

Natural History Note

Long-Term Habitat Selection and Chronic Root Herbivory: Explaining the Relationship between Periodical Cicada Density and Tree Growth

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ABSTRACT: Periodical cicadas (*Magicicada* spp.) are insect herbivores that feed on host tree roots, but their distribution among hosts is determined largely by the oviposition of female cicadas in the previous generation. A pattern of decreasing tree growth rates with increasing cicada densities is predicted when considering the costs of chronic root herbivory, but the opposite pattern is expected when considering adaptive habitat selection. Here, we report observations indicating that the relationship between periodical cicada densities and host tree growth rates is hump shaped. We suggest that both herbivory and habitat selection are likely to be key processes explaining this pattern, resulting in regions of positive and negative correlation. These results suggest that the effects of cicada herbivory are most apparent at relatively high cicada densities, while habitat selection tends to distribute cicada herbivory on host trees that are able to compensate for cicada root herbivory up to threshold cicada densities.

Keywords: chronic belowground root herbivory, long-term habitat selection, periodical cicadas (*Magicicada* spp.), host-parasite interaction, interaction threshold, forest fragment expansion.

Relatively few studies have investigated the effects of chronic herbivory on long-lived plants, either aboveground or belowground. Among the existing studies, sev-

eral have shown substantial declines in host growth and performance associated with chronic herbivory. For example, both Morrow and LaMarche (1978) and Trotter et al. (2002) demonstrated that chronic aboveground insect herbivory substantially reduced the growth of trees in natural forest systems. These results are consistent with a transition matrix model developed by Doak (1992), which suggests that even at very low intensities, chronic herbivory can substantially reduce the growth of long-lived plants.

Periodical cicadas (*Magicicada* spp.) are long-lived, root-feeding insect herbivores. Soon after hatching, periodical cicada nymphs establish belowground feeding sites on the roots of their host trees (White and Strehl 1978). For more than 99% of their 13- or 17-year ontogeny, these nymphal cicadas live in short tunnels or mud cells, feeding on dilute xylem fluid from host roots (Marlatt 1907; Beamer 1928; White and Lloyd 1975; Maier 1980; Williams and Simon 1995). Because cicada root herbivory occurs belowground, many of its ecological effects are not readily apparent (Hunter 2001). However, this form of herbivory likely imposes costs on the host tree in terms of increased water stress, reduced nutrient assimilation efficiency, and damage to fine roots (White and Lloyd 1975; White and Strehl 1978; Karban 1984). The cumulative effects of cicada herbivory on host trees are potentially large. Periodical cicadas are among the most abundant forest herbivores in North America across a large geographic range, with emergence densities commonly ranging from 30,000 to 3.5 million individuals ha⁻¹ (Dybas and Davis 1962; Williams and Simon 1995). Previous observations of periodical cicadas have suggested that high cicada densities in apple orchards contribute to reductions in fruit yield and tree growth over time (Banta 1960; Hamilton 1961; Hamilton and Cleveland 1964; Karban 1982), while studies of periodical cicadas in natural forests suggest that cicada herbivory can slow the growth of host trees (Karban 1980; Koenig and Liebhold 2003). These observations suggest that the relationship between cicadas and their host trees is primarily an antagonistic host-parasite interaction, leading to the

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expectation of a negative relationship between nymphal cicada densities and the growth of their host trees.

The distribution of nymphal cicadas among host trees is determined in part by the oviposition decisions of adult female cicadas in the previous generation. Adult female cicadas insert eggs into pencil-sized tree branches of selected host trees (fig. A1 in the online edition of the *American Naturalist*). Approximately 6 weeks after oviposition, the next generation of nymphal cicadas hatches from these eggs, falls to the ground, and begins digging for suitable host roots. Previous field studies suggest that cicadas show strong preferences for ovipositing on host trees in high-light environments (White 1980; White and Lloyd 1985; Williams et al. 1993; Yang 2006), possibly because local light environments are robust long-range predictors of host tree growth rates and root densities (Cole and Lorimer 1994; Naidu and Delucia 1997). Several observations suggest that the growth and survival of cicada nymphs are maximized on the roots of rapidly growing host trees (White and Lloyd 1975, 1985; Maier 1980). For both males and females, larger cicadas have fitness greater than that of smaller cicadas (Brown and Chippendale 1973; Karban 1983), suggesting an adaptive explanation for observed patterns of habitat selection. Consistent with the plant vigor hypothesis (Price 1991), patterns of cicada habitat selection suggest that cicadas preferentially oviposit on host trees that show the best prospects for long-term future growth (Yang 2006).

Herbivory and habitat selection are both important processes that affect the relationship between periodical cicadas and their host trees (fig. 1), but these processes suggest alternative hypotheses for the relationship between cicada density and host tree growth in natural systems. If

this relationship is primarily characterized by the costs of chronic herbivory, host tree growth should decline with increasing cicada density (H_1). Conversely, if this relationship is largely characterized by the habitat selection decisions of the ovipositing female, host tree growth and cicada density should be positively correlated, due to the positive effects of high-light environments on both cicada oviposition density and tree growth (H_2). The observation of no significant correlation between cicada densities and tree growth would support the null hypothesis (H_0). Here, we report the results of field studies aimed at evaluating these hypotheses. This paired analysis of host tree increment cores and emergence hole densities provides a unique opportunity to retroactively measure patterns of tree growth over a 17-year-long plant-herbivore interaction.

Material and Methods

We conducted field studies to examine the relationship between nymphal cicada densities and long-term host tree growth rates. These studies were conducted in 2002, 2004, and 2007, at three distant forest sites, using three different tree species. Each year, we collected paired, retrospective observations of past cicada density and tree growth. We used the density of cicada emergence holes immediately below individual trees to measure natural variation in the density of belowground cicada herbivores over the previous 17-year period and collected increment cores from these same trees to determine their average annual growth rates during the 17-year interaction.

In 2002, we surveyed a population of 26 sugar maples (*Acer saccharum*) in an approximately 2-ha area of mixed deciduous forest at the Powdermill Nature Reserve near

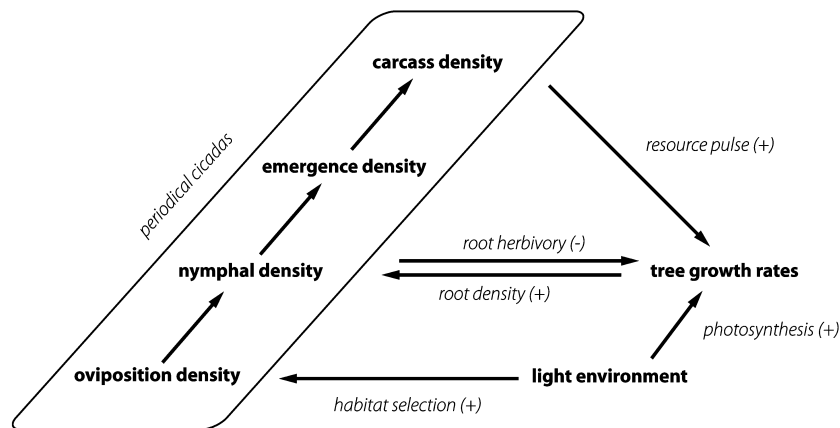


Figure 1: Schematic diagram illustrating how periodical cicada interactions with their abiotic environment and their long-term host trees change over the course of their life history. Arrows indicate the direction of interaction effects, arrow labels indicate the ecological mechanism for these interactions, and plus and minus signs indicate the nature of the expected qualitative effect.

Rector, Pennsylvania (Carnegie Museum of Natural History, 40°9'52"N, 79°15'59"W). This site was characterized by mesic, low-slope, fine-loamy soils of the Ernest and Atkins series, in a contiguous area of mature secondary-growth forest dominated by maple (*Acer* spp.) and oak (*Quercus* spp.) trees, bounded by roads and old fields. We selected mature trees (mean diameter at breast height [dbh] \pm SD, 20.3 \pm 4.8 cm) with relatively straight trunks and some canopy exposure for this study in order to maximize the quality of our increment cores (Stokes and Smiley 1968) and provide a comparable host tree population; beyond these factors, our selection of focal trees was haphazard in order to provide a broad sample of cicada densities in the population. We used these same criteria to select trees in each subsequent year. Each tree was cored with an increment borer at 1.3-m height. We also measured the diameter of each tree at this height and the distance from each focal tree to its nearest neighboring canopy tree. We counted cicada emergence holes in a 1-m² area cleared of leaf litter and humus immediately below the canopy of the focal tree. Surveys of cicada hole densities were conducted on June 7, 2002, after all local emergence activity of brood VIII was complete.

In 2004, we conducted a similar survey in an approximately 36-ha forested area at the Stonebridge Farm (39°0'13"N, 78°6'52"W) near Ashby, Virginia. This forest was characterized by low-slope, Lodi silt loam in a mature oak-dominated secondary-growth forest bounded by old fields and planted saplings. We conducted measurements of cicada emergence hole densities coordinated with host tree increment core collections from 26 tulip trees (*Liriodendron tulipifera*). Because of the high density of surface rocks and roots at this site, we counted cicada emergence holes in 0.5-m² quadrats beneath each tree. Surveys of cicada hole densities were conducted on May 26, 2004, after all local emergence activity of brood X was complete. We also measured the diameter of each focal tree at 1.3-m height (mean dbh \pm SD, 32.3 \pm 10.3 cm).

In 2007, we conducted our survey in an approximately 1-ha area of the Will County Forest Preserve (Illinois Nature Preserves, Lower Plum Creek South, 41°27'4"N, 87°33'15"W). This site was partly bounded by the oxbow of a small (approximately 9-m width) stream and characterized by occasionally flooded mesic soils (Lawson silt loam, 0%–2% slopes). The forest composition at this site included oaks (*Quercus* spp.), hickories (*Carya* spp.), and cottonwoods (*Populus deltoides*). Emergence holes were counted in 1-m² quadrats adjacent to the trunks of 30 American basswood (*Tilia americana*) trees on June 12, 2007, after the completion of local cicada emergence of brood XIII. We measured the dbh and estimated the nearest-neighbor distances of adjacent canopy trees for each focal tree.

Tree core samples were collected, mounted, and prepared following standard methods (Stokes and Smiley 1968; Grissino-Mayer 2003). Increment cores collected in 2002 were measured using a stage micrometer at the USDA Forest Service Northern Research Station Forestry Sciences Laboratory in Morgantown, West Virginia; growth increments from tree cores collected in 2004 and 2007 were measured from high-resolution digital scans using image analysis software (ImageJ, National Institutes of Health, Bethesda, MD; <http://rsb.info.nih.gov/ij/>). The age of each tree in the data set was estimated using the formula $[(d/2) - b]/a$, where d represents tree dbh, b represents the thickness of the phloem and bark layers, a represents the annual growth increment averaged over all available data, and all parameters were measured in a common unit of length. The mean age of trees in this data set was estimated to be 41 years (\pm 15 years SD). Three tulip trees from the 2004 study were estimated to be <19 years old and were excluded from these analyses. Our tree cores often included readable increments extending close to the pith, so that direct counts of annual increments accounted for a large fraction (mean = 76.3%, SD = 14.6%) of the estimated tree age. This fact increases our confidence in these estimates of tree age. Although these methods cannot provide an absolute determination of tree age, they offer a useful and reliable estimate appropriate for these analyses.

We used a mixed-model ANOVA to investigate the relationship between past belowground cicada densities and the 17-year average annual growth increment. In this study, we used a 17-year average growth increment to reduce the annual variation in the data set and focus on long-term ecological processes. The examination of narrower time intervals within the 17-year cicada generation did not provide any additional insights, and comparisons between time intervals are beyond the scope of this study design. Initial hypotheses suggested first-order regressions of average annual tree growth on the Y-axis against belowground cicada densities on the X-axis. However, early exploratory analysis of data from the 2002 field season indicated a hump-shaped relationship between these variables. Therefore, we evaluated a more complex model including cicada density as both first- and second-order fixed variables in a polynomial regression. We included year, location, and tree species as a single random blocking factor (hereafter, site). We evaluated this complete model including all interaction terms, in addition to a stepwise evaluation of all simpler models, including first-order (i.e., linear) polynomial regressions. These interaction terms were found to be nonsignificant and were excluded in subsequent analyses. Nearest-neighbor distances from 2002 and 2007 were also evaluated as potential covariates in these analyses but were found to be uninformative. We used the Akaike Information Criterion (AIC) to determine

the minimally complex model that maximizes explanatory goodness of fit using the complete data set for all combinations and subsets of factors in the complete model. Assumptions of residual normality were confirmed using a normal quantile plot and a Shapiro-Wilk test ($W = 0.95$).

In order to measure fine-scale spatial variation in the density of cicada emergence holes, in 2007 we oriented each square quadrat so that one corner was adjacent to the tree trunk and a diagonal of the quadrat pointed toward the center of the host tree trunk. This quadrat was divided into two adjacent triangular 0.5-m² areas, one near and one far from the tree trunk. This allowed us to systematically measure the density of emergence holes in equal areas near and far from the tree trunk. The density of cicadas near and far from host trees was compared using a paired t -test. Cicada densities were log transformed before analysis to improve residual normality, though identical conclusions were observed using untransformed data. Assumptions of residual normality (Shapiro-Wilk's $W = 0.98$) and homoscedasticity (Levene's test, $P = 1.0$) were confirmed.

Results

The relationship between cicada density and tree growth was hump shaped. At low cicada densities, increasing cicada densities were associated with greater tree growth, but at higher cicada densities, trees with more cicadas grew more slowly. More precisely, the relationship between cicada density and tree growth was best fit by a concave-down quadratic regression line in the overall analysis (first-order fit, $AIC = 15.3$, $R^2_{adj} = 0.44$ vs. second-order fit, $AIC = 10.2$, $R^2_{adj} = 0.49$). In the quadratic regression analysis, both first- and second-order cicada density terms were significant (fig. 2; first-order term, $P = .007$; second-order term, $P = .011$). At the sugar maple site in 2002, the critical threshold point separating regions of positive and negative slopes occurred at a cicada density of 74.3 holes m⁻²; at the tulip tree site in 2004, it occurred at 55.4 holes m⁻²; and at the basswood site in 2007, it occurred at 72.3 holes m⁻².

Older trees grew less rapidly than younger ones (fig. 2). Average annual growth increments decreased with increasing host tree age in each survey (2002: $R^2_{adj} = 0.38$, $P = .0005$; 2004: $R^2_{adj} = 0.45$, $P = .0003$; 2007: $R^2_{adj} = 0.17$, $P = .0148$; fig. A2 in the online edition of the *American Naturalist*). In climatic reconstructions using dendrochronology, it is conventional to remove the effect of tree age, in order to leave a residual "index" that reflects short-term climatic variation in tree growth (Fritts 1976). In this analysis, however, tree age is of ecological interest as a factor that may influence cicada oviposition through

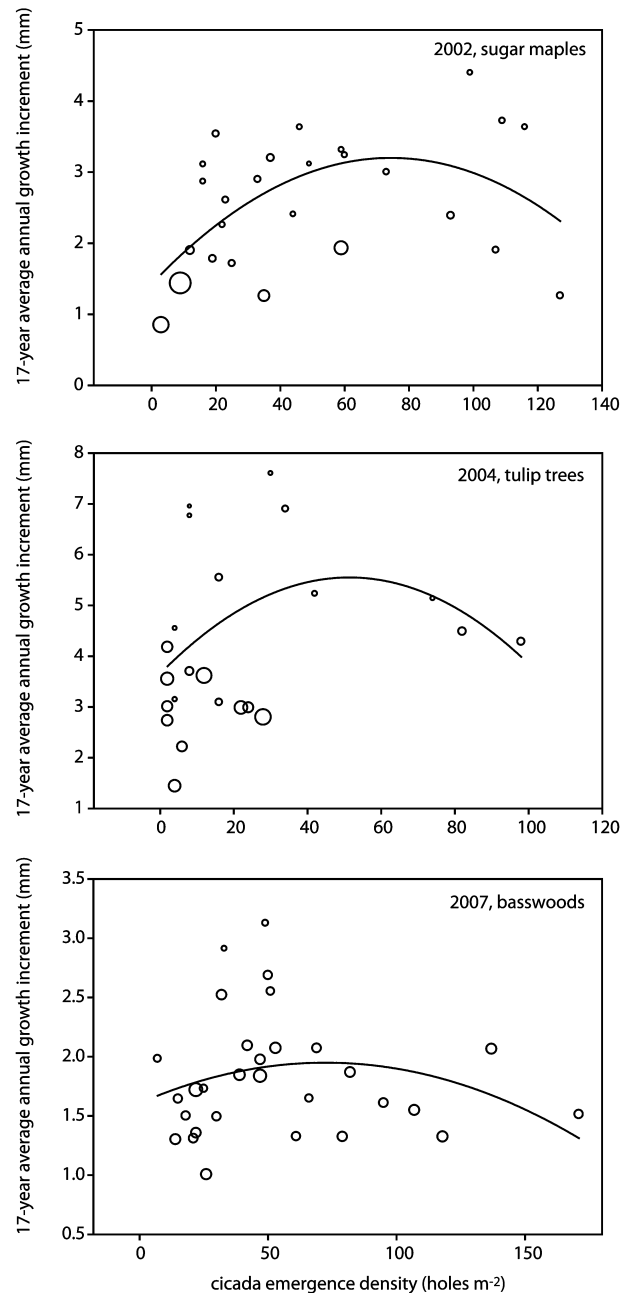


Figure 2: Seventeen-year averages of host tree growth rates show a hump-shaped relationship along an axis of increasing cicada densities. Lines indicate quadratic regressions, and circle size is proportional to estimated host tree age.

its associations with the light environment. In particular, older trees are more likely to be located in the interior of expanding forest fragments, while younger trees are more likely to be located near forest edges (Ranney et al. 1981). Because the habitat selection mechanism suggests that

more exposed trees experience increased oviposition, the distribution of cicadas on trees of different ages and age-related patterns of tree growth are ecological processes of interest. In addition, the detrending procedures typically used for climatic reconstructions may not be appropriate for the comparatively short time series in this analysis, especially given the relatively long period of the cicada-host association relative to the host age. Nonetheless, we repeated these analyses using the residuals of linear regressions of estimated tree age versus the 17-year average annual growth increment for each site, in order to examine these data without the effects of tree age on the average annual growth increment (fig. A2). An otherwise identical analysis of the complete data set using these residual data showed the same qualitative results as an analysis using the original data; both first- and second-order cicada density terms were significant (fig. A3 in the online edition of the *American Naturalist*; first-order term, $P = .0490$; second-order term, $P = .029$), while the explanatory model that included a quadratic term showed the lowest AIC value compared with the linear model and all simpler models (first-order fit, $AIC = -32.2$ vs. second-order fit, $AIC = -34.7$). Although these analyses support the same qualitative conclusions, the resulting quadratic patterns are somewhat weaker. This suggests that the quadratic pattern of these data is not an incidental result of tree age, though the distribution of cicadas on trees of different ages may represent a pattern of ecological interest.

The belowground distribution of cicada nymphs was concentrated close to the trunks of host trees. In 2007, cicada densities were 88% higher in the area near the base of the host tree than in adjacent equal-sized areas farther from the host tree (fig. 3; $P < .0001$).

Discussion

These results indicate a hump-shaped relationship between cicada density and host tree growth (fig. 2) that was evident in each of three years at three distinct sites in populations of three different forest tree species. The best-fit regression line describes a pattern of increasing tree growth with increasing cicada densities up to a site-specific threshold between 55.4 and 74.3 cicadas m^{-2} ; beyond this threshold, increasing cicada densities are correlated with decreasing host tree growth. The region of negative correlation between cicada density and tree growth on the right side of this regression fits the expectation of a host-parasite interaction (H_1). This negative correlation supports the conclusions of previous studies suggesting that chronic cicada herbivory reduces the productivity of host trees (Karban 1980, 1982; Koenig and Liebhold 2003). Consistent with expectations, this pattern was most apparent at high cicada densities. We suggest that the positive correlation between

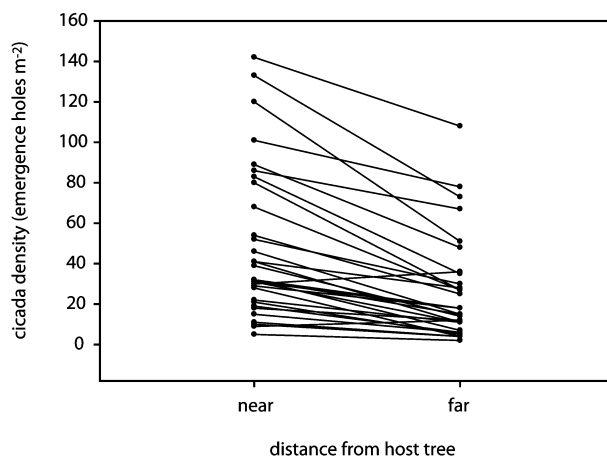


Figure 3: Belowground cicada densities are patchily distributed in space, with higher cicada densities near tree trunks. Lines connect pairs of near and far hole counts for equal-sized areas under the canopy of the same host tree.

host tree growth rates and cicada densities observed on the left side of this regression results from preferential oviposition in environments favorable to long-term host tree growth (H_2). Previous studies suggest that the highest densities of cicada oviposition and emergence occur along forest edges (White 1980; White and Lloyd 1985), and this pattern appears to be driven by habitat selection decisions in response to the light environment around potential host trees (Yang 2006). Studies in other deciduous forests suggest that the light environment around forest trees is a good long-range predictor of future tree growth (Cole and Lorimer 1994). Thus, a positive correlation between tree growth and cicada densities could result if both cicada oviposition and tree growth increase in high-light environments. The regions of positive correlation on the left side of figure 2 suggest that the effects of habitat selection decisions made by female cicadas 17 years earlier dominated the relationship between cicada density and tree growth at low cicada densities until the year of emergence.

Although the observed patterns are consistent with both habitat selection and herbivory mechanisms, inference about causation is limited in all correlative approaches. In particular, the combined effects of both habitat selection and herbivory do not necessarily predict the hump-shaped relationship that was observed. For example, if the effects of habitat selection and herbivory were countervailing and compensatory over the same range of cicada densities, no detectable correlation would be expected. Given the proposed mechanism, nonquadratic patterns of data are possible. However, given the observation of a quadratic relationship, we suggest that a combination of habitat

selection and herbivory processes provides the most likely explanation.

This interpretation involving habitat selection appears to be supported by the nonrandom distribution of tree ages in this analysis. In 2002 and 2004, most of the older trees showed relatively low cicada emergence densities. This pattern could result if older trees are more likely to be located in the interior of forests, where cicada oviposition densities are lower, while younger trees are more likely to be located near forest edges, where cicada oviposition is most intense (White 1980; Williams et al. 1993; Rodenhouse et al. 1997). This pattern of spatial demography is generally true in expanding forest areas (Ranney et al. 1981) and is consistent with observations of more rapid tree growth rates near forest edges (McDonald and Urban 2004). These studies suggest that younger trees are most likely located along forest edges in expanding forest fragments. The forest sites that we studied in 2002 and 2004 were both expanding, with forest edges advancing into adjacent old fields. Both of these forest sites showed older trees supporting relatively low cicada densities (fig. 2). By comparison, the forest site we studied in 2007 was interior but bounded by the oxbow of a small stream. This stream created a canopy gap, but the forest edges at this site were relatively stationary, and the age structure was relatively uniform. This site showed a quadratic relationship between tree growth and cicada density but did not show any contributing pattern of host tree age structure. This analysis of tree age offers some additional support for the hypothesis that habitat selection contributes to the region of positive correlation between tree growth and cicada density.

Our primary hypothesis for the region of positive correlation between tree growth and cicada densities is that both tree growth and cicada density are positively correlated with high-light environments. However, two alternative hypotheses may also have contributed to this pattern. First, faster-growing trees may have been able to support higher densities of cicadas than slower-growing trees. Observations of high cicada densities in managed orchards and suburban environments (White and Lloyd 1975; White et al. 1979; Cook et al. 2001; Cook and Holt 2002) show that fertilized host trees in high-light environments can support very high cicada densities, and similar observations have been made in other plant-herbivore systems (Price 1994). However, this study is not able to separate the effects of preference (high oviposition densities) from the effects of nymphal performance (high rates of nymphal survival). A second alternative hypothesis is that the accumulation of dead cicada carcasses in the emergence year represents a resource pulse for the host tree, which contributes to increased host tree growth. This hypothesis assumes that significant between-tree variation in

both long-term growth rates and the density of cicada emergence in the present is explained by the density of cicada carcass deposition in the emergence year 17 years ago. Resource pulses of cicada carcasses have been shown to affect the nutrient uptake, growth, and reproduction of understory plants in the emergence year (Yang 2004; L. H. Yang, unpublished manuscript), but the effects of these pulsed enrichment events on the growth of long-lived trees remain unresolved. However, we note that these alternative mechanisms are not exclusive and should probably be considered in addition to mechanisms of habitat selection.

The distribution of cicadas in the belowground environment appears to be strongly structured by the distribution of host trees in the environment, with higher cicada densities emerging near the base of host trees (fig. 3). The patchy distribution of cicadas over landscape scales has been well documented previously (Dybas and Davis 1962; Whiles et al. 2001); our current observations indicate that the distribution of cicadas in the soil is also patchily distributed over much smaller spatial scales and that patches of high cicada density are centered on host trees. The observed spatial distribution of cicada emergence holes relative to host trees confirms that the between-host tree scale represents an appropriate one for this investigation.

Taken together, this work suggests that the observed relationship between tree growth and cicada density is unlikely to be adequately explained by any single mechanism. Instead, this study suggests that both habitat selection and herbivory are important factors that mediate the long-term interaction between periodical cicadas and their host plants. While previous studies have demonstrated the effects of both mechanisms acting separately (Karban 1980; Koenig and Liebhold 2003; Yang 2006), this study documents an unanticipated natural pattern consistent with the combined effects of both mechanisms. In combination, these mechanisms may contribute to the observation of both positive and negative correlations, separated by threshold cicada densities. The observation of an interaction threshold raises additional questions regarding the relationship between cicadas and their host trees. Future studies will be necessary to understand how multiple types of interactions could combine to create an interaction threshold. For example, the observed relationship between tree growth and cicada density could result if host trees are able to compensate for the costs of cicada herbivory at low densities. Some long-lived plants are able to effectively compensate for low levels of chronic herbivory. For example, Seastedt et al. (1983) found that low levels of canopy consumption did not detectably reduce the productivity of black locust (*Robinia pseudoacacia*) and red maple (*Acer rubrum*) trees.

The implications of this work are twofold. First, the observation that chronic cicada herbivory reduces tree

growth rates at high densities supports previous calls for caution in the reconstruction of climatic histories based on dendrochronological records under the assumption of an overriding abiotic signal (Morrow and LaMarche 1978; Trotter et al. 2002). Herbivores as numerous as periodical cicadas can also be important drivers of tree growth and possibly other ecosystem processes. These findings suggest that the preferential distribution of cicadas on fast-growing host trees may have an equalizing effect on tree growth rates within a local site. By preferentially ovipositing at high densities along sunlit forest edges, chronic cicada herbivory may slow the expansion of forest fragments within the cicada range.

More broadly, this study reflects the inherent difficulty of measuring the effects of an ecological stressor when the incidence of the stressor is itself related to variation in individual quality. In many plant-herbivore interactions, for example, the incidence of herbivory reflects variation in the quality of host plants (e.g., Price 1991). Similar issues are relevant to the study of optimal clutch sizes in birds, where the quality of the parental pair can determine their individual optimal clutch size (Pettifor et al. 2001). The reciprocal interaction between individual quality and the level of the stressor presents a common ecological motif represented in both of these examples. However, this study demonstrates that observed, retrospective patterns in natural systems can yield useful insights into the relative importance of multiple ecological processes even in systems that present obstacles for direct manipulation.

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Literature Cited

- Banta, E. S. 1960. Apple orchard decline. *Proceedings of the Ohio State Horticultural Society* 118:88–90.

- Beamer, R. 1928. Studies of the Kansas Cicadidae. *University of Kansas Science Bulletin* 18:155–230.
- Brown, J. J., and G. M. Chippendale. 1973. Nature and fate of the nutrient reserves of the periodical (17 year) cicada. *Journal of Insect Physiology* 19:607–614.
- Cole, W. G., and C. G. Lorimer. 1994. Predicting tree growth from crown variables in managed northern hardwood stands. *Forest Ecology and Management* 67:159–175.
- Cook, W. M., and R. D. Holt. 2002. Periodical cicada (*Magicicada cassini*) oviposition damage: visually impressive yet dynamically irrelevant. *American Midland Naturalist* 147:214–224.
- Cook, W. M., R. D. Holt, and J. Yao. 2001. Spatial variability in oviposition damage by periodical cicadas in a fragmented landscape. *Oecologia* (Berlin) 127:51–61.
- Doak, D. F. 1992. Lifetime impacts of herbivory for a perennial plant. *Ecology* 73:2086–2099.
- Dybas, H. S., and D. D. Davis. 1962. A population census of seventeen-year periodical cicadas (Homoptera: Cicadidae: *Magicicada*). *Ecology* 43:432–444.
- Fritts, H. C. 1976. *Tree rings and climate*. Academic Press, London.
- Grissino-Mayer, H. D. 2003. A manual and tutorial for the proper use of an increment borer. *Tree-Ring Research* 59:63–79.
- Hamilton, D. 1961. Periodical cicadas, *Magicicada* spp., as pests in apple orchards. *Proceedings of the Indiana Academy of Science* 71:116–121.
- Hamilton, D., and M. Cleveland. 1964. Periodical cicadas in 1963, brood 23. *Proceedings of the Indiana Academy of Science* 73:167–170.
- Hunter, M. D. 2001. Out of sight, out of mind: the impacts of root-feeding insects in natural and managed systems. *Agricultural and Forest Entomology* 3:3–9.
- Karban, R. 1980. Periodical cicada nymphs impose periodical oak tree wood accumulation. *Nature* 287:326–327.
- . 1982. Experimental removal of 17-year cicada nymphs and growth of apple trees. *Journal of the New York Entomological Society* 90:74–81.
- . 1983. Sexual selection, body size and sex-related mortality in the cicada *Magicicada cassini*. *American Midland Naturalist* 109:324–330.
- . 1984. Opposite density effects of nymphal and adult mortality for periodical cicadas. *Ecology* 65:1656–1661.
- Koenig, W. D., and A. M. Liebhold. 2003. Regional impacts of periodical cicadas on oak radial increment. *Canadian Journal of Forest Research* 33:1084–1089.
- Maier, C. T. 1980. A moleseye view of 17-year periodical cicada nymphs, *Magicicada septendecim* (Hemiptera, Homoptera, Cicadidae). *Annals of the Entomological Society of America* 73:147–152.
- Marlatt, C. L. 1907. The periodical cicada. *Bulletin of the USDA Bureau of Entomology* 71:1–181.
- McDonald, R. I., and D. L. Urban. 2004. Forest edges and tree growth rates in the North Carolina Piedmont. *Ecology* 85:2258–2266.
- Morrow, P. A., and V. C. LaMarche. 1978. Tree ring evidence for chronic insect suppression of productivity in subalpine *Eucalyptus*. *Science* 201:1244–1246.
- Naidu, S. L., and E. H. Delucia. 1997. Growth, allocation and water relations of shade-grown *Quercus rubra* L. saplings exposed to a late-season canopy gap. *Annals of Botany* 80:335–344.
- Pettifor, R. A., C. M. Perrins, and R. H. McCleery. 2001. The individual optimization of fitness: variation in reproductive output,

- including clutch size, mean nestling mass and offspring recruitment, in manipulated broods of great tits *Parus major*. *Journal of Animal Ecology* 70:62–79.
- Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62:244–251.
- . 1994. Phylogenetic constraints, adaptive syndromes, and emergent properties: from individuals to population dynamics. *Researches on Population Ecology* 36:3–14.
- Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67–92 in R. L. Burgess and D. M. Sharpe, eds. *Forest island dynamics in man-dominated landscapes*. Springer, New York.
- Rodenhouse, N. L., P. J. Bohlen, and G. W. Barrett. 1997. Effects of woodland shape on the spatial distribution and density of 17-year periodical cicadas (Homoptera: Cicadidae). *American Midland Naturalist* 137:124–135.
- Seastedt, T. R., D. A. Crossley, and W. W. Hargrove. 1983. The effects of low-level consumption by canopy arthropods on the growth and nutrient dynamics of black locust and red maple trees in the southern Appalachians. *Ecology* 64:1040–1048.
- Stokes, M. A., and T. L. Smiley. 1968. *An introduction to tree-ring dating*. University of Chicago Press, Chicago.
- Trotter, R. T., N. S. Cobb, and T. G. Whitham. 2002. Herbivory, plant resistance, and climate in the tree ring record: interactions distort climatic reconstructions. *Proceedings of the National Academy of Sciences of the USA* 99:10197–10202.
- Whiles, M. R., M. A. Callahan, C. K. Meyer, B. L. Brock, and R. E. Charlton. 2001. Emergence of periodical cicadas (*Magicicada cassini*) from a Kansas riparian forest: densities, biomass and nitrogen flux. *American Midland Naturalist* 145:176–187.
- White, J. 1980. Resource partitioning by ovipositing cicadas. *American Naturalist* 115:1–28.
- White, J., and M. Lloyd. 1975. Growth rates of 17-year and 13-year periodical cicadas. *American Midland Naturalist* 94:127–143.
- . 1985. Effect of habitat on size of nymphs in periodical cicadas (Homoptera, Cicadidae, *Magicicada* spp.). *Journal of the Kansas Entomological Society* 58:605–610.
- White, J., and C. E. Strehl. 1978. Xylem feeding by periodical cicada nymphs on tree roots. *Ecological Entomology* 3:323–327.
- White, J., M. Lloyd, and J. H. Zar. 1979. Faulty eclosion in crowded suburban periodical cicadas: populations out of control. *Ecology* 60:305–315.
- Williams, K. S., and C. Simon. 1995. The ecology, behavior, and evolution of periodical cicadas. *Annual Review of Entomology* 40:269–295.
- Williams, K. S., K. G. Smith, and F. M. Stephen. 1993. Emergence of 13-year periodical cicadas (Cicadidae, *Magicicada*): phenology, mortality, and predator satiation. *Ecology* 74:1143–1152.
- Yang, L. H. 2004. Periodical cicadas as resource pulses in North American forests. *Science* 306:1565–1567.
- . 2006. Periodical cicadas use light for oviposition site selection. *Proceedings of the Royal Society B: Biological Sciences* 273:2993–3000.

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An adult 17-year periodical cicada prepares for its first flight. Photograph by Louie Yang.