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Permalink

https://escholarship.org/uc/item/1k95s1tp

Journal

Ecology, 100(6)

ISSN

0012-9658

Authors

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Publication Date

2019-06-01

DOI

10.1002/ecy.2705

Supplemental Material

https://escholarship.org/uc/item/1k95s1tp#supplemental

Running head: Cicadas increase tree growth

The effects of pulsed fertilization and chronic herbivory by periodical cicadas on tree growth

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Abstract

While many studies have investigated plant growth in the context of episodic herbivory and pressed resource availability, relatively few have examined how plant growth is affected by pulsed resources and chronic herbivory. Periodical cicadas (*Magicicada* spp.) adults represent a pulsed detrital subsidy that fertilizes plants, while live cicada nymphs are long-lived root-feeding herbivores. Previous studies of cicada herbivory effects have been inconclusive, and previous studies of cicada-mediated fertilization did not examine effects on trees, or on a multi-year timescale. Here we describe the results of a three-year experiment that factorially manipulated the presence and absence of cicada fertilization and herbivory in a population of 100 American sycamore (*Platanus occidentalis*) trees. We found that cicada fertilization strongly increased tree growth in the year of emergence, creating differences in tree size that persisted at least two years later. By comparison, we did not detect reductions in tree growth associated with cicada herbivory in any year of this experiment. However, cicada herbivory reduced the densities of, and damage from, other aboveground herbivores. These results suggest that cicadas affect the size structure of forests over multiple years, and raise questions about how cicada-mediated fertilization and herbivory will affect tree growth over longer timescales.

Keywords: resource pulses, pulsed detrital subsidy, chronic belowground herbivory, periodical cicadas, *Magicicada* spp., tree growth, root herbivores, pulsed fertilization, temporally explicit ecology, absolute and relative growth rates, amplification, attenuation

Introduction

Both resource limitation and herbivory can limit plant growth (e.g., Hawkes and Sullivan 2001). While many studies have documented these effects, most studies investigate systems in which herbivory is pulsed (episodic) and resource availability is pressed (continuous). Experimental studies often manipulate herbivory in episodic bouts that mimic herbivore damage consistent with population outbreaks, seasonal dynamics or other transient phenomena (Zvereva et al. 2012) while assuming that nutrient availability is a relatively constant characteristic determined by edaphic factors, and unlikely to change on an experimental timescale. While the paradigm of pulsed herbivory and pressed nutrient resources is common, examples of the converse - chronic herbivory and pulsed resources - are also widespread. Terrestrial plants are actually more likely to experience low levels of chronic herbivory as opposed to episodic bouts of severe herbivory (Cyr and Pace 1993), and even low levels of background herbivory can strongly affect plant growth (Zvereva et al. 2012) and reproduction (Mueller et al. 2005) over longer timescales. Likewise, the belowground nutrient resources available to plants are often highly dynamic on multiple timescales (Bardgett et al. 2005), and often show episodic pulses as a result of inputs from the aboveground community or changing abiotic conditions (Yang et al. 2010). However, few studies have experimentally examined the combined consequences of pulsed resources and pressed herbivory on plant growth.

Periodical cicadas present a natural context in which to examine questions about pulsed resources and chronic herbivory. Periodical cicadas are among the most abundant herbivores of deciduous trees in North America both in terms of numbers and biomass, with emergence densities as high as 372 cicadas per m^2 in continuous floodplain forests and 579 cicadas per m^2 in fertilized landscapes (Dybas and Davis 1962, Karban 2014). The species with more northern ranges develop belowground for 17 years before their emergence, while the species with more southern ranges develop for 13 years prior to emergence (Marlatt 1907, Williams and Simon 1995). During this prolonged development, cicada nymphs actively feed on xylem fluid from plant roots (White and Strehl 1978). After emergence, the adult stage lasts only 2-4 weeks (Marlatt 1907), and this ephemeral abundance of cicadas effectively satiates their potential predators in the aboveground community (Lloyd and Dybas 1966, Karban 1982a, Williams et al. 1993). As a consequence, most adult cicadas are not killed or consumed; instead, dead adults accumulate on the forest floor where their nutrients return to the rhizosphere as a detrital subsidy (Whiles et al. 2001, Yang 2004, 2006a)(Fig. 1a). In the late summer of the emergence year, the next generation of first instar cicadas hatches from eggs laid in trees (Fig. 1b), falls to the ground and begins digging to find suitable roots. Although this unusual natural history has been well-documented, the relationship between periodical cicadas and their host trees as herbivores and as resource pulses is not well-understood.

Because cicadas feed belowground, their role as herbivores is easy to overlook and difficult to measure. In an analysis of tree rings, Karban (1980) observed that 20 scrub oaks (*Quercus ilicifolia*) with cicada herbivory grew 30% less in the emergence year and in the four years that followed when compared with 15 scrub oaks growing without cicadas. However, a subsequent study examining the growth of 294 individual trees representing six species in the two years following the 1998 cicada emergence in Kansas did not find any significant relationship between tree growth and cicada oviposition density for four of the six species (Cook and Holt 2002). This study did find that the growth of red cedar (*Juniperus virginiana*) was positively correlated with cicada densities, and the growth of elm (*Ulmus rubra*) was negatively correlated with cicada oviposition densities, but both relationships were confounded with stem density. At a larger spatial scale, Koenig and Liebhold (2003) found that oak (*Quercus* spp.) trees in counties with emergences of cicadas grew 4% less during the emergence year when compared with trees in counties without emergences; this pattern was not observed for non-host pine (*Pinus* spp.) trees. More recently, in an analysis of tree rings from three host species (26 sugar maple, *Acer saccharum*; 26 tulip trees, *Liriodendron tulipifera*; and 30 American basswood, *Tilia americana*) from three sites in three years (Pennsylvania, USA in 2002; Virginia, USA in 2004; and Illinois, USA in 2007), Yang and Karban (2009) observed a consistent hump-shaped relationship between cicada emergence density and the mean annual growth rate over the preceding 17 years. This hump-shaped relationship was hypothesized to reflect the combined effects of two opposing processes: the region of positive correlation was probably caused by female cicadas preferentially ovipositing on faster growing trees, while the region of negative correlation reflected the accumulating cost of chronic herbivory (Yang and Karban 2009).

The differences in the conclusions of these observational studies are likely due to differences in methodology as much as biological differences between sites or species. For example, several studies indicate that cicada oviposition density is a poor predictor of cicada nymph densities, perhaps due to strong density dependence for young nymphs belowground (Karban 1984, 1985, Clay et al. 2009); this suggests that oviposition density may not provide a good quantitative measure of future nymphal herbivory. Moreover, the observation of potentially confounding factors (such as tree density, e.g. Cook and Holt 2002) and interacting processes (such as habitat selection, e.g. Yang and Karban 2009) limits our ability to assess the effects of cicada herbivory from purely observational studies. However, manipulative experiments to evaluate the effects of cicada nymphal herbivory on tree growth have also had mixed results. For example, the experimental removal of cicada nymphs from three apple trees (*Malus pumilia*) significantly increased radial tree growth relative to seven control trees, but replication in this experiment was low (Karban 1982b). In a subsequent experiment, the addition of cicada eggs failed to measurably affect acorn production or rootlet density in 10 scrub oak trees (*Quercus ilicifolia*) compared with 10 control trees (Karban 1985). An ambitious and well-replicated experiment that reduced cicada densities on three species of potential host trees (*Acer rubra*, *Cornus florida*, and *Cercis canadensis*) failed to show any effects of cicada herbivores on growth or reproduction in the emergence year or the years immediately following (Flory and Mattingly 2008). In summary, across both observational and experimental studies, the effects of feeding cicada nymphs on their host trees remain unclear.

Cicadas may also affect tree growth through pulsed fertilization resulting from the decomposition of adult carcasses in the emergence year. As nymphs, cicadas store resources in their collective biomass over time, and return these nutrients on the soil surface when they die. Previous work suggests that this pulse of nutrients can have important effects on forest ecosystems. Both bacterial and fungal biomasses increased in the soil within days after experimental subsidies of cicada carcasses (Yang 2004). Invertebrate decomposers also increased in abundance during this time (Yang 2006). The decomposition of cicada carcasses at realistic densities increased the availability of soil ammonium and nitrate by several fold during the emergence year (Yang 2004). This fertilization effect has been found to have consequences at higher trophic levels as well. Fertilized individuals of American bellflower (*Campanulastrum americanum*), a common herbaceous understory plant, grew larger, showed increased N concentrations in their leaves and produced larger seeds than controls that were not fertilized with cicada carcasses (Yang 2004, 2013). Mammalian herbivores preferred to feed on fertilized bellflowers relative to unfertilized controls and removed more biomass from the fertilized individuals (Yang 2008). However, the generality of these results, and particularly the effects of cicada fertilization on the growth of trees, is not currently known. Moveover, little is known about the combined and interactive effects of pulsed fertilization and chronic belowground herbivory.

The primary goal of this study was to experimentally evaluate the negative effects of root herbivory by periodical cicada nymphs and the positive effects of fertilization from the deposition of dead cicada bodies on the growth of forest trees. Specifically, we asked if belowground herbivory by early instar cicadas would reduce the height and diameter of American sycamore (*Platanus occidentalis*) trees during the emergence year and over the next two years. In a factorial design, we also asked whether subsidies of cicada bodies would increase tree growth in the emergence year and each of the following two years, and whether cicada fertilization and herbivory interact to affect tree growth. During the course of this experiment, we also quantified two unexpected herbivore outbreaks at our study site, and used these opportunities to examine the factorial effects of pulsed fertilization and chronic belowground herbivory on the magnitude of future aboveground herbivory by insects. We hypothesized that pulsed belowground fertilization would increase aboveground herbivory, while chronic belowground herbivory would decrease aboveground herbivory.

Methods

This experiment was conducted at the Kansas University Field Station (KUFS) near Lawrence (39.011346° N, 95.206254° W). This site is in the alluvial bottomlands north of the Kansas River. Prior to 1860, the site was forested but by the early part of the 20th century the land was cultivated (Fitch and McGregor 1956). Our experimental site was well within the range of Brood IV periodical cicadas, and cicadas were observed emerging on the field station property at the forested Suzanne Ecke McColl Nature Reserve approximately 3 km away in May 2015. Since our experimental site had been in cultivation for many decades, it supported no periodical cicadas prior to the start of the experiment.

We planted 100 bare-root American sycamore (*Platanus occidentalis*) seedlings (approximately 50 cm height from root crown to top) from the Kansas Forest Service (Kansas Forest Service, Conservation Tree Planting Program, Manhattan, KS) on April 29, 2014. We chose American sycamore for this study because it is fast-growing, hardy, and was originally present, although not dominant, at this site before it was converted to agriculture (Fitch and McGregor 1956). To reduce competition from grasses and other plants, we surrounded the seedlings with weed barrier fabric (Kansas Forest Service), covered with 15-20 cm of mulch. We planted 100 seedlings in four rows, separating trees by 5m. This distance is sufficient to isolate cicada nymphs introduced to specific trees (White and Lloyd 1975, Maier 1980). Grasses were mowed between the rows.

All of our trees survived throughout the experiment (Fig. 1c-d). We varied the presence of live cicada nymphs (i.e. “herbivory”) and the presence of dead cicada bodies (i.e., “fertilization”) in a 2x2 full factorial design, with 25 trees randomly assigned to each treatment group (herbivory only, fertilization only, herbivory and fertilization, and control).

We put dead adult cicada bodies below trees that were assigned to receive cicada fertilization. Live adult *M. cassini* cicadas were collected from Brood IV in Lawrence, KS on 27-28 May 2015. These individuals were frozen soon after being collected. We added 155g of dead cicadas (approximately 300 cicadas) to the soil surface in an area of approximately 1 m^2 beneath the canopy of each tree assigned to this treatment (Fig. 1a). This is within the range of cicada emergence and deposition densities that have been observed during natural emergence events (Williams and Simon 1995, Yang 2004).

We introduced live cicada nymphs to trees that were assigned to the herbivory treatment. Twigs of maples (*Acer* sp.), elms (*Ulmus* sp.) and redbuds (*Cercis canadensis*) containing cicada eggnest incisions were collected and introduced to their new host trees on 29 July 2015 and 7 August 2015, approximately six weeks following the peak of the mating and oviposition (Fig. 1b). The majority of cicada individuals at our study site were

M. cassini. These two dates were selected to bracket the time that first-instar nymphs hatch from their twig-borne eggcases. Eggnests were collected from Hidden Valley Camp in Lawrence, KS (38.958720° N, 95.282936° W). For the 29 July 2015 introduction, the ends of twigs were dipped in a protective coating (Doc Farwell's Seal and Heal, Farwell Products, Wenatchee, WA) immediately after clipping to reduce desiccation and to increase successful hatching of nymphs (White 1981). We placed the eggnests on the surface of the soil leaning against the trunk on the day following clipping for each tree assigned to receive cicada nymphs. This technique has been used to successfully introduce cicada nymphs in previous experiments (White 1981, Karban 1985). A separate sample of twigs was dissected on 7 August 2015 to estimate the proportion of unhatched and viable eggs in these twigs.

In total, we estimate that we introduced at least 150 eggnests at each tree; each eggnest contains 20-30 eggs (Williams and Simon 1995), although only 50-95% of these are likely to have hatched successfully (White 1981) under ideal circumstances, and our dissections indicated that only 25% of the eggs were still unhatched on 7 August 2015. Accounting for previously hatched eggs and unsuccessful hatching, we conservatively estimate that we introduced between 188-534 live cicada nymphs to each tree. Previous studies suggest that the density of surviving nymphs just 2 years after the emergence is not strongly correlated with initial oviposition densities (Karban

1984, 1985, Clay et al. 2009), suggesting that nymphal densities are likely to be limited by other factors.

We measured the height of each tree on 28 May 2015, 7 August 2015, 30 May 2016, and 12 July 2017. We measured the trunk diameter at 50 cm above ground at each of those dates using dial calipers. In each year, 4-6 trees had multiple trunks; in these cases, we measured the height and diameter of each trunk, and used the maximum of each measurement to represent the tree. We observed qualitatively identical results if these trees were excluded. We quantified tree growth in height and diameter using absolute growth rates (AGR) and relative growth rates (RGR). Absolute growth rates reflect growth in measurement units per day (cm day^{-1} for height, and mm day^{-1} for diameter), while relative growth rates reflect proportional growth per day (cm cm^{-1} day^{-1} for height, and mm mm^{-1} day^{-1} for diameter). Both metrics were calculated using standard formulae (e.g., Hunt 1982), assessed independently for each measurement interval (28 May 2015 to 7 August 2015; 7 August 2015 to 30 May 2016; 30 May 2016 to 12 July 2017). Because plant size was measured non-destructively at each observation, this procedure allowed a separate measurement of each growth rate (AGR and RGR) for each measurement (height and diameter) for each tree in each measurement interval.

We constructed two sets of linear models in order to evaluate the effects of herbivory, fertilization and their interaction on measures of plant size and growth. The first set of models analyzed tree height and trunk diameter as separate response variables; these analyses assess how well cicada herbivory (nymphs introduced or absent) and fertilization (carcasses introduced or absent) explain variation in measured tree size. Each year of observations was analyzed in a separate model and all models included pre-treatment (May 2015) measurements as a covariate. We did not observe significant herbivory × fertilization interaction effects in any of these analyses, and therefore assessed each main effect relative to a model that excluded the interaction effect. The significance of each factor was tested using likelihood ratio tests with a χ^2 approximation. These analyses were conducted in R, using the *lm* function (R Core Team 2018). We confirmed the assumptions of residual normality and homoscedasticity using quantile (Q-Q) plotting and plots of residuals against fitted values.

The second set of models analyzed the absolute growth rate (AGR) and relative growth rate (RGR) of tree height and diameter specific to each measured interval. Because these growth rates were calculated independently for each interval (i.e., they reflect the marginal growth rate since the start of the interval, not the cumulative growth since the beginning of the experiment), these models provide a way to assess if the effects of cicada herbivory and fertilization varied over time. Our initial linear mixed models assessed the role of cicada herbivory, cicada fertilization, observation date (rescaled to a mean=0 and standard deviation=1) and all interaction terms as fixed factors, and tree identity as a random factor to account for the structure of repeated measurements. Because these models indicated significant fertilization × observation date interaction effects, we subsequently analyzed the AGR and RGR of tree height and diameter for each interval separately. These analyses assess when the effects of cicada herbivory and fertilization occurred. In each interval, we examined linear models including cicada herbivory, cicada fertilization and their interaction, using likelihood ratio tests with a χ^2 approximation to test for the significance of each factor. Assumptions of residual normality and homoscedasticity were confirmed using quantile (Q-Q) plotting and plots of residuals against fitted values.

In 2017, we observed and quantified unanticipated outbreaks of bagworms (*Thyridopteryx ephemeraeformis*) and Japanese beetles (*Popillia japonica*) at our field site. We counted the bagworms on each experimental tree to quantify bagworm densities, and visually estimated Japanese beetle damage as the proportion of sampled leaves with foliar beetle damage. Because the bagworm data was strongly zero-inflated, we used the *hurdle* function in the *pscl* package in R (Jackman 2017) to model bagworm counts as the outcome of two processes: a binomial process determining the proportion of non-zero observations, and a Poisson process determining observed non-zero counts (Zeileis et al. 2008). Japanese beetle damage was logit transformed prior to analysis, and analyzed in a linear model including fertilization, herbivory and their interaction as factors.

For all analyses, effect sizes were calculated based on model coefficients to account for differences in initial measurements, and reported relative to control means. Because the analysis of main effects in these models evaluate directional *a priori* hypotheses, we assessed their significance using one-tailed tests accounting for the direction of observed and predicted effects (Cho and Abe 2013). All analyses were conducted in R version 3.5.1 (R Core Team 2018) using the Rmarkdown format in Rstudio version 1.1.456 (RStudio Team 2016).

Results

Trees that received cicada carcass fertilization showed tree heights (Fig. 2a) and trunk diameters (Fig. 2b) that were greater than those of unfertilized trees in each year of this study (*2015*: 5.2% greater height, $t_{97}=3.87$, $p<0.0001$; 13.8% larger diameter, $t_{97}=4.13$, $p<0.0001$; *2016*: 5.0% greater height, $t_{97}=3.51$, $p= 0.0003$; 7.4% larger diameter, $t_{97}=2.84$, $p= 0.0028$; *2017*: 5.4% greater height, $t_{97}=1.94$, $p= 0.028$; 9.7% larger diameter, $t_{97}=2.2$, $p= 0.015$).

The addition of live cicada nymphs (herbivory) did not have a significant effect on tree heights (Fig. 2a) and trunk diameters (Fig. 2b) in any year of this study (*2015*: 0.13% greater height, $t_{97}=-0.095$, $p=0.54$; 2.4% larger diameter, $t_{97}= -0.0001$, $p=0.50$; *2016*: 0.19% greater height, $t_{97}= -0.47$, $p=0.68$; 1.8% smaller diameter, $t_{97}= 0.081$, $p=0.47$; *2017*: 4.0% greater height, $t_{97}= -1.33$, p=0.91; 0.32% larger diameter, $t_{97}= -0.38$, p=0.65). There were no significant herbivory × fertilization interaction effects on tree height (*2015*: $F_{1,96}=0$, $p=0.996$; *2016*: $F_{1,96}=0.12$, $p=0.73$; *2017*: $F_{1,96}=0.15$, $p=0.7$) or diameter (*2015*: $F_{1,96}=0.74$, $p=0.39$; *2016*: $F_{1,96}=0.25$, $p=0.62$; *2017*: $F_{1,96}=0.23$, $p=0.63$). These results suggest that cicada fertilization in the emergence year caused measurable increases in tree size that persisted throughout the following three years.

The effect of fertilization on tree height and trunk diameter growth rates (Fig. 2c-f) varied by year (tree height AGR: fertilization × date, p=0.063; tree height RGR: fertilization × date, p=0.036; trunk diameter AGR: fertilization × date, p=0.00097; trunk diameter RGR: fertilization × date, p=0.0001). Fertilization increased the AGR of tree height in the year of emergence (*2015*: 17.9% higher AGR, $t_{98}= 3.77$, $p=0.0001$), but did not affect AGR in subsequent years (*2016*: 6.3% higher AGR, $t_{98}=1.4$, $p=0.09$; *2017*: 1.3% higher AGR, $t_{98}=0.24$, $p=0.41$). A similar pattern was observed for the AGR of trunk diameter (*2015*: 38.3% higher AGR, $t_{98}=4.03$, $p<0.0001$; *2016*: 2.4% higher AGR, $t_{98}= 0.39$, $p=0.35$; *2017*: 8.4% higher AGR, $t_{98}=0.46$, $p=0.32$). Analyses of the RGR of tree height (*2015*: 19.7% higher RGR, $t_{98}= 3.82$, $p=0.00012$; *2016*: 2.9% higher RGR, $t_{98}=0.70$, $p=0.24$; *2017*: 0.12% higher RGR, $t_{98}=0.023$, $p=0.49$) and trunk diameter (*2015*: 40.7% higher RGR, $t_{98}=4.55$, $p<0.0001$; *2016*: 0.8% smaller RGR, $t_{98}= -0.18$, $p=0.57$; *2017*: 2.2% smaller RGR, $t_{98}= -0.32$, $p=0.63$) showed the same pattern. In all growth rate analyses, there was a strong and significant effect of fertilization in the emergence year, followed by smaller and non-significant effects in subsequent years.

By comparison, there were no significant effects of herbivory on relative or absolute growth rates for tree height or trunk diameter in any year of the study (Fig. 2c-f). The AGR of tree height (*2015*: 0.6% lower AGR, $t_{98}=0.13$, $p=0.45$; *2016*: 1.9% higher AGR, $t_{98}=-0.43$, $p=0.67$; *2017*: 6.9% higher AGR, $t_{98}=-1.2$, $p=0.89$) and trunk diameter (*2015*: 1.3% lower AGR, $t_{98}=0.17$, $p=0.43$; *2016*: 3.5% lower AGR, $t_{98}=0.57$, $p=0.29$; *2017*: 6.5% lower AGR, $t_{98}=0.85$, $p=0.20$) was not significantly affected by nymphal herbivory in any year. The same pattern was observed for the RGR of tree height (*2015*: 3.8% higher RGR, $t_{98}=-3.8$, $p=0.78$; *2016*: 6.0% higher RGR, $t_{98}=0.70$, $p=0.24$; *2017*: 9.2% higher RGR, $t_{98}=-1.79$, $p=0.96$) and trunk diameter (*2015*: 3.9% higher RGR, $t_{98}=-0.51$, $p=0.69$; *2016*: 0.8% lower RGR, $t_{98}=-0.16$, $p=0.57$; *2017*: 0.97% lower RGR, $t_{98}=0.15$, $p=0.44$).

Of the trees surveyed in 2017, 47% did not have any visible bagworms, and the binomial component of the hurdle model did not detect any significant effects of fertilization, herbivory or their interaction on the likelihood of positive bagworm counts (fertilization, $z=-0.57$, $p=0.71$; herbivory, $z=-0.57$, $p=0.28$; herbivory × fertilization, $z=0.205$, $p=0.84$). However, the analysis of non-zero counts suggested a significant herbivory × fertilization interaction ($z=-3.19$, $p=0.0014$). A subsequent analysis of main effects showed that trees experiencing belowground cicada herbivory had 17% lower non-zero bagworm counts (Fig. 3a, $z=-2.7$, $p=0.003$), while trees receiving cicada fertilization had 15% higher non-zero bagworm counts (Fig. 3b, $z=1.9$, $p=0.03$), though these differences were strongly affected by a single tree with high bagworm densities. However, we observed a similar pattern with foliar damage by Japanese beetles. Trees with cicada nymphs added showed less Japanese beetle damage than trees with nymphs absent (Fig. 3c, 23.7% damage with nymphs present, compared with 30.5% damage with nymphs absent; $t_{98}=1.9$, $p=0.03$). Beetle damage was not affected by cicada fertilization (27.9% damage with subsidy absent, compared with 26.3% damage with subsidy present; $t_{98}=-0.32$, $p=0.63$) or the herbivory × fertilization interaction ($F_{1,97}=0.005$, $p=0.94$).

Discussion

Our findings show that subsidies of dead periodical cicadas increased tree growth in the year of emergence, creating significant differences in tree size that persisted throughout this study. These observed differences in tree size were observed over multiple years, but emerged from a transient period of significantly increased growth occurring only in the emergence year, immediately following cicada deposition and decomposition. Thus, although these changes in tree growth rate were ephemeral, they created differences in tree height and trunk diameter that persisted through multiple growing seasons. These findings raise additional questions about how long the observed size differences will persist, and whether these differences will increase, decrease or be maintained over time.

By comparison, chronic belowground herbivory did not significantly affect tree growth in any year of this experiment. This suggests that trees are able to adequately tolerate or compensate for the effects of chronic belowground herbivory in years immediately following emergence. Periodical cicadas have been previously shown to actively seek out oviposition host trees that are on forest edges or have greater light exposure (White 1980, Yang 2006b, Yang and Karban 2009), and observational studies suggested that cicada growth and survival belowground may be higher on rapidly growing trees (White and Lloyd 1975, White et al. 1979). Whereas some previous studies have documented reductions in tree growth associated with the presence or density of cicada nymphs during early development (Karban 1980, 1982b, Koenig and Liebhold 2003), other studies did not observe evidence for cicada-mediated reductions in tree growth during this early period (Karban 1985, Cook and Holt 2002, Flory and Mattingly 2008). By comparison, the findings of Yang and Karban (2009) suggested that the negative effects of cicada herbivory were particularly evident above a density threshold using a metric of growth that integrated over the entire 17-year cicada development period. Thus, while we did not observe evidence for cicada-mediated reductions in tree growth in this current study, it remains possible that such reductions would be observable at higher cicada densities or later in the cicada development, as the nymphs become larger.

The responses of aboveground herbivores suggest that chronic belowground herbivory may reduce the likelihood or intensity of subsequent aboveground herbivory two years after the emergence year. This pattern could result from induced plant defenses, differential host plant selection, competition, or other mechanisms that have previously been shown to influence the interactions between belowground and aboveground herbivores (Masters et al. 1993, Bardgett and Wardle 2003, Blossey and Hunt-Joshi 2003, Bezemer et al. 2003). Japanese beetles also feed on root tissue as larvae, and could plausibly compete directly with periodical cicada nymphs, though are generally described as feeding on relatively shallower and non-woody roots (Potter and Held 2002). A similar pattern was observed in bagworms, which do not compete with periodical cicadas for access to plant roots, suggesting that direct competition for root feeding resource is unlikely to explain this pattern. While belowground herbivores can have large effects on aboveground herbivores in some systems mediated by changes in plant quality or quantity, future studies will be necessary to identify the mechanisms of observed effects in this system.

Cicada fertilization also increased the density of bagworms when present. This result is consistent with previous studies suggesting that fertilization by cicadas increase the nutrient quality of plant tissue, making it more attractive to selectively feeding herbivores (Yang 2004, 2008). However, cicada fertilization did not have a significant effect on measures of Japanese beetle damage, suggesting that the occurrence, persistence or magnitude of these fertilization effects on aboveground herbivory may be species-specific.

In combination, the findings of this study indicate that both pulsed fertilization with dead cicada adults and chronic belowground herbivory by live cicada nymphs affects host trees. The effects of pulsed fertilization are consistent with previous studies documenting the effects of insect biomass deposition on the belowground components of ecosystems generally (Schowalter and Crossley 1983, Yang 2004, 2006a, Gratton et al. 2008, Yang and Gratton 2014), and with cicada fertilization effects on plant growth specifically (Yang 2013). However, while Yang (2013) examined the short-term growth of herbaceous plants in a greenhouse context, the current study examines the trajectory of cicada fertilization effects on the growth of trees over a multi-annual timescale. Here we find that the effects of pulsed fertilization are strong relative to those of chronic herbivory, with short-term (intra-annual) effects on tree growth rate that lead to expectedly persistent (inter-annual) consequences for tree size.

Looking forward, these findings suggest an uncommon opportunity to examine the degree to which a resource pulse can have persistent, attenuating or amplifying effects in future studies. If the size differences between fertilized and unfertilized trees that were observed in the first two years after the emergence year were maintained over longer timescales, it would suggest that a relatively brief episode of pulsed fertilization in the emergence year is capable of creating persistent differences in the size structure of forests. If these differences attenuate over the coming years, it could suggest that negative feedback mechanisms such as selective herbivory are acting to reduce tree size differences over time, or simply that the tree size differences caused by a resource pulse erode over time due to the accumulated influence of stochastic factors. Conversely, if these initial size differences become larger over time, it would suggest that relatively small and ephemeral differences in growth rate cause initial differences in tree size that can be amplified over time by positive feedback mechanisms such as asymmetric competition for light and other resources (Weiner 1990). Future studies will be necessary to evaluate the long-term consequences of pulsed fertilization and chronic herbivory for tree growth.

This study offers new insights into the interactions between cicadas and their surrounding community, suggesting potential implications for a broader understanding of pulsed fertilization and chronic herbivory in forest dynamics. This study contributes to our understanding of cicada effects on forests by experimentally comparing the effects of cicada herbivory and fertilization. While we do not yet know the effects of cicada-mediated herbivory and fertilization across the entire cicada developmental period, the results of this study do suggest that the negative effects of cicada herbivory for tree growth are not coincident with the positive effects of cicada fertilization. Across the broad range of periodical cicadas, cicada-mediated fertilization could increase tree growth along forest edges where cicadas aggregate, potentially accelerating forest expansion. More broadly, the results of this study suggest how persistent effects can arise from pulsed perturbations, while pressed perturbations could have effects that are potentially more limited in time.

Acknowledgements

We thank Bruce Johanning, Vaughn Salisbury, Ben Sikes, Dean Kettle and the Kansas University Field Station for invaluable assistance in the field.

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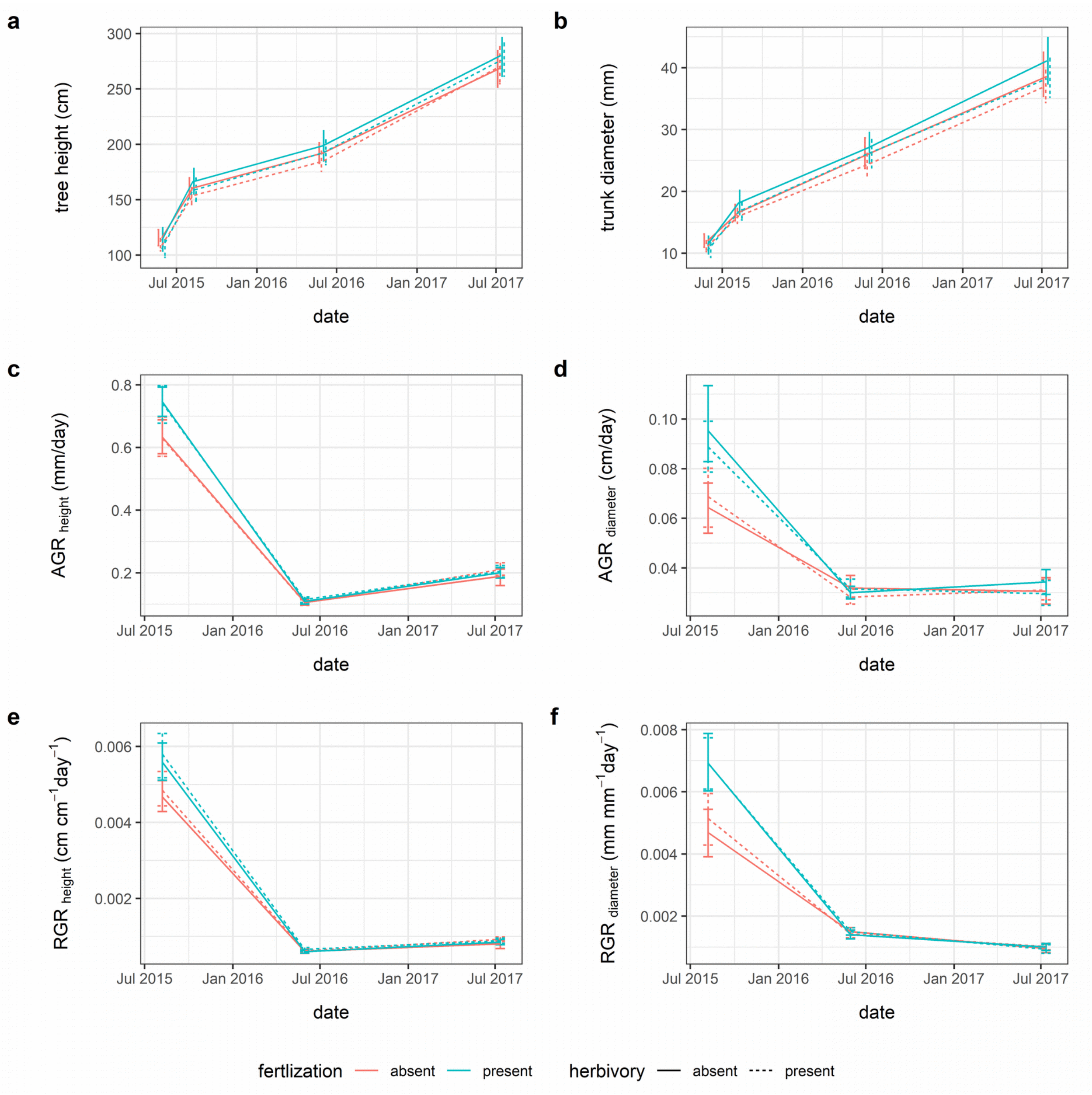
Figure 1. a) Dead cicada carcasses can represent a significant pulsed detrital subsidy. b) Cicadas oviposit into eggnest incision in woody branches. c) Experimental trees in May 2015. d) The same trees in July 2017.

Figure 2. Fertilization with dead cicada carcasses increased a) tree height and b) trunk diameter. The fertilization effect is shown as the difference between blue and red lines, especially when comparing within herbivory treatments. This effect persisted for two years after the emergence year, caused by a transient increase in the growth rate of trees in the first year (c-f). We did not detect any significant effect of cicada herbivory on tree growth. Data represent means ± 95% CL.

Figure 3. a) Fewer bagworms were observed on trees with cicadas present. b) More bagworms were observed on trees that received cicada subsidies. c) Trees with cicadas present also had less foliar damage by Japanese beetles compared with control trees. All data represent back-transformed means ± SE.

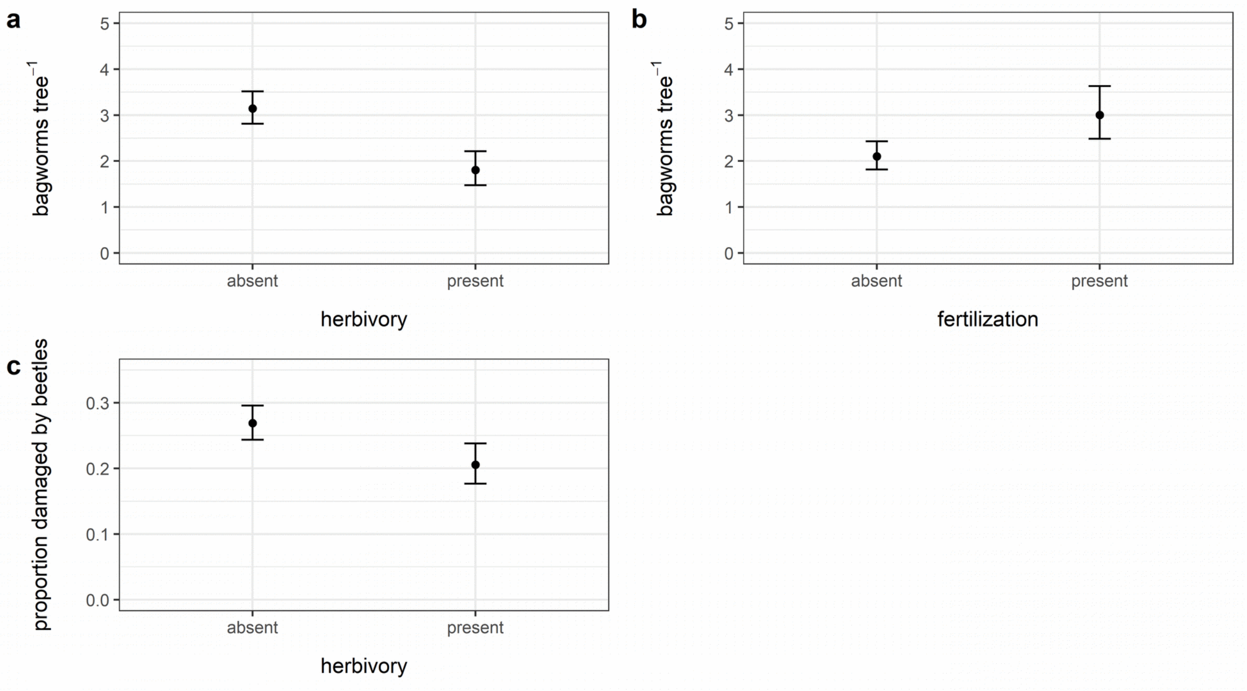
Figure 1

Figure 2



a
tree height (cm)
300
250
200
150
100
Jul 2015
Jan 2016
Jul 2016
Jan 2017
Jul 2017
date
b
trunk diameter (mm)
40
30
20
10
c
AGR height (mm/day)
0.8
0.6
0.4
0.2
d
AGR diameter (cm/day)
0.10
0.08
0.06
0.04
e
RGR height (cm cm-1day-1)
0.006
0.004
0.002
f
RGR diameter (mm mm-1day-1)
0.008
0.006
0.004
0.002
fertlization
absent
present
herbivory
absent
present

636Figure 3



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