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# Periodical Cicada (Magicicada cassini) Oviposition Damage: Visually Impressive yet Dynamically Irrelevant

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ABSTRACT.—Selective herbivory by animals can have significant effects on the succession of a plant community. Damage resulting from major insect outbreaks has been shown to alter species dominance and competitive balance of woody plants in temperate North America. In this study we examine the effects over three seasons of a visually striking herbivory event: periodical cicada (*Magicicada cassini*) oviposition into an early successional tree community in the prairie-forest ecotone in eastern Kansas. Oviposition damage during cicada emergence in 1998 was large in overall magnitude, highly variable in space and varied by host tree species. From 1998–2000 we monitored four measures of tree growth on individuals of each tree species on the study site, and infructescence production on the dominant species (rough leaved dogwood, *Cornus drummondii*). Cicada damage in 1998 was regressed against each measure of tree performance in following years. Only a few statistically significant results were found. Overall, we concluded that the widespread oviposition damage from periodical cicadas did not have any important effects on successional dynamics of the host plants, suggesting that the trees appeared to compensate sufficiently for physiological damage during the emergence. We suggest that documenting the absence of substantial impacts from episodes of herbivory is useful in gauging the general significance of herbivory in succession.

## INTRODUCTION

In many ecosystems, selective herbivory can lead to important changes in plant community dynamics (Crawley, 1983; Samson *et al.*, 1992). Highly dynamic communities, such as those undergoing secondary succession, appear to be notably sensitive to herbivory (Weltzin *et al.*, 1997; Ostfeld *et al.*, 1997; Schweiger, 1998). Recently, we (Cook *et al.*, 2001) documented spatial variation in oviposition damage on tree saplings by the periodical cicada (*Magicicada cassini*) in 1998 in an old field undergoing succession. The overall damage was extensive, with >87% of sampled individuals being attacked, often heavily. We suggested that this dramatic episode of insect herbivory could affect tree community dynamics. In this paper we evaluate the impacts of cicada emergence on tree community dynamics by documenting inter- and intraspecific changes in individual growth rates over the next 2 y, and variation in reproductive output for the dominant tree species, rough-leaved dogwood (*Cornus drummondii*).

Major insect outbreaks can have important effects on plant communities. In the eastern United States the introduced gypsy moth (*Lymantria dispar*) attacks many tree species and in outbreak years can defoliate large areas (Williams *et al.*, 1991). The spruce budworm (*Choristoneura fumiferana*) exhibits population explosions in coniferous forests of North America, leading to damage sufficient to be considered a major pest species. Budworm outbreaks damage spruce and so help maintain dominance by fir (Zoladeski and Maycock, 1990), and also indirectly increase understory plant diversity (De Grandpre and Bergeron,

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1997). Plants may often be able to compensate for herbivory damage within a growing season, but changes in fitness in long-lived species may not be detectable until years later (Sacchi and Connor, 1999). Due to their great numbers and concentrated emergences, periodical cicadas could have comparable effects on the plant community. In this study we investigated whether differential herbivory by periodical cicadas decreases dominance by a heavily damaged tree species over three growing seasons subsequent to the pulse of emergence.

*Potential cicada effects.*—Periodical cicadas impose energetic drains on trees by several modes of resource exploitation. After mating, females create linear series of conspicuous slits for oviposition on the underside of small tree branches (Miller and Crowley, 1998). The branch portion distal to the slits quickly loses its leaves and the end may droop [a phenomenon called ''flagging'' (Williams and Simon, 1995)]. Repair requires the plant to use resources otherwise available for growth and reproduction; slits placed in larger branches also allow entry to pathogens (Anderson *et al.*, 1979). Oviposition by the nonperiodical Apache cicada (*Diceroprocta apache*) has been reported to affect agricultural crop yields (Elmer, 1964); and periodical cicadas can have effects on tree architecture that may not be conspicuous until following years and may also stunt growth or flowering (Smith and Linderman, 1974). Nymphs live underground for up to 17 y, extracting nutrients from tree root xylem. The tremendous density of cicadas could cumulatively impose a substantial belowground herbivore load on host plants (White and Strehl, 1978). Periodical and nonperiodical cicada nymphs have been shown to affect host plant growth (Karban, 1980; White and Sedcole, 1993) and could potentially reduce an individual tree's capacity for reproduction (although not necessarily, *see* Karban, 1985). Although adult cicadas feed by sucking plant fluids, the long-term impact of oviposition is likely to exceed greatly that of adult feeding, and the impacts of nymphal feeding should be even greater (Williams and Simon, 1995).

*The 1998 emergence.*—In June 1998 a population of periodical cicadas (*Magicicada cassini*) invaded a successional tree community at an experimentally fragmented study site in eastern Kansas (Cook *et al.*, 2001), having emerged in an adjacent woodland. The study site is presently dominated by early successional tree species, which show strong spatial patterns in occurrence and density. These patterns are correlated with fragment area and distance to source pools (Yao *et al.*, 1999). Oviposition by cicadas inflicted conspicuous damage on nearly all of the tree species present at the site, with heavier damage per stem on large habitat patches, on patches near to the forest, and on trees in less dense stands.

Because the dominant early successional tree species (rough-leaved dogwood, *Cornus drummondii*) was disproportionally damaged by the cicadas (by some measures, experiencing up to 5 times the levels of damage of other, later successional species), in the previous paper we hypothesized that this could lead to changes in the successional trajectory at the study site. The present paper investigates the possibility that 1998 cicada damage suppressed the subsequent growth or reproduction of trees, or indirectly increased growth by triggering compensatory mechanisms. The design of our ongoing study will also permit assessment of even longer-term damage in the coming years (*e.g.*, due to nymphal feeding).

*Hypotheses.*—We hypothesized that the magnitude of damage inflicted on a stem by cicadas in 1998 on each tree species would be inversely related to the growth and reproductive performance of that individual in following seasons. In particular, we predicted that: (1) Growth in height of the host species would be inversely related to the amount of damage inflicted during emergence. If trees had sufficient stored reserves to grow unimpeded during the season of the emergence, differences in damage could nonetheless be reflected in differential growth in subsequent years. (2) Fruit production (infructescences) in dogwoods would be inversely proportional to the amount of damage inflicted in 1998. As flowering was already in progress during the cicada emergence, we considered the possibility that differences in performance might not be observed until the following years. (3) At the community level, we expected to find statistical relationships between cicada damage and tree performance in the most damaged species in the community (dogwood) and not in the other host species with light herbivory. There is often a correlation between successional status and vulnerability to herbivory, and rough-leaved dogwood is one of the first woody colonizers of successional habitats in our region. Thus, we expected a more significant statistical relationship between oviposition damage and growth in dogwood than in other tree species.

If the above hypotheses are correct, this would indicate that differential oviposition damage by cicadas in 1998 is leading to changes in plant community dynamics. Additionally, there has been considerable debate over the mechanisms by which plants compensate for herbivory damage (McNaughton, 1983; Trumble *et al.*, 1993; Belsky *et al.*, 1993; Agrawal, 2000). If we were to observe significant negative relationships between 1998 cicada damage and tree growth and fecundity, this would suggest that the plants are not compensating. By contrast, absence of effects suggests the potential action of compensatory mechanisms.

## METHODS

*Study site.*—Data for this study were collected at the Kansas Fragmentation Study, located in the Nelson Environmental Study Area, Kansas Field Station and Ecological Reserves, in southern Jefferson County, Kansas. The study site, initiated in 1984, was designed to examine the impacts of patch size and landscape position on succession (Robinson *et al.*, 1992; Holt *et al.*, 1995; Schweiger *et al.*, 2000). Currently, the site is dominated by small rapidly maturing trees (rough-leaved dogwood, *Cornus drummondii*; slippery elm, *Ulmus rubra*; eastern red cedar, *Juniperus virginiana*; ash, *Fraxinus* sp.; box elder, *Acer negundo*; honey locust, *Gleditsia triacanthos*; smooth sumac, *Rhus glabra*). By the late 1990s dogwood comprised the large majority (over 93%) of individual trees (Yao *et al.*, 1999).

*Study design.*—In 1998, before the periodical cicada emergence, potential host trees of each available species were selected from (at that time) a set of nearly 4000 individually marked and monitored stems. To assess spatial variability in oviposition damage we used a 3-way factorial design, based on three variables: patch size, distance to the nearest forest and local stem density. We stratified our sampling to ensure, wherever possible, equal sample sizes for each (area) × (distance) × (density) class (*see* Cook *et al.*, 2001 for a complete description). Sample sizes varied greatly by host species, and a complete spatial analysis was possible only for dogwood. Most individual trees were located in permanent plant quadrats, allowing precise estimates of local stem density, but to increase the sample sizes of species other than dogwood we included individuals of those species from outside the quadrats. Because of this, some trees in the sample did not have available estimates of local stem density. Two indices of cicada oviposition damage were measured in Nov. 1998: mean slit damage (the average proportion of the outer 50 cm damaged on the farthest emergent branch in each cardinal direction) and flag damage (total number of flagged twigs observed, normalized by the tree's crown volume). Crown volume was estimated in 1998 by multiplying tree height by measurements of maximal crown width in the N-S and E-W directions.

Tree heights and base diameters (DAB) were measured for each individual tree during the summers of 1998, 1999 and 2000. From these data, changes in height, % height, DAB and % DAB were calculated for the 1998 to 1999 and 1998 to 2000 time periods. For each tree species both damage indices were plotted against growth for the two periods, and

TABLE 1.—Slopes of regression between 1998 cicada damage and tree growth between 1998 and 1999, and 1998 and 2000. HT = Growth in height. HT% = % Growth in height. DAB = Growth in DAB. DAB% = % Growth in DAB. '+' = Significant positive regression slope at $\alpha = 0.05$. '−' = significant negative regression slope at $\alpha = 0.05$. '0' = No significant regression slope at $\alpha = 0.05$. 'NA' = No test due to missing data

| | | Flag damage | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1998–1999 | | | | 1998–2000 | | | |
| Species | N | HT | HT% | DAB | DAB% | HT | HT% | DAB | DAB% |
| Dogwood | 198 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Box elder | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ash | 18 | 0 | 0 | NA | NA | 0 | 0 | NA | NA |
| Honey locust | 9 | 0 | 0 | NA | NA | 0 | 0 | NA | NA |
| Red cedar | 36 | 0 | 0 | 0 | 0 | + | + | 0 | 0 |
| Slippery elm | 22 | — | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | Slit damage | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1998–1999 | | | | 1998–2000 | | | |
| Species | N | HT | HT% | DAB | DAB% | HT | HT% | DAB | DAB% |
| Dogwood | 198 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 |
| Box elder | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ash | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Honey locust | 9 | 0 | 0 | NA | NA | 0 | 0 | NA | NA |
| Red cedar | 36 | 0 | 0 | NA | NA | 0 | 0 | NA | NA |
| Slippery elm | 22 | 0 | 0 | 0 | 0 | + | + | 0 | 0 |

regressions of growth on damage were calculated for each pairing. For dogwoods, the number of fruit clusters (infructescences) produced by a sample of 138 trees was counted in the autumns of 1998, 1999 and 2000. These data were compared to both measures of the 1998 cicada damage. Because local stem density has been demonstrated to have significant effects on both dogwood growth and survival, and on the likelihood of colonization by periodical cicadas at our site (Cook *et al.*, 2001; Yao, 2001), we also examined potential confounding stem density effects in two ways. For dogwoods, we ran multiple regressions on height change, % height change, DAB change and % DAB change with local stem density and each damage measure as the predictor variables. For the other host species (which did not have sufficient sample sizes for multiple regressions), we regressed growth on cicada damage separately for each stem density class in all cases where growth and damage had significant regression slopes.

## RESULTS

Overall, most analyses failed to show statistical relationships between cicada damage in 1998 and tree performance in following years.

*Tree growth following cicada damage.*—Cicada damage measures had very few significant statistical relationships with either total growth in height or % growth in height for host tree species. Growth in height and % growth in height in dogwood, the dominant tree species in the community, had essentially no relationship with either measure of cicada damage in 1998 (Table 1, Fig. 1). Multiple regressions of stem density and cicada damage on dogwood growth in height and % growth in height revealed no slopes significantly

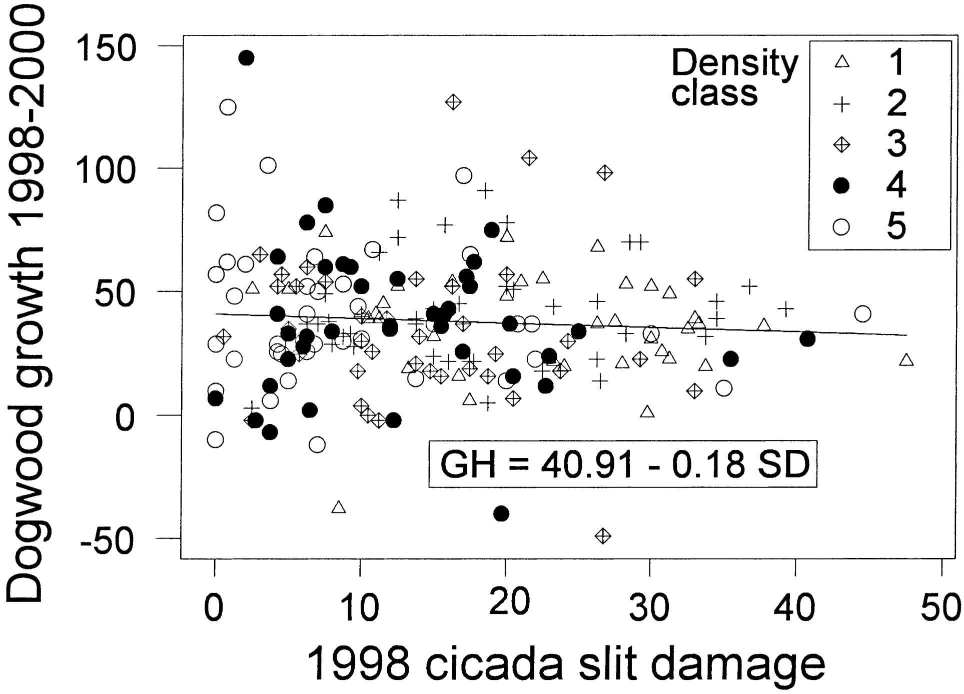

FIG. 1.—Linear regression of dogwood growth in height (cm) from 1998–2000 as a function of 1998 cicada slit damage (average damage per 50 cm of branch). Symbols indicate local stem density class (1 = 1–2 stems >2 m per 4 × 4 quadrat; 2 = 3–5 stems; 3 = 6–10 stems; 4 = 11–15 stems; 5 = >15 stems), although regression includes all data points. For regression, GH = mean growth in height (cm), adjusted by a linear term proportional to cicada slit damage (SD). Note: change in tree height may be negative due to storm damage and other physical stresses

different from zero, and no multiple regression explained more than 4% of variation in the data.

There were only two statistically significant relationships between 1998 cicada damage and growth in tree height (*see* Table 1). Red cedar growth (1998–2000) was positively associated with 1998 flag damage (positive regression slope, $P = 0.045$; *see* Fig. 2), and elm growth (1998–1999) was negatively associated with 1998 flag damage (negative regression slope, $P = 0.020$; *see* Fig. 3). However, the association of red cedar growth and flag damage was confounded with local stem density; cedar growth in the lowest stem density class (1–2 stems per 4 m$^2$) had a positive relationship with flag damage ($N = 14$, positive regression slope, $P < 0.02$), whereas cedars in the other density classes showed no significant association ($N = 18$, positive regression slope, $P = 0.30$). Cedars in the lowest damage class grew slightly more than those in the other damage classes [1998–2000 *t*-test $P = 0.21$ (ns)]. The association of elm growth and cicada damage was also confounded by density. Whereas flag damage did not significantly interact with stem density for elms during cicada colonization in 1998, 1998–1999 growth of elms in the highest density class had a significant negative relationship with flag damage ($N = 15$, negative regression slope, $P = 0.046$), whereas elms in the other classes had no such relationship ($N = 5$, negative regression slope, $P = 0.945$). Cicada flag damage had a positive relationship with 1998–2000% growth in height in red

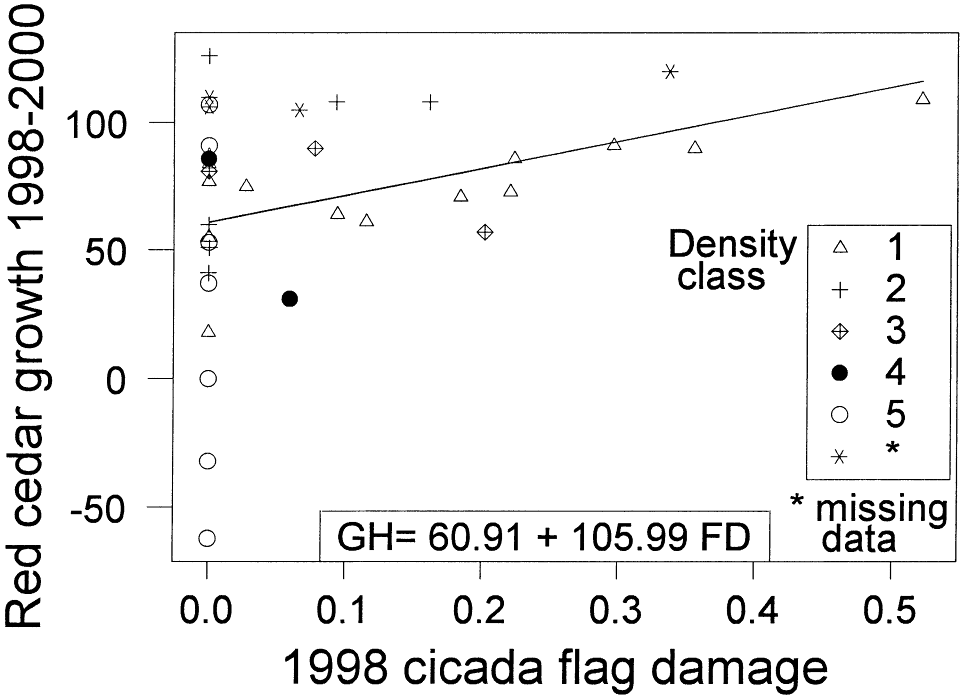

FIG. 2.—Linear regression of red cedar growth in height (cm) from 1998–2000 on 1998 cicada flag damage (number of flags per cu m crown volume). Symbols indicate local stem density class (1 = 1–2 stems >2 m per 4 × 4 quadrat; 2 = 3–5 stems; 3 = 6–10 stems; 4 = 11–15 stems; 5 = >15 stems, * = missing data), although regression includes all data points. For regression, GH = mean growth in height (cm), adjusted by a linear term proportional to cicada flag damage (FD). Note: change in tree height may be negative due to storm damage and other physical stresses

cedars (positive regression slope, P = 0.030), the same pattern observed for growth in height for that year, and cicada slit damage also had a positive association with 1998–1999 honey locust % growth (positive regression slope, P = 0.028). However, there were not sufficient estimates of local stem density for honey locust to investigate potential confounding effects.

Dogwood DAB growth (1998–2000) had a significant *positive* relationship with cicada slit damage, in contrast to our hypotheses (*see* Table 1). However, this association explained less than 4% of variation in the data, and no multiple regression including local stem density and any density-cicada damage interaction for any time period had a statistically significant slope. There were three significant relationships between cicada damage and DAB growth or % DAB growth in other species (ash and honey locust lacked sufficient sample sizes for this analysis): a significant negative relationship between 1998–2000% DAB growth and 1998 slit damage in box elders (negative regression slope, P = 0.037), and positive relationships between slit damage and both 1998–1999 and 1998–2000 DAB growth in elms (positive regression slopes, P = 0.017 and P = 0.009, respectively). All of the sampled box elders were in the highest density class, so we were unable to investigate confounding effects of local stem density in that species. Elms in the highest stem density class (N = 15) had lower DAB growth than elms in the other density classes (N = 6) from 1998–2000 (*t*-test, P =

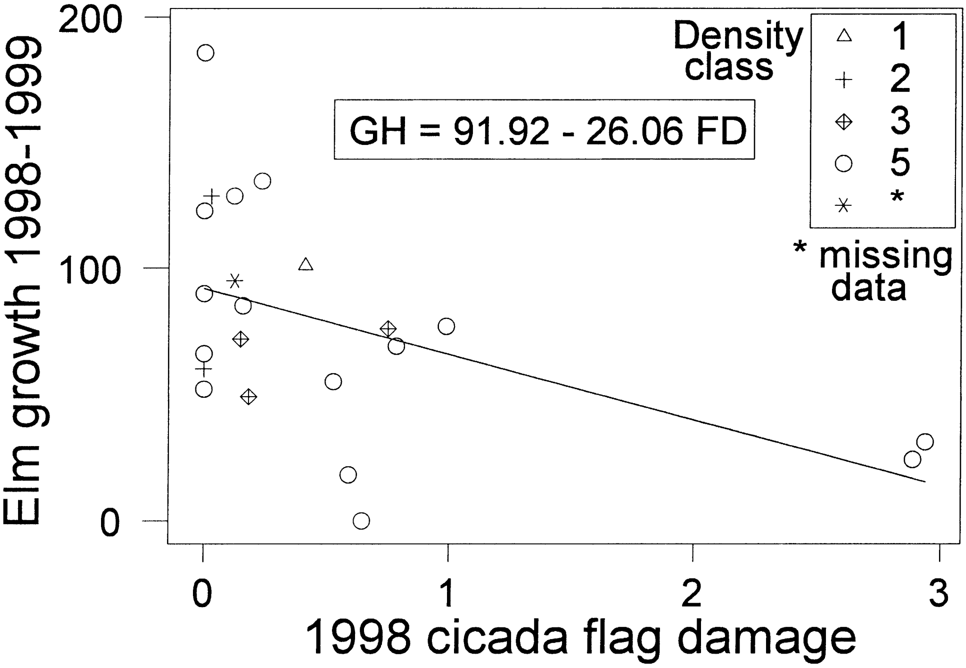

FIG. 3.—Linear regression of slippery elm growth in height (cm) from 1998–1999 on 1998 cicada flag damage (number of flags per cu m crown volume). Symbols indicate local stem density class (1 = 1–2 stems >2 m per 4 × 4 quadrat; 2 = 3–5 stems; 3 = 6–10 stems; 4 = 11–15 stems; 5 = >15 stems, * = missing data), although regression includes all data points. For regression, GH = mean growth in height (cm), adjusted by a linear term proportional to cicada flag damage (FD). Note: change in tree height may be negative due to storm damage and other physical stresses

0.039), and from 1998–1999 (*t*-test, P = 0.036). Within that highest density class, there was no statistical association between DAB growth and 1998 slit damage from 1998–1999 (positive regression slope, P = 0.440) or from 1998–2000 (positive regression slope, P = 0.440).

*Dogwood fruiting following cicada damage.*—There were no significant relationships between infructescence production by dogwoods in any year and either measure of cicada damage in 1998. Each set of fruiting data was distributed in a highly nonnormal and nonlinear fashion, and plots of 1998 damage vs. fruiting either depict a wide scatter in 1998 and 1999 (*see* Fig. 4) or a tight cluster of low fruiting points surrounded by wide-flung outliers in 2000. There was a mild drought in 2000, so fruit production overall was depressed that year. Given the lack of pattern, formal statistics do not seem appropriate due to the violation of many distributional assumptions. The average infructescence production varied widely between years, likely as a result of local climatic fluctuations, but within-year comparisons failed to show any significant patterns that could be attributed to cicada oviposition damage.

## DISCUSSION

The patterns of growth and reproduction in the tree community did not, in general, reveal the hypothesized relationships between cicada oviposition and tree growth and fecundity.

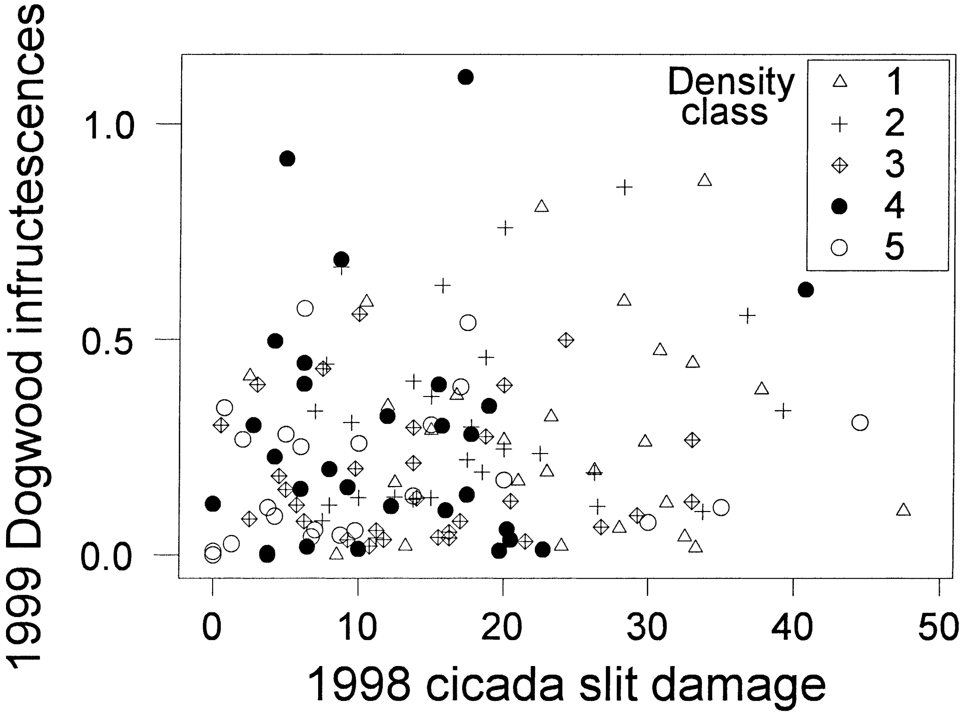

FIG. 4.—Dogwood infructescences/crown volume in 1999 as a function of 1998 cicada slit damage (average damage per 50 cm of branch). Separated by local stem density class (1 = 1–2 stems >2 m per 4 × 4 quadrat; 2 = 3–5 stems; 3 = 6–10 stems; 4 = 11–15 stems; 5 = >15 stems)

*Effects on dogwood growth.*—Whereas the oviposition damage to dogwood, the dominant tree in the community, was extensive and visually impressive (Cook *et al.*, 2001), there was no meaningful resulting statistical association between 1998 cicada damage and either growth or reproduction in dogwoods between 1998 and 2000. The one statistically significant association between dogwood DAB growth and cicada slit damage we observed appears on closer inspection to be a masked effect of stem density and the covariation of damage and density. This general finding is consistent with the conclusions of Miller (1997) and Miller and Crowley (1998), who observed in urban woodlots and arboretums that oviposition damage by periodical cicadas resulted in significant pruning of the affected trees, but did not have lasting effects on the trees' fitness. Our results reveal a similar pattern for trees in a more natural setting, surrounded by competitors, where one might have expected an intensification of impacts from oviposition damage.

*Effects on growth of other species.*—Cicada oviposition damage did have significant associations with measures of growth in some less dominant tree species: red cedar, slippery elm and honey locust. Most of these associations, however, were confounded by variation in local stem density, indicating that some of these trends are primarily effects of the original spatial variation in cicada oviposition or tree location correlated with tree density (*see* Cook *et al.*, 2001). Increased growth by red cedars with flag damage was observed primarily in trees with low local stem densities. As cedars were damaged at lower rates than any other affected species, it seems unlikely that cicada damage was primarily responsible for spurring increases in growth. Nevertheless, the linear increase in growth of low-density cedars with cicada flag damage from 1998 to 2000 is intriguing, and could suggest that cicada damage indeed spurred compensatory growth in those individuals.

The 1998–1999 decrease in growth with 1998 flag damage by elms in dense stands is consistent with other observations at the site; elms are attacked heavily by both small and large mammals, and this appears to impede their growth (Schweiger, 1998). If resource limitation is more severe in dense stands, it is to be expected that damaged trees would have more difficulty displaying compensatory growth. However, the positive association of both 1998–1999 and 1998–2000 DAB growth with 1998 slit damage in elms counters that suggestion. Regardless, these trends may be better explained by greater growth of elms under conditions of low competition or statistical flukes due to low sample size. Most of these (contradictory) effects on elms were observed in only one sample year.

Cicada slit damage was positively associated with % growth in height in 1998–1999 in honey locusts, a pattern which may be consistent with the possibility of physiological compensation. Yet we were unable to explore confounding effects of stem density in that case because the relationship is based on a small sample size and, moreover, it was not observed in 2000. Cicada slit damage was negatively associated with 1998–2000 % DAB growth in box elders, unconfounded by density effects; this may be evidence that growth was impeded by cicada damage for box elder. However, the biological relevance of each of these results is put in question by at least one of these concerns, such as the lack of similar trends with a second damage estimator or the appearance of the trend in only one of the sampling years or small sample sizes. As most results shown in Table 1 were null, there was little evidence overall that either dogwood growth, or that of any of the secondary species in the community, was strongly associated with 1998 cicada damage.

*Effects on dogwood fruiting.*—Although the average dogwood infructescence production varied tremendously between years, there is no statistical evidence that fruiting was associated with 1998 cicada damage in any year. We had hypothesized that the oviposition damage would lead to selective allocation of plant resources away from fruiting to other needs such as compensatory growth, but this hypothesis was not borne out by the third reproductive season after the cicada emergence.

Overall, there is only weak (or no) evidence that oviposition damage inflicted on the site's tree community in 1998 caused any shifts in population or community successional trajectories by 2000. The dominant tree species, dogwood, was not demonstrably affected in either growth or reproductive output, indicating that the conspicuous (and disproportionate) damage to that species was below the threshold where it significantly affected the species' fitness. There were some suggestions in our results that growth of other species (red cedar, elm, box elder, honey locust) was affected, but no pattern is clear. Our first hypothesis stated that host tree growth would be inversely related to 1998 cicada damage; in most cases there was no statistical relationship, and there were more positive than negative statistical associations. Our second hypothesis predicted an inverse relationship between dogwood fruit production and 1998 cicada damage; there was no evidence of any biologically meaningful relationship. Finally, we predicted a stronger statistically negative relationship between growth and cicada damage in dogwood than in other tree species; if anything, there were weaker effects on dogwood. With respect to our original hypotheses, it seems unlikely that changes in tree community dynamics will occur as a direct result of periodical cicada ovipositional damage.

*Implications.*—The study of tree demography at this site is ongoing, and it is conceivable that impacts of oviposition damage from the 1998 cicada emergence will loom larger over time. However, we would not predict this outcome, given the results reported here. By contrast, previous studies have observed effects of below-ground herbivory by cicada nymphs on plant growth, physiology and fecundity (Karban, 1980; Karban, 1985; Powell and Myers, 1988; Gange and Brown, 1989; White and Sedcole, 1993; Masters and Brown, 1995). Future work at the study site may yet reveal differences in tree growth or reproduction or changes in successional trajectory attributable to spatial variation in nymphal cohorts established in 1998.

There is a traditional bias against the publication of null or negative results. The recent growth of interest in meta-analysis as a tool for discerning broad patterns among sites or systems has highlighted the importance of documentation of well-corroborated negative results (Gurevitch and Hedges, 1999; Osenberg *et al.*, 1999; Gurevitch *et al.*, 2000; Palmer, 2000). As noted in the introduction, understanding the importance of herbivory on successional dynamics is an important challenge. Documenting the absence of effects of apparent oviposition damage in our successional system indicates that herbivory is not necessarily a force that always drives secondary succession.

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