams and Simon, 1995). Marlatt (1907) reported six morphologically and behaviorally distinct species of periodical cicadas throughout the United States (17 y cicadas: *Magicicada septendecim, M. cassini, M. septendecula* and 13 y cicadas: *M. tredecim, M. tredecassini, M. tredecula*). Recently a 4th species (*M. neotredecim*) of 13 y cicada has been identified based on reproductive character displacement of acoustic mating signal (Marshall and Cooley, 2000) and confirmed with genetic analysis (Cooley *et al.*, 2001). A given brood consists of multiple *Magicicada* species that all emerge synchronously.

Hypotheses.—We test three alternative hypotheses about periodical cicadas' influence on ring growth in trees:

(1) *Nymphal feeding hypothesis.*—Because the primary niche of periodical cicadas is as a root parasite, trees may be most affected during the extended nymphal stage when water and mineral resources are drained from the tree, resulting in reduced ring growth especially in the years prior to emergence when cicada nymphs reach their largest size (Fig. 1A). Concomitantly, growth in ring widths should be released the year of emergence because of the cessation of root parasitism. During the emergence year, most of the growing season occurs post-emergence. However, Karban (1980) found that below-ground feeding of cicada nymphs on scrub oak (*Quercus ilicifolia*) trees reduced incremental growth by as much as 30% in the year of emergence.

Oviposition damage hypothesis.—Oviposition scarring (where female cicadas cut egg nests into small branches) may cause enough damage to small branches to result in decreased growth during the year of emergence or the following year or two (Fig. 1B). For example, Koenig and Liebhold (2003) documented a 4% reduction in tree growth in oak (*Quercus* spp.) trees growing in the range of periodical cicadas during the year of emergence and suggested that cicada emergences produce a landscape-level effect. However, White (1981) found that egg survival was increased when the branches were not damaged to the point of flagging suggesting that branch mortality is accidental and not preferred.

(2) *Oviposition damage hypothesis.*—If both release from the cessation of nymphal feeding and suppression from oviposition damage later in the season occur in the same individual, these two factors may balance out such that no response or only the dominant response will be evident in tree growth. Further, the cessation of nymphal feeding during the emergence year is followed later by resumption of feeding by the next cicada generation following egg hatch. Newly hatched nymphs are very small and have very high mortality (*see* Karban, 1984, 1997); but the densities of early instars are many orders of magnitude higher than later instars and, therefore, may have a significant impact on host tree growth.

(3) *Nutrient pulse hypothesis.*—The biomass transport and nutrient cycling associated with up to 3,000,000 insects per hectare emerging and then dying may cause a growth pulse in trees after the emergence event (Fig. 1C). Yang (2004) created a nutrient pulse in American bellflower (*Campanulastrum americanum*) by artificially enriching soil with 140 cicadas/m^2, resulting in larger seed size and leaves with significantly higher nitrogen concentration compared to unenriched controls.

Objectives.—Various studies provide some support for all three of these hypotheses, but no study has systematically studied the direct effect of cicadas on tree growth increments on multiple host tree species in a region. The goal of our research was to examine the direct effect of periodical cicadas on their host trees. More specifically, we tested if (1) there is any detectable effect on tree growth correlated with the life cycle of periodical cicadas, and if (2) there are differential responses among host tree species that might correspond with cicada preference. Most dendroentomological research has focused on the loss of photosynthetic tissue (*i.e.*, buds and leaves) and tree growth caused by defoliating insects such as western

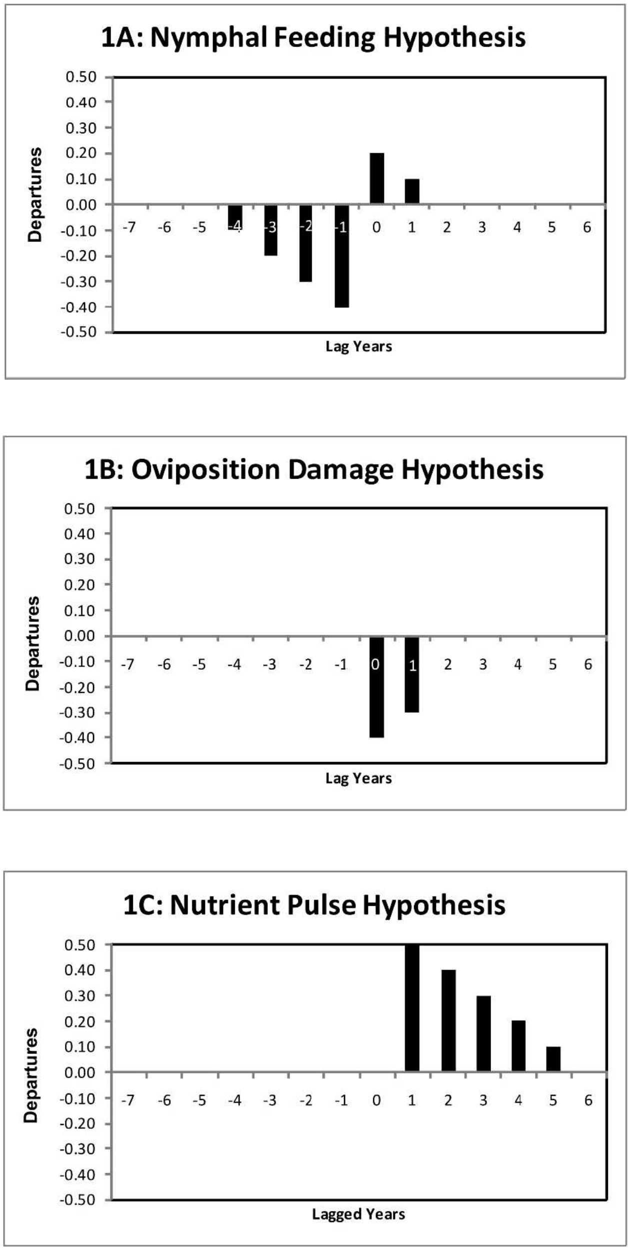

FIG. 1.—Three hypothetical responses of the trees to cicada damage. The y-axis represents an increase in tree-ring width above the origin and a decrease in tree-ring width below the origin. The relative heights of the bars also indicate where we expect to see the greatest response to cicada effects. 1A, the Nymphal Feeding Hypothesis, shows decreasing growth as the cicada nymphs mature in the soil with a release in the trees after emergence. 1B, the Oviposition Damage Hypothesis, shows decreased growth in year zero or year one related to oviposition scarring by the female cicadas. 1C, Nutrient Pulse Hypothesis, shows an increase in growth some time after the emergence do to the nutrient cycling of the cicada carcasses

spruce budworm (*Choristoneura occidentalis*) (Swetnam *et al.*, 1985; Swetnam and Lynch, 1993; Ryerson *et al.*, 2003), tussock moth (*Orgyia* sp.) (Mason *et al.*, 1997) and pandora moth (*Coloradia pandora*) (Speer *et al.*, 2001; Pohl *et al.*, 2006). Other studies (Parish *et al.*, 1999; Hedgren *et al.*, 2003; Muzika and Guyette, 2004) have emphasized the effects of bark beetles (*i.e.*, *Dryocoetes confusus*, *Enaphalodes rufulus* and *Ips typographus*) that girdle the trees by eating the cambium, resulting in the ultimate death of the trees. However, only a few limited studies (Karban, 1980; Cook and Holt, 2002; Koenig and Liebhold, 2003; Yang and Karban, 2009) have focused on root parasites generally or periodical cicadas specifically and their effects on hardwood tree growth, and none have examined the effect of these insects on multiple tree species at the individual tree to forest stand levels. We used dendroentomological approaches to quantify the effect of periodical cicadas on a suite of eastern deciduous forest tree species and to determine if these insects may differentially affect tree species during the course of succession.

METHODS

Field collection of samples.—Five tree species at four separate sites were sampled for this research. All sites were chosen because they exhibited high levels of cicada emergence according to local observers. Twenty black oak (*Quercus velutina*) trees and 18 sassafras (*Sassafras albidum*) trees were sampled at Greene-Sullivan State Forest (the only site in this study affected by Brood XXIII 13 y cicadas) in southwestern Indiana; 18 white ash (*Fraxinus americana*) trees were sampled at the Marry Lea Environmental Center near Fort Wayne in northeastern Indiana; 23 sugar maple (*Acer saccharum*) trees were sampled at Griffy Woods near Bloomington in southcentral Indiana; and 10 pin oak (*Q. palustris*) trees were sampled in suburban yards in Bloomington, Indiana (Fig. 2). Greene-Sullivan State Forest is a forest interior site in the early stages of succession because it was established after coal mining and agriculture use in the early 1900s. It has relatively steep topography which is a remnant from coal strip mines and tailings piles. The area sampled in the Marry Lea Environmental Center has little topography and the ash trees were located at the edge of the stand bordering an agricultural field. Griffy Woods is part of the Indiana University Research and Teaching Preserve located just outside of Bloomington. Samples were taken along the Weir Trail in a mature deciduous forest on a gently northwest facing slope. Finally, remaining trees were sampled in suburban areas around Bloomington. Cicada loads were particularly heavy on these trees as they were some of the few mature trees in this suburban landscape. These suburban sites had little competition for light and received occasional watering. Given that one species was sampled at a single site, we recognize that differences among species may reflect site differences and possibly levels of cicada infestation (although sites were chosen based on expert opinion that infestations were very heavy). However, our primary comparisons are between years for a single species at a single site.

A total of 180 cores were examined in this study (two cores per tree). Tree cores were taken on opposite sides of each tree, parallel to the landscape contour using a Haglof 5.15mm increment borer at breast height (~1.4 m above the ground). The samples were packaged in paper straws to prevent warping while the sample dries and to prevent the loss of core pieces in the field. The straws were marked with a three-letter site designation, sample number, species abbreviation and date in order to track the cores throughout the laboratory analysis.

Laboratory analysis of samples.—The tree cores were air dried in a fume hood for 2 wk and then cores were mounted on pre-fabricated wooden core mounts with Elmer's^{TM} white glue with the cross-sectional view facing up. All information from the straw (*i.e.*, three-letter site name, sample number, species abbreviation and date) was transferred to the core mount.

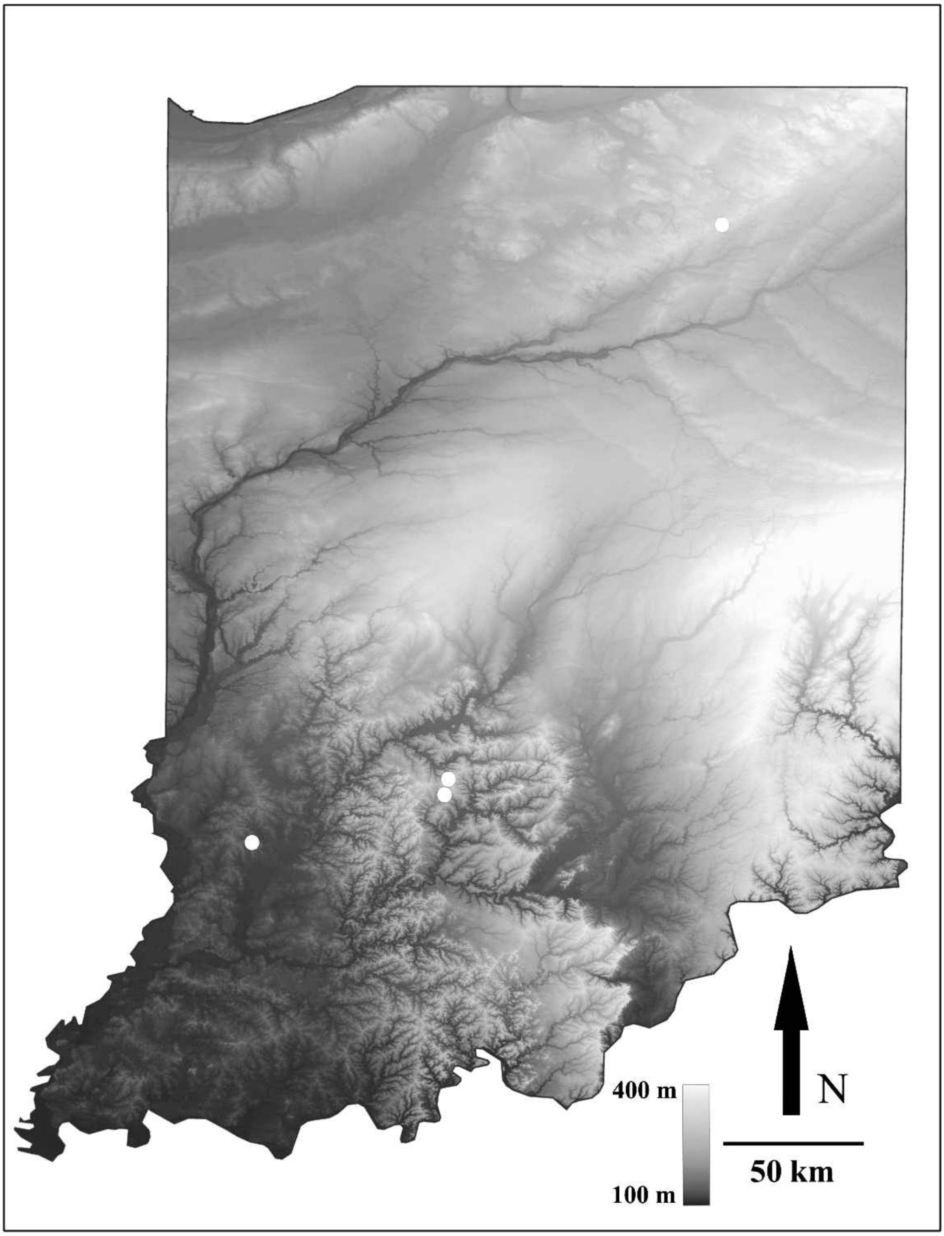

FIG. 2.—Location of the field sampling sites. The white dots show the location of the four sites that we sampled. The shaded relief represents topography that ranges from a low of 99 m elevation in the southwestern corner of the state to 383 m elevation in the central eastern portion of the state. Two tree species were sampled at Greene-Sullivan State Forest in the southwestern portion of the map. City trees were sampled in Bloomington, Indiana in the south-central portion of Indiana and one site was located in Griffy Woods which is located just north of Bloomington and is a an Indiana University Nature Preserve. The final site was located at Merry Lea Environmental Center in the northeastern portion of Indiana near the town of Fort Wayne

The specimens were then belt sanded with ANSI^{TM} (American National Standards Institute) 80 (177–210 μm), 120 (105–125 μm), 220 (53–74 μm), 320 (32.5–36.0 μm) and 400 (20.6–23.6 μm) grit sandpaper in order to expose existing tree rings to the naked eye (Orvis and Grissino-Mayer, 2002). Core samples were further hand sanded with 30, 15 and 9 micron 3M^{TM} sanding film to expose the cell structure of all of the rings to facilitate crossdating.

All samples were crossdated using skeleton plots to develop a master chronology for each site and tree species (Stokes and Smiley, 1968). Ring widths were then measured to 0.001mm precision using a standard dissecting microscope and a Velmex^{TM} measuring system. The computer program COFECHA was used to check for measurement errors and validate the dating (Holmes, 1983; Grissino-Mayer, 2001). Interseries correlation was used to determine the stand-level signal where 1.0 is perfect synchrony of growth across the stand. Mean sensitivity is a measure of year-to-year variability and is a measure of how well a stand is recording a variable environmental signal with 0.20 considered a good value and 0.18 being acceptable (Fritts, 1976). A 40 y cubic smoothing spline was used to standardize all of the cores using the computer program ARSTAN (Cook and Holmes, 1986) to remove noise from long-term climate and other environmental factors while maintaining more than 96% of the variance at the 17 y or 13 y time scale associated with the periodical cicada lifecycle.

The climate response of each tree species was determined using a correlation matrix comparing the master index chronologies for each species to 66 climate variables of monthly temperature, precipitation and Palmer Drought Severity Index (PDSI: Palmer 1965) for Indiana Climate Division 3, 7 or 8 depending upon where the sites were located. PDSI is calculated with both precipitation and temperature and is a better measure of available moisture for the trees (Cook *et al.*, 1999). All climate correlations were tested with 95% confidence limits. Simple linear regression was used to remove the signal from the dominant climate parameter for each species chronology.

The residual chronology from the regression analysis for each species was examined to determine the effect of periodical cicadas on tree growth through time. The effects from all of the outbreaks on a site were combined by conducting a superposed epoch analysis. In this analysis, all of the emergence years are shifted to year zero and the tree growth of the preceding 7 y and post 6 y is analyzed to find repeated patterns of effect. These graphs were used to test our three hypotheses by determining if growth was significantly different prior to, during or after the emergence years. The nymphal feeding hypothesis would be supported if the superposed epoch analysis showed a decrease in growth in the years prior to the emergence year (year zero) or an increase in growth in year zero (Fig. 1). The oviposition damage hypothesis would be supported if year 0 or year 1 showed a decrease in growth. Finally, the nutrient pulse hypothesis would be supported if an increase in growth was observed for several years after year zero. Significance was determined by using a Monte Carlo simulation with 1000 events using 95% confidence limits.

RESULTS

Chronologies ranging in length from 63 to 98 y cover multiple emergence events (a minimum of four up to eight emergences) for the analysis of the effect of periodical cicadas on tree growth, and so provide a historical perspective on potential cicada impacts on trees. All chronologies had strong chronology statistics, demonstrating that they responded to a stand-level signal and were sensitive to environmental forcing factors (Table 1). Interseries correlations ranged from 0.645 (for black oak) to 0.388 (for pin oak), demonstrating strong stand-level signal for each species (although pin oak from our suburban trees had a lower than normal correlation, probably reflecting individual yard maintenance). The cores were

TABLE 1.—Chronology statistics for all species. Series intercorrelation is a statistic that demonstrates the correlation of each core to the master chronology and is a measure of stand-level signal. Mean sensitivity measures the year-to-year variability and is a measure of sensitivity. The chronology length reports the length of the oldest core

Common name	Scientific name	Series intercorrelation	Mean sensitivity	Number of trees	Chronology length (years)
Sugar Maple	*Acer saccharum*	0.453	0.362	23	64
White Ash	*Fraxinus americana*	0.459	0.204	18	74
Sassafras	*Sassafras albidum*	0.514	0.186	18	76
Pin Oak	*Quercus palustris*	0.388	0.209	10	63
Black Oak	*Quercus velutina*	0.645	0.189	20	98

mathematically broken into 50 y segments then correlated back to the master chronology for each site; 88% of all segments dated significantly at the 99% confidence level. For the other 12% of the segments that fell below the 99% confidence level in dating, we visually re-examined the wood and determined the discrepancy to be associated with individual tree response to environmental factors and not due to incorrect dating.

All five species had a significant response to climate. Annual growth of sassafras correlated the highest with mean Jun. precipitation (r = 0.406), pin oak growth correlated the best with total summer precipitation (r = 0.366), black oak growth correlated with Jul. PDSI (r = 0.527), sugar maple growth correlated with mean Jun. temperature (r = −0.392) and white ash growth correlated best with summer PDSI (r = 0.338) (Table 2). This analysis was conducted to remove the greatest climate response from the chronologies. The rest of the analysis was conducted using the residuals that resulted from a regression analysis with the above-mentioned variables.

None of the five tree species showed a decrease in growth prior to emergence or a release in growth the year of emergence, effectively rejecting the nymphal feeding hypothesis that the cicadas are most debilitating to tree growth during their late nymphal stages (Fig. 3). However, sassafras and pin oak exhibited a consistent, significant decrease in growth 1 y following emergence, consistent with the oviposition damage hypothesis (Fig. 3). Black oak showed a significant negative response 3 y after emergence, which could possibly be a longer-term lag effect from oviposition damage. None of the five species showed an increase in growth one to 3 y after emergence, which would be predicted by the nutrient pulse hypothesis. However, three of the species (pin oak, black oak and sugar maple) all showed an increase in growth 5 y after emergence (Fig. 3). White ash from the Marry Lea Environmental Center had no significant response to the cicada emergence.

TABLE 2.—Climate response for all species. PDSI stands for Palmer Drought Severity Index

Common name	Scientific name	Month with the highest correlation	Correlation	P value
Sugar Maple	*Acer saccharum*	Jun. temperature	−0.392	<0.01
White Ash	*Fraxinus americana*	Summer PDSI	0.338	<0.01
Sassafras	*Sassafras albidum*	Jun. precipitation	0.406	<0.01
Pin Oak	*Quercus palustris*	Summer precipitation	0.366	<0.01
Black Oak	*Quercus velutina*	Jul. PDSI	0.527	<0.01

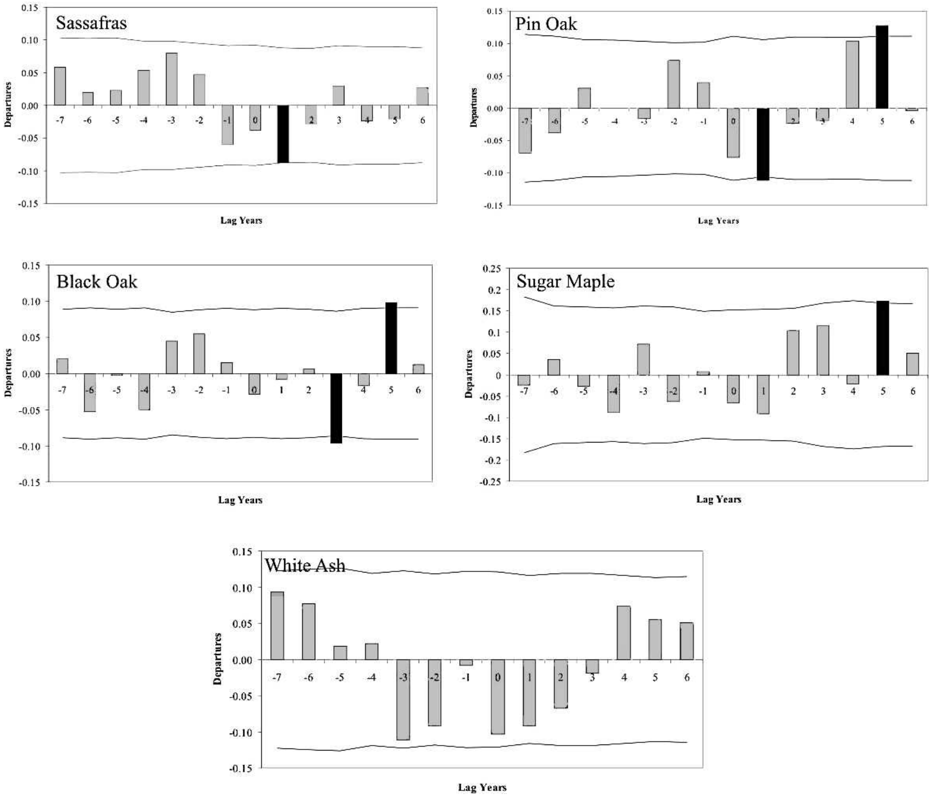

FIG. 3.—Superposed Epoch Analysis (SEA) of the climate residuals. These values are departures of tree-ring growth from the mean of the chronology where year zero represents the growth from the stacked cicada emergence years along with growth for lag years prior to and post emergence. Darker bars designate significant departures at the 95% confidence level and the horizontal lines are the 95% confidence intervals as determined by a bootstrap method. (A) Sassafras from Greene-Sullivan State Forest (6 events), (B) Pin oak from Bloomington city trees (4 events), (C) Black oak from Greene-Sullivan State Forest (8 events), (D) Sugar Maple from Griffy Woods (4 events), (E) White Ash from Marry Lea Environmental Center (5 events)

DISCUSSION

The four species chronologies from the forest sites (sugar maple, white ash, sassafras and black oak) resulted in chronology statistics that are similar to other well-dated chronologies of the same species developed in the eastern deciduous forest (Speer, unpublished data). As expected, the pin oak chronology had the lowest series intercorrelation in this study and was relatively low for an oak chronology. Because these trees were scattered through a suburban area in private yards, they were open grown, subject to watering and possibly fertilized from treatment of surrounding grass. Because of these mitigating effects, these pin oak trees were not limited by one common factor such as drought, resulting in a low series intercorrelation. While the correlation was relatively low, the pin oak chronology was still properly dated (as were the other species chronologies) as demonstrated by visual cross-dating.

The nymphal feeding hypothesis (Fig. 1A) that cicadas have their strongest negative effect on tree growth during their extended period as a root parasite was not supported by our data. It was surprising that none of the tree species examined in this study showed decreased growth due to long-term root parasitism. There was no evidence from the five sites examined that cicadas cause any reduction in growth prior to emergence. Nymphal cicadas draw water and nutrients from the xylem in the roots as those roots uptake water from the soil. The nymphal cicada load (up to 300 emergence holes per square meter, Clay *et al.*, 2009a) on a tree is likely to result in an increased resistance to the tree's ability to uptake water. Increasing resistance can be compensated through producing more stomata or having them open longer, subsequently transpiring more water and uptaking more water from their roots. It would be possible to test this mechanism to see if there is a stable isotopic change in the wood chemistry caused by more exchange with the atmosphere for trees with a heavy cicada load versus lower loads.

The oviposition damage hypothesis (Fig. 1B) was supported for two and possibly three of the tree species. Both sassafras and pin oak showed a significant decrease in growth 1 y after emergence, suggesting that oviposition damage was significant enough to decrease growth the following year. Black oak also exhibited a significant decrease in growth after the emergence, but it was lagged by 3 y. This is possibly due to the longer cycle of growth in black oak trees relative to carbon storage in the tree. For example, black oak trees take 2 y for their acorns to mature compared to 1 y for the white oak group (Speer, 2001). Therefore a reaction to the reduction in photosynthates from the canopy may be delayed through carbon and nutrient storage in the tree, until that reduction overwhelms the reserves of the tree. Pin oak acorns also take 2 y to mature, but the suburban pin oaks examined here are less likely to be resource limited than trees in unmanaged habitats. We recognize that the very high densities of first instar nymphs soon after hatching could also suppress tree growth and parallel the effects of oviposition damage, although this young nymphal effect is more likely to be a long-term effect (2–3 y) than oviposition damage because the young nymphs continue to feed until mortality reduces their numbers.

The reduction of pin oak growth associated with oviposition scarring observed here is consistent with Koenig and Liebhold's (2003) finding that on the regional scale, oak trees exhibited a 4% decrease in growth the year of emergence although they detected no consistent lag effects. In the Koenig and Liebhold study trees were not selected because of known cicada outbreaks on their sites but rather because the trees grew within the range of particular periodical cicada broods, potentially underestimating the effects of cicadas on oak growth. Our results demonstrate reduced growth of sassafras and two oak species but not in red maple and white ash, following cicada emergences.

Based on oviposition scarring data collected for the genera examined here during the 2004 Brood X emergence around Bloomington IN (Clay *et al.*, 2009b), white ash was the most preferred by cicadas, followed by red oak (closest studied to our black oak), sugar maple, sassafras and finally pin oak. This species preference is the opposite of the sensitivity of trees to the effects of the cicadas based on tree-growth response. White ash showed no effect and sassafras and pin oak demonstrated the greatest response to oviposition scarring.

This differential species response to damage could be due to adaptation or differing cicada loads at each site through time. We know that all of our sites were heavily affected by cicadas during the most recent outbreak (2004 for the Bloomington, Griffy Woods, and Marry Lea sites and 2002 for the Greene-Sullivan site), but we do not have data for past emergences on these sites. Future work with a larger sample depth and replication within species on different sites should be able to better separate differential species responses to cicada damage from response to differing site characteristics.

The nutrient pulse hypothesis was supported (Fig. 1C) but on a longer time span (5 y) than we predicted. We expected nutrient cycling to be relatively quick in this system, as

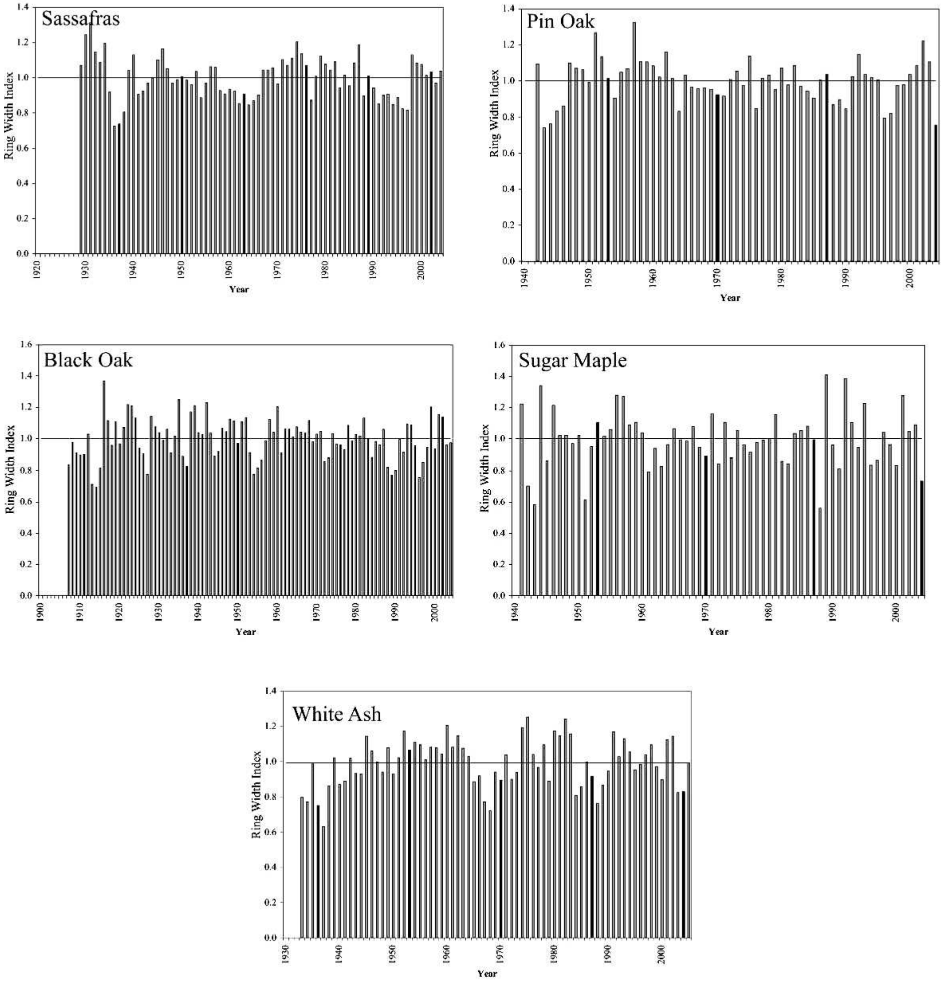

FIG. 4.—Climate Residuals plotted with a line showing average tree growth and darker bars designating the emergence years. (A) Sassafras from Greene-Sullivan State Forest (6 events), (B) Pin oak from Bloomington city trees (4 events), (C) Black oak from Greene-Sullivan State Forest (8 events), (D) Sugar Maple from Griffy Woods (4 events), (E) White Ash from Marry Lea Environmental Center (5 events)

decaying cicada carcasses were very evident during the weeks following emergence. Yang (2004) also demonstrated a flush of growth and higher nitrogen concentrations in bell flower in the same season as his artificial loading with cicadas. The 5 y lag in growth response we observed in pin oak, black oak and sugar maple could indicate the time it takes for nutrients to become available to trees combined with a lag response of wood production. It is also possible that high mortality of second and third instar nymphs provides a delayed nutrient pulse directly to the root system (Karban, 1980). These possibilities could be tested experimentally by collection and removal of adult cicada carcasses before they decompose in defined areas and comparing subsequent tree growth with control areas.

Pin oak trees in suburban habitats exhibited a greater effect from cicadas than did forest interior trees. This may be an edge effect, as cicadas tend to congregate at the forest edge or on isolated well-lit trees, or it may be a species-specific response. Without replication of species across different sites, it is difficult to distinguish site effects from species effects, but this significant response in pin oak was not reflected in black oak on another site. Further work with multiple species on multiple sites will help to differentiate these factors. The heavy cicada load on suburban tree resources seems to concentrate the effect of the cicadas, resulting in significant damage from oviposition scarring and a possible lagged release due to nutrient cycling (Williams and Simon, 1995).

Given that we can look back through the history of tree response to periodical cicadas with dendrochronology, we can determine if cicadas had a different effect on the trees growth from one emergence to another as the trees mature (Fig. 4). No such effect was observed across the four to eight individual emergence events experienced by each species. Cicadas tend to move towards edge location with more light to form their chorusing groups. Because of this, researchers have suggested that edge locations (such as our Marry Lea site) or younger stands are likely to have the greatest concentration of insects. This would result in greater damage to young trees and less cicada activity as the stand ages and fills in. Such a trend was not evident from our data although greater damage to younger trees could be compensated for by the faster growth of younger trees.

CONCLUSIONS

The results from this study suggest that extended nymphal feeding has no detectable effect on tree growth but that oviposition damage (or early instar nymphal feeding) did have a significant negative effect on post-emergence growth of three of the five species examined here. Further, three of the five species also exhibited longer term growth increase following emergence consistent with the nutrient pulse hypothesis. Interestingly, the tree species that are most preferred for oviposition by cicadas were the least affected and showed little growth response. The preferred trees may have evolved under the continuing pressure of oviposition scarring or alternatively, short-term, post-emergence nutrient pulses may counterbalance the effect of scarring on these tree species. Further dendrochronological studies with replication within species across multiple sites should show if this is a repeated and consistent pattern between species. If this pattern holds true, our data suggest that the tree species favored by periodical cicadas for oviposition will compete better in succession under parasitism from cicadas.

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LITERATURE CITED

ABRAMS, M. D., D. A. ORWIG AND T. E. DEMEO. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine-mixed-oak forest in the southern Appalachians, USA. *J. Ecol.*, **83**:123–133.

AYRES, M. P. AND M. J. LOMBARDERO. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci. Tot. Envir.*, **262**:263–286.

BUCKLEY, T. R., C. SIMON AND G. K. CHAMBERS. 2001. Phylogeography of the New Zealand cicada *Maoricicada campbelli* based on mitochondrial DNA sequences: Ancient clades associated with Cenozoic environmental change. *Evolution*, **55**(7):1395–1407.

CARSON, W. P., J. P. CRONIN AND Z. T. LONG. 2004. A general rule for predicting when insects will have strong top-down effects on plant communities: On the relationship between insect outbreaks and host concentration, p. 193–211. *In:* W. W. Weisser and E. Siemann (eds.). Insects and ecosystem function, vol. 173. Ecological studies. Springer-Verlag Academic Publishing, Berlin.

——— AND R. B. ROOT. 2000. Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect. *Ecol. Monog.*, **70**(1):73–99.

CLAY, K., A. L. SHELTON AND C. WINKLE. 2009a. Differential susceptibility of tree species to oviposition by periodical cicadas. *Ecol. Entom.*, **34**:277–286.

———, ——— AND ———. 2009b. Effects of ovipostion by periodical cicadas on tree growth. *Can. J. For. Res.*, **39**:1688–1697.

COOK, E. R. AND R. L. HOLMES. 1986. Users manual for program ARSTAN, p. 50–56. *In:* R. L. Holmes, R. K. Adams and H. C. Fritts (eds.). Tree-ring chronologies of western North America: California, eastern Oregon, and northern Great Basin. Chronology Series 6. Laboratory of Tree-Ring Research, The University of Arizona, Tucson, Arizona.

———, D. M. MEKO, D. W. STAHLE AND M. K. CLEAVELAND. 1999. Drought reconstructions for the continental United States. *J. Climate*, **12**:1145–1162.

COOK, W. M. AND R. D. HOLT. 2002. Periodical cicada (*Magicicada cassini*) oviposition damage: Visually impressive yet dynamically irrelevant. *Am. Midl. Nat.*, **147**:214–224.

———, ——— AND J. YAO. 2001. Spatial variability in oviposition damage by periodical cicadas in a fragmented landscape. *Oecologia*, **127**:51–61.

COOLEY, J. R., C. SIMON, D. C. MARSHALL, K. SLON AND C. EHRHARDT. 2001. Allochronic speciation, secondary contact, and reproductive character displacement in periodical cicadas (Hemiptera: *Magiciada* spp.): genetic, morphological, and behavioural evidence. *Mol. Ecol.*, **10**(3):661–671.

COUPE, M. D. AND J. F. CAHILL, JR. 2003. Effects of insects on primary production in temperate herbaceous communities: A meta-analysis. *Ecol. Entom.*, **28**:511–521.

DALE, V. H., L. A. JOYCE, S. MCNULTY, R. P. NEILSON, M. P. AYRES, M. D. FLANNIGAN, P. J. HANSON, L. C. IRLAND, A. E. LUGO, C. J. PETERSON, D. SIMBERLOFF, F. J. SWANSON, B. J. STOCKS AND B. M. WOTTON. 2001. Climate change and forest disturbances. *BioScience*, **51**(9):723–734.

DYBAS, H. S. AND M. LLOYD. 1962. Isolation by habitat in two synchronized species of periodical cicadas. *Ecology*, **43**(3):444–459.

FORSYTHE, JR., H. Y. 1977. Effect of sun-exposure on emergence of 17-year cicadas. *Ohio J. Sci.*, **77**(4):183–185.

FRITTS, H. C. 1976. Tree rings and climate. Academic Press, London. 567 p.

GRISSINO-MAYER, H. D. 2001. Evaluating crossdating accuracy: A manual and tutorial for the computer program COFECHA. *Tree-Ring Res.*, **57**(2):205–221.

HEDGREN, P. O., L. M. SCHROEDER AND J. WESLIEN. 2003. Tree killing by *Ips typographus* (*Coleoptera: Scolytidae*) at stand edges with and without colonized felled spruce trees. *Agric. For. Entom.*, **5**:67–74.

HOLMES, R. L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.*, **43**:69–75.

JOHNSON, W. T. AND H. H. LYON. 1991. Insects that feed on trees and shrubs, 2nd edition. Cornell University Press, Ithaca, New York. p. 490–492.

KARBAN, R. 1980. Periodical cicada nymphs impose periodical oak tree wood accumulation. *Nature*, **287**:326–327.

———. 1984. Opposite density effects of nymphal and adult mortality for periodical cicadas. *Ecology*, **65**(5):1656–1661.

———. 1997. Evolution of prolonged development: A life table analysis for periodical cicadas. *Am. Nat.*, **150**(4):446–461.

KOENIG, W. D. AND A. M. LIEBHOLD. 2003. Regional impacts of periodical cicadas on oak radial increment. *Can. J. For. Res.*, **33**:1084–1089.

LAMARCHE, JR., V. C. AND K. K. HIRSCHBOECK. 1984. Frost rings in trees as records of major volcanic eruptions. *Nature*, **307**(5946):121–126.

MARLATT, C. L. 1907. The periodical cicada. USDA Bureau of Entomology, Bulletin No. 71. Government Printing Office, Washington, D.C. 181 p.

MARSHALL, D. C. AND J. R. COOLEY. 2000. Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim*. *Evolution*, **54**(4):1313–1325.

MASON, R. R., B. E. WICKMAN AND H. G. PAUL. 1997. Radial growth response of Douglas-fir and grand fir to larval densities of the Douglas-fir Tussock moth and the western spruce budworm. *For. Sci.*, **43**(2):194–205.

MATTSON, W. J. AND N. D. ADDY. 1975. Phytophagous insects as regulators of forest primary production. *Science*, **190**(4214):515–522.

MEDLEY, K. E., C. M. POBOCIK AND B. M. OKEY. 2003. Historical changes in forest cover and land ownership in a Midwestern U.S. landscape. *Ann. Assoc. Am. Geog.*, **93**(1):104–120.

MORROW, P. A. AND V. C. LAMARCHE, JR. 1978. Tree ring evidence for chronic insect suppression of productivity in subalpine eucalyptus. *Science*, **201**(4362):1244–1246.

MUZIKA, R. AND R. P. GUYETTE. 2004. A dendrochronological analysis of red oak borer abundance, p. 102–105. *In:* M. A. Spetich (ed.). Upland oak ecology symposium: History, current conditions, and sustainability. USDA Forest Service, General Tech. Report SRS-73: Southern Research Station, Asheville, North Carolina. 311 p.

ORVIS, K. H. AND H. D. GRISSINO-MAYER. 2002. Standardizing the reporting of abrasive papers used to surface tree-ring samples. *Tree-Ring Research*, **58**(1/2):47–50.

PALMER, W. C. 1965. Meteorological drought. USDC Weather Bureau Research Paper Number 45. 58 p.

PARISH, R., J. A. ANTOS AND M.-J. FORTIN. 1999. Stand development in an old-growth subalpine forest in southern interior British Columbia. *Can. J. For. Res.*, **29**:1347–1356.

POHL, K. A., K. S. HADLEY AND K. B. ARABAS. 2006. Decoupling tree-ring signatures of climate variation, fire, and insect outbreaks in central Oregon. *Tree-Ring Research*, **62**(2):37–50.

REED, D. K., G. L. REED AND D. W. HAMILTON. 1963. The 13-year cicada – conclusion of an experiment started in 1963. *Proc. Indiana Acad. Sci.*, **73**:167–170.

RYERSON, D. E., T. W. SWETNAM AND A. M. LYNCH. 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, U.S.A. *Can. J. For. Res.*, **33**:1010–1028.

SCHOWALTER, T. D. 1996. Insect ecology: An ecosystem approach. Academic Press, San Diego, California. 483 p.

SPEER, J. H. 2001. Oak mast history from dendrochronology: A new technique demonstrated in the Southern Appalachian Region. Dissertation, University of Tennessee. 241 p.

———, T. W. SWETNAM, B. E. WICKMAN AND A. YOUNGBLOOD. 2001. Changes in pandora moth outbreak dynamics during the past 622 years. *Ecology*, **82**(3):679–697.

STOKES, M. A. AND T. L. SMILEY. 1968. An introduction to tree-ring dating. The University of Arizona Press, Tucson, Arizona. 73 p.

SWETNAM, T. W. AND A. M. LYNCH. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecol. Monog.*, **63**(4):399–424.

———, M. A. THOMPSON AND E. K. SUTHERLAND. 1985. Spruce budworms handbook: Using dendrochronology to measure radial growth of defoliated trees. USDA Forest Service, Agriculture Handbook No. 639: Government Printing Office, Washington, D.C. 39 p.

WHITE, J. 1981. Flagging: Host defences versus oviposition strategies in periodical cicadas (*Magicicada* spp., Cicadidae, Homptera). *Can. Entom.*, **113**:727–738.

——— AND C. E. STREHL. 1978. Xylem feeding by periodical cicada nymphs on tree roots. *Ecol. Entom.*, **3**:323–327.

WILLIAMS, K. S. AND C. SIMON. 1995. The ecology, behavior and evolution of periodical cicadas. *Ann. Rev. Ecol. System.*, **40**:269–295.

YANG, L. H. 2004. Periodical Cicadas as Resource Pulses in North American Forests. *Science*, **306**(5701):1565–1568.

——— AND R. KARBAN. 2009. Long-Term Habitat Selection and Chronic Root Herbivory: Explaining the Relationship between Periodical Cicada Density and Tree Growth. *Am. Nat.*, **173**:105–112.

YOUNG, F. N. AND G. KRITSKY. 1987. Observations on periodical cicadas (brood X), *In:* Indiana in 1987 *(Homoptera: Cicadidae)*. *Proc. Indiana Acad. Sci.*, **97**:323–329.

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