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1**Running head:** Cicadas increase tree growth

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

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8

9Abstract

10While many studies have investigated plant growth in the context of episodic
11herbivory and pressed resource availability, relatively few have examined
12how plant growth is affected by pulsed resources and chronic herbivory.
13Periodical cicadas (*Magicicada* spp.) adults represent a pulsed detrital
14subsidy that fertilizes plants, while live cicada nymphs are long-lived root-
15feeding herbivores. Previous studies of cicada herbivory effects have been
16inconclusive, and previous studies of cicada-mediated fertilization did not
17examine effects on trees, or on a multi-year timescale. Here we describe the
18results of a three-year experiment that factorially manipulated the presence
19and absence of cicada fertilization and herbivory in a population of 100
20American sycamore (*Platanus occidentalis*) trees. We found that cicada
21fertilization strongly increased tree growth in the year of emergence,
22creating differences in tree size that persisted at least two years later. By
23comparison, we did not detect reductions in tree growth associated with
24cicada herbivory in any year of this experiment. However, cicada herbivory
25reduced the densities of, and damage from, other aboveground herbivores.
26These results suggest that cicadas affect the size structure of forests over
27multiple years, and raise questions about how cicada-mediated fertilization
28and herbivory will affect tree growth over longer timescales.

29**Keywords:** resource pulses, pulsed detrital subsidy, chronic belowground
30herbivory, periodical cicadas, *Magicicada* spp., tree growth, root herbivores,

31pulsed fertilization, temporally explicit ecology, absolute and relative growth

32rates, amplification, attenuation

33

34

35Introduction

36Both resource limitation and herbivory can limit plant growth (e.g., Hawkes
37and Sullivan 2001). While many studies have documented these effects,
38most studies investigate systems in which herbivory is pulsed (episodic) and
39resource availability is pressed (continuous). Experimental studies often
40manipulate herbivory in episodic bouts that mimic herbivore damage
41consistent with population outbreaks, seasonal dynamics or other transient
42phenomena (Zvereva et al. 2012) while assuming that nutrient availability is
43a relatively constant characteristic determined by edaphic factors, and
44unlikely to change on an experimental timescale. While the paradigm of
45pulsed herbivory and pressed nutrient resources is common, examples of the
46converse - chronic herbivory and pulsed resources - are also widespread.
47Terrestrial plants are actually more likely to experience low levels of chronic
48herbivory as opposed to episodic bouts of severe herbivory (Cyr and Pace
491993), and even low levels of background herbivory can strongly affect plant
50growth (Zvereva et al. 2012) and reproduction (Mueller et al. 2005) over
51longer timescales. Likewise, the belowground nutrient resources available to
52plants are often highly dynamic on multiple timescales (Bardgett et al.
532005), and often show episodic pulses as a result of inputs from the
54aboveground community or changing abiotic conditions (Yang et al. 2010).
55However, few studies have experimentally examined the combined
56consequences 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 m² in continuous floodplain forests and 579 cicadas per m² 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.

80Because cicadas feed belowground, their role as herbivores is easy to
81overlook and difficult to measure. In an analysis of tree rings, Karban (1980)
82observed that 20 scrub oaks (*Quercus ilicifolia*) with cicada herbivory grew
8330% less in the emergence year and in the four years that followed when
84compared with 15 scrub oaks growing without cicadas. However, a
85subsequent study examining the growth of 294 individual trees representing
86six species in the two years following the 1998 cicada emergence in Kansas
87did not find any significant relationship between tree growth and cicada
88oviposition density for four of the six species (Cook and Holt 2002). This
89study did find that the growth of red cedar (*Juniperus virginiana*) was
90positively correlated with cicada densities, and the growth of elm (*Ulmus*
91*rubra*) was negatively correlated with cicada oviposition densities, but both
92relationships were confounded with stem density. At a larger spatial scale,
93Koenig and Liebhold (2003) found that oak (*Quercus* spp.) trees in counties
94with emergences of cicadas grew 4% less during the emergence year when
95compared with trees in counties without emergences; this pattern was not
96observed for non-host pine (*Pinus* spp.) trees. More recently, in an analysis
97of tree rings from three host species (26 sugar maple, *Acer saccharum*; 26
98tulip trees, *Liriodendron tulipifera*; and 30 American basswood, *Tilia*
99*americana*) from three sites in three years (Pennsylvania, USA in 2002;
100Virginia, USA in 2004; and Illinois, USA in 2007), Yang and Karban (2009)
101observed a consistent hump-shaped relationship between cicada emergence
102density and the mean annual growth rate over the preceding 17 years. This

103hump-shaped relationship was hypothesized to reflect the combined effects
104of two opposing processes: the region of positive correlation was probably
105caused by female cicadas preferentially ovipositing on faster growing trees,
106while the region of negative correlation reflected the accumulating cost of
107chronic herbivory (Yang and Karban 2009).

108The differences in the conclusions of these observational studies are likely
109due to differences in methodology as much as biological differences between
110sites or species. For example, several studies indicate that cicada oviposition
111density is a poor predictor of cicada nymph densities, perhaps due to strong
112density dependence for young nymphs belowground (Karbon 1984, 1985,
113Clay et al. 2009); this suggests that oviposition density may not provide a
114good quantitative measure of future nymphal herbivory. Moreover, the
115observation of potentially confounding factors (such as tree density, e.g.
116Cook and Holt 2002) and interacting processes (such as habitat selection,
117e.g. Yang and Karban 2009) limits our ability to assess the effects of cicada
118herbivory from purely observational studies. However, manipulative
119experiments to evaluate the effects of cicada nymphal herbivory on tree
120growth have also had mixed results. For example, the experimental removal
121of cicada nymphs from three apple trees (*Malus pumilia*) significantly
122increased radial tree growth relative to seven control trees, but replication in
123this experiment was low (Karbon 1982b). In a subsequent experiment, the
124addition of cicada eggs failed to measurably affect acorn production or
125rootlet density in 10 scrub oak trees (*Quercus ilicifolia*) compared with 10

126control trees (Karban 1985). An ambitious and well-replicated experiment
127that reduced cicada densities on three species of potential host trees (*Acer*
128*rubra*, *Cornus florida*, and *Cercis canadensis*) failed to show any effects of
129cicada herbivores on growth or reproduction in the emergence year or the
130years immediately following (Flory and Mattingly 2008). In summary, across
131both observational and experimental studies, the effects of feeding cicada
132nymphs on their host trees remain unclear.

133Cicadas may also affect tree growth through pulsed fertilization resulting
134from the decomposition of adult carcasses in the emergence year. As
135nymphs, cicadas store resources in their collective biomass over time, and
136return these nutrients on the soil surface when they die. Previous work
137suggests that this pulse of nutrients can have important effects on forest
138ecosystems. Both bacterial and fungal biomasses increased in the soil within
139days after experimental subsidies of cicada carcasses (Yang 2004).
140Invertebrate decomposers also increased in abundance during this time
141(Yang 2006). The decomposition of cicada carcasses at realistic densities
142increased the availability of soil ammonium and nitrate by several fold during
143the emergence year (Yang 2004). This fertilization effect has been found to
144have consequences at higher trophic levels as well. Fertilized individuals of
145American bellflower (*Campanulastrum americanum*), a common herbaceous
146understory plant, grew larger, showed increased N concentrations in their
147leaves and produced larger seeds than controls that were not fertilized with
148cicada carcasses (Yang 2004, 2013). Mammalian herbivores preferred to

149feed on fertilized bellflowers relative to unfertilized controls and removed
150more biomass from the fertilized individuals (Yang 2008). However, the
151generality of these results, and particularly the effects of cicada fertilization
152on the growth of trees, is not currently known. Moreover, little is known
153about the combined and interactive effects of pulsed fertilization and chronic
154belowground herbivory.

155The primary goal of this study was to experimentally evaluate the negative
156effects of root herbivory by periodical cicada nymphs and the positive effects
157of fertilization from the deposition of dead cicada bodies on the growth of
158forest trees. Specifically, we asked if belowground herbivory by early instar
159cicadas would reduce the height and diameter of American sycamore
160(*Platanus occidentalis*) trees during the emergence year and over the next
161two years. In a factorial design, we also asked whether subsidies of cicada
162bodies would increase tree growth in the emergence year and each of the
163following two years, and whether cicada fertilization and herbivory interact
164to affect tree growth. During the course of this experiment, we also
165quantified two unexpected herbivore outbreaks at our study site, and used
166these opportunities to examine the factorial effects of pulsed fertilization and
167chronic belowground herbivory on the magnitude of future aboveground
168herbivory by insects. We hypothesized that pulsed belowground fertilization
169would increase aboveground herbivory, while chronic belowground herbivory
170would decrease aboveground herbivory.

171**Methods**

172This experiment was conducted at the Kansas University Field Station (KUFS)
173near Lawrence (39.011346° N, 95.206254° W). This site is in the alluvial
174bottomlands north of the Kansas River. Prior to 1860, the site was forested
175but by the early part of the 20th century the land was cultivated (Fitch and
176McGregor 1956). Our experimental site was well within the range of Brood IV
177periodical cicadas, and cicadas were observed emerging on the field station
178property at the forested Suzanne Ecke McColl Nature Reserve approximately
1793 km away in May 2015. Since our experimental site had been in cultivation
180for many decades, it supported no periodical cicadas prior to the start of the
181experiment.

182We planted 100 bare-root American sycamore (*Platanus occidentalis*)
183seedlings (approximately 50 cm height from root crown to top) from the
184Kansas Forest Service (Kansas Forest Service, Conservation Tree Planting
185Program, Manhattan, KS) on April 29, 2014. We chose American sycamore
186for this study because it is fast-growing, hardy, and was originally present,
187although not dominant, at this site before it was converted to agriculture
188(Fitch and McGregor 1956). To reduce competition from grasses and other
189plants, we surrounded the seedlings with weed barrier fabric (Kansas Forest
190Service), covered with 15-20 cm of mulch. We planted 100 seedlings in four
191rows, separating trees by 5m. This distance is sufficient to isolate cicada

192nymphs introduced to specific trees (White and Lloyd 1975, Maier 1980).

193Grasses were mowed between the rows.

194All of our trees survived throughout the experiment (Fig. 1c-d). We varied
195the presence of live cicada nymphs (i.e. “herbivory”) and the presence of
196dead cicada bodies (i.e., “fertilization”) in a 2x2 full factorial design, with 25
197trees randomly assigned to each treatment group (herbivory only,
198fertilization only, herbivory and fertilization, and control).

199We put dead adult cicada bodies below trees that were assigned to receive
200cicada fertilization. Live adult *M. cassini* cicadas were collected from Brood IV
201in Lawrence, KS on 27-28 May 2015. These individuals were frozen soon after
202being collected. We added 155g of dead cicadas (approximately 300
203cicadas) to the soil surface in an area of approximately 1 m² beneath the
204canopy of each tree assigned to this treatment (Fig. 1a). This is within the
205range of cicada emergence and deposition densities that have been
206observed during natural emergence events (Williams and Simon 1995, Yang
2072004).

208We introduced live cicada nymphs to trees that were assigned to the
209herbivory treatment. Twigs of maples (*Acer* sp.), elms (*Ulmus* sp.) and
210redbuds (*Cercis canadensis*) containing cicada eggnest incisions were
211collected and introduced to their new host trees on 29 July 2015 and 7
212August 2015, approximately six weeks following the peak of the mating and
213oviposition (Fig. 1b). The majority of cicada individuals at our study site were

214*M. cassini*. These two dates were selected to bracket the time that first-instar
215nymphs hatch from their twig-borne eggcases. Egg nests were collected
216from Hidden Valley Camp in Lawrence, KS (38.958720° N, 95.282936° W).
217For the 29 July 2015 introduction, the ends of twigs were dipped in a
218protective coating (Doc Farwell's Seal and Heal, Farwell Products,
219Wenatchee, WA) immediately after clipping to reduce desiccation and to
220increase successful hatching of nymphs (White 1981). We placed the
221egg nests on the surface of the soil leaning against the trunk on the day
222following clipping for each tree assigned to receive cicada nymphs. This
223technique has been used to successfully introduce cicada nymphs in
224previous experiments (White 1981, Karban 1985). A separate sample of
225twigs was dissected on 7 August 2015 to estimate the proportion of
226unhatched and viable eggs in these twigs.

227In total, we estimate that we introduced at least 150 egg nests at each tree;
228each egg nest contains 20-30 eggs (Williams and Simon 1995), although only
22950-95% of these are likely to have hatched successfully (White 1981) under
230ideal circumstances, and our dissections indicated that only 25% of the eggs
231were still unhatched on 7 August 2015. Accounting for previously hatched
232eggs and unsuccessful hatching, we conservatively estimate that we
233introduced between 188-534 live cicada nymphs to each tree. Previous
234studies suggest that the density of surviving nymphs just 2 years after the
235emergence is not strongly correlated with initial oviposition densities (Karbon

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 ($\text{cm cm}^{-1} \text{ day}^{-1}$ for height, and $\text{mm mm}^{-1} \text{ day}^{-1}$ 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

258growth. The first set of models analyzed tree height and trunk diameter as
259separate response variables; these analyses assess how well cicada
260herbivory (nymphs introduced or absent) and fertilization (carcasses
261introduced or absent) explain variation in measured tree size. Each year of
262observations was analyzed in a separate model and all models included pre-
263treatment (May 2015) measurements as a covariate. We did not observe
264significant herbivory $\times$ fertilization interaction effects in any of these
265analyses, and therefore assessed each main effect relative to a model that
266excluded the interaction effect. The significance of each factor was tested
267using likelihood ratio tests with a χ^2 approximation. These analyses were
268conducted in R, using the *lm* function (R Core Team 2018). We confirmed the
269assumptions of residual normality and homoscedasticity using quantile (Q-Q)
270plotting and plots of residuals against fitted values.

271The second set of models analyzed the absolute growth rate (AGR) and
272relative growth rate (RGR) of tree height and diameter specific to each
273measured interval. Because these growth rates were calculated
274independently for each interval (i.e., they reflect the marginal growth rate
275since the start of the interval, not the cumulative growth since the beginning
276of the experiment), these models provide a way to assess if the effects of
277cicada herbivory and fertilization varied over time. Our initial linear mixed
278models assessed the role of cicada herbivory, cicada fertilization,
279observation date (rescaled to a mean=0 and standard deviation=1) and all
280interaction terms as fixed factors, and tree identity as a random factor to

281account for the structure of repeated measurements. Because these models
282indicated significant fertilization × observation date interaction effects, we
283subsequently analyzed the AGR and RGR of tree height and diameter for
284each interval separately. These analyses assess when the effects of cicada
285herbivory and fertilization occurred. In each interval, we examined linear
286models including cicada herbivory, cicada fertilization and their interaction,
287using likelihood ratio tests with a χ^2 approximation to test for the significance
288of each factor. Assumptions of residual normality and homoscedasticity were
289confirmed using quantile (Q-Q) plotting and plots of residuals against fitted
290values.

291In 2017, we observed and quantified unanticipated outbreaks of bagworms
292(*Thyridopteryx ephemeraeformis*) and Japanese beetles (*Popillia japonica*) at
293our field site. We counted the bagworms on each experimental tree to
294quantify bagworm densities, and visually estimated Japanese beetle damage
295as the proportion of sampled leaves with foliar beetle damage. Because the
296bagworm data was strongly zero-inflated, we used the *hurdle* function in the
297*pscl* package in R (Jackman 2017) to model bagworm counts as the outcome
298of two processes: a binomial process determining the proportion of non-zero
299observations, and a Poisson process determining observed non-zero counts
300(Zeileis et al. 2008). Japanese beetle damage was logit transformed prior to
301analysis, and analyzed in a linear model including fertilization, herbivory and
302their 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

325 were no significant herbivory $\times$ fertilization interaction effects on tree height
 326 (2015: $F_{1,96}=0$, $p=0.996$; 2016: $F_{1,96}=0.12$, $p=0.73$; 2017: $F_{1,96}=0.15$, $p=0.7$)
 327 or diameter (2015: $F_{1,96}=0.74$, $p=0.39$; 2016: $F_{1,96}=0.25$, $p=0.62$; 2017:
 328 $F_{1,96}=0.23$, $p=0.63$). These results suggest that cicada fertilization in the
 329 emergence year caused measurable increases in tree size that persisted
 330 throughout the following three years.

331 The effect of fertilization on tree height and trunk diameter growth rates (Fig.
 332 c-f) varied by year (tree height AGR: fertilization $\times$ date, $p=0.063$; tree
 333 height RGR: fertilization $\times$ date, $p=0.036$; trunk diameter AGR: fertilization $\times$
 334 date, $p=0.00097$; trunk diameter RGR: fertilization $\times$ date, $p=0.0001$).
 335 Fertilization increased the AGR of tree height in the year of emergence
 336 (2015: 17.9% higher AGR, $t_{98}=3.77$, $p=0.0001$), but did not affect AGR in
 337 subsequent years (2016: 6.3% higher AGR, $t_{98}=1.4$, $p=0.09$; 2017: 1.3%
 338 higher AGR, $t_{98}=0.24$, $p=0.41$). A similar pattern was observed for the AGR of
 339 trunk diameter (2015: 38.3% higher AGR, $t_{98}=4.03$, $p<0.0001$; 2016: 2.4%
 340 higher AGR, $t_{98}=0.39$, $p=0.35$; 2017: 8.4% higher AGR, $t_{98}=0.46$, $p=0.32$).
 341 Analyses of the RGR of tree height (2015: 19.7% higher RGR, $t_{98}=3.82$,
 342 $p=0.00012$; 2016: 2.9% higher RGR, $t_{98}=0.70$, $p=0.24$; 2017: 0.12% higher
 343 RGR, $t_{98}=0.023$, $p=0.49$) and trunk diameter (2015: 40.7% higher RGR,
 344 $t_{98}=4.55$, $p<0.0001$; 2016: 0.8% smaller RGR, $t_{98}=-0.18$, $p=0.57$; 2017: 2.2%
 345 smaller RGR, $t_{98}=-0.32$, $p=0.63$) showed the same pattern. In all growth rate
 346 analyses, there was a strong and significant effect of fertilization in the

347emergence year, followed by smaller and non-significant effects in
348subsequent years.

349By comparison, there were no significant effects of herbivory on relative or
350absolute growth rates for tree height or trunk diameter in any year of the
351study (Fig. 2c-f). The AGR of tree height (2015: 0.6% lower AGR, $t_{98}=0.13$,
352 $p=0.45$; 2016: 1.9% higher AGR, $t_{98}=-0.43$, $p=0.67$; 2017: 6.9% higher AGR,
353 $t_{98}=-1.2$, $p=0.89$) and trunk diameter (2015: 1.3% lower AGR, $t_{98}=0.17$,
354 $p=0.43$; 2016: 3.5% lower AGR, $t_{98}=0.57$, $p=0.29$; 2017: 6.5% lower AGR,
355 $t_{98}=0.85$, $p=0.20$) was not significantly affected by nymphal herbivory in any
356year. The same pattern was observed for the RGR of tree height (2015: 3.8%
357higher RGR, $t_{98}=-3.8$, $p=0.78$; 2016: 6.0% higher RGR, $t_{98}=0.70$, $p=0.24$;
3582017: 9.2% higher RGR, $t_{98}=-1.79$, $p=0.96$) and trunk diameter (2015: 3.9%
359higher RGR, $t_{98}=-0.51$, $p=0.69$; 2016: 0.8% lower RGR, $t_{98}=-0.16$, $p=0.57$;
3602017: 0.97% lower RGR, $t_{98}=0.15$, $p=0.44$).

361Of the trees surveyed in 2017, 47% did not have any visible bagworms, and
362the binomial component of the hurdle model did not detect any significant
363effects of fertilization, herbivory or their interaction on the likelihood of
364positive bagworm counts (fertilization, $z=-0.57$, $p=0.71$; herbivory, $z=-0.57$,
365 $p=0.28$; herbivory $\times$ fertilization, $z=0.205$, $p=0.84$). However, the analysis of
366non-zero counts suggested a significant herbivory $\times$ fertilization interaction
367($z=-3.19$, $p=0.0014$). A subsequent analysis of main effects showed that
368trees 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 $\times$ 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

390observed size differences will persist, and whether these differences will
391increase, decrease or be maintained over time.

392By comparison, chronic belowground herbivory did not significantly affect
393tree growth in any year of this experiment. This suggests that trees are able
394to adequately tolerate or compensate for the effects of chronic belowground
395herbivory in years immediately following emergence. Periodical cicadas have
396been previously shown to actively seek out oviposition host trees that are on
397forest edges or have greater light exposure (White 1980, Yang 2006b, Yang
398and Karban 2009), and observational studies suggested that cicada growth
399and survival belowground may be higher on rapidly growing trees (White and
400Lloyd 1975, White et al. 1979). Whereas some previous studies have
401documented reductions in tree growth associated with the presence or
402density of cicada nymphs during early development (Karbon 1980, 1982b,
403Koenig and Liebhold 2003), other studies did not observe evidence for
404cicada-mediated reductions in tree growth during this early period (Karbon
4051985, Cook and Holt 2002, Flory and Mattingly 2008). By comparison, the
406findings of Yang and Karban (2009) suggested that the negative effects of
407cicada herbivory were particularly evident above a density threshold using a
408metric of growth that integrated over the entire 17-year cicada development
409period. Thus, while we did not observe evidence for cicada-mediated
410reductions in tree growth in this current study, it remains possible that such
411reductions would be observable at higher cicada densities or later in the
412cicada development, as the nymphs become larger.

413The responses of aboveground herbivores suggest that chronic belowground
414herbivory may reduce the likelihood or intensity of subsequent aboveground
415herbivory two years after the emergence year. This pattern could result from
416induced plant defenses, differential host plant selection, competition, or
417other mechanisms that have previously been shown to influence the
418interactions between belowground and aboveground herbivores (Masters et
419al. 1993, Bardgett and Wardle 2003, Blossey and Hunt-Joshi 2003, Bezemer
420et al. 2003). Japanese beetles also feed on root tissue as larvae, and could
421plausibly compete directly with periodical cicada nymphs, though are
422generally described as feeding on relatively shallower and non-woody roots
423(Potter and Held 2002). A similar pattern was observed in bagworms, which
424do not compete with periodical cicadas for access to plant roots, suggesting
425that direct competition for root feeding resource is unlikely to explain this
426pattern. While belowground herbivores can have large effects on
427aboveground herbivores in some systems mediated by changes in plant
428quality or quantity, future studies will be necessary to identify the
429mechanisms of observed effects in this system.

430Cicada fertilization also increased the density of bagworms when present.
431This result is consistent with previous studies suggesting that fertilization by
432cicadas increase the nutrient quality of plant tissue, making it more
433attractive to selectively feeding herbivores (Yang 2004, 2008). However,
434cicada fertilization did not have a significant effect on measures of Japanese

435beetle damage, suggesting that the occurrence, persistence or magnitude of
436these fertilization effects on aboveground herbivory may be species-specific.

437In combination, the findings of this study indicate that both pulsed
438fertilization with dead cicada adults and chronic belowground herbivory by
439live cicada nymphs affects host trees. The effects of pulsed fertilization are
440consistent with previous studies documenting the effects of insect biomass
441deposition on the belowground components of ecosystems generally
442(Schowalter and Crossley 1983, Yang 2004, 2006a, Gratton et al. 2008, Yang
443and Gratton 2014), and with cicada fertilization effects on plant growth
444specifically (Yang 2013). However, while Yang (2013) examined the short-
445term growth of herbaceous plants in a greenhouse context, the current study
446examines the trajectory of cicada fertilization effects on the growth of trees
447over a multi-annual timescale. Here we find that the effects of pulsed
448fertilization are strong relative to those of chronic herbivory, with short-term
449(intra-annual) effects on tree growth rate that lead to expectedly persistent
450(inter-annual) consequences for tree size.

451Looking forward, these findings suggest an uncommon opportunity to
452examine the degree to which a resource pulse can have persistent,
453attenuating or amplifying effects in future studies. If the size differences
454between fertilized and unfertilized trees that were observed in the first two
455years after the emergence year were maintained over longer timescales, it
456would suggest that a relatively brief episode of pulsed fertilization in the

457emergence year is capable of creating persistent differences in the size
458structure of forests. If these differences attenuate over the coming years, it
459could suggest that negative feedback mechanisms such as selective
460herbivory are acting to reduce tree size differences over time, or simply that
461the tree size differences caused by a resource pulse erode over time due to
462the accumulated influence of stochastic factors. Conversely, if these initial
463size differences become larger over time, it would suggest that relatively
464small and ephemeral differences in growth rate cause initial differences in
465tree size that can be amplified over time by positive feedback mechanisms
466such as asymmetric competition for light and other resources (Weiner 1990).
467Future studies will be necessary to evaluate the long-term consequences of
468pulsed fertilization and chronic herbivory for tree growth.

469This study offers new insights into the interactions between cicadas and their
470surrounding community, suggesting potential implications for a broader
471understanding of pulsed fertilization and chronic herbivory in forest
472dynamics. This study contributes to our understanding of cicada effects on
473forests by experimentally comparing the effects of cicada herbivory and
474fertilization. While we do not yet know the effects of cicada-mediated
475herbivory and fertilization across the entire cicada developmental period, the
476results of this study do suggest that the negative effects of cicada herbivory
477for tree growth are not coincident with the positive effects of cicada
478fertilization. Across the broad range of periodical cicadas, cicada-mediated
479fertilization could increase tree growth along forest edges where cicadas

480aggregate, potentially accelerating forest expansion. More broadly, the
481results of this study suggest how persistent effects can arise from pulsed
482perturbations, while pressed perturbations could have effects that are
483potentially more limited in time.

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487**Literature Cited**

- 488Bardgett, R. D., W. D. Bowman, R. Kaufmann, and S. K. Schmidt. 2005. A
489 temporal approach to linking aboveground and belowground ecology.
490 Trends in Ecology & Evolution 20:634–641.
- 491Bardgett, R. D., and D. A. Wardle. 2003. Herbivore-Mediated Linkages
492 Between Aboveground and Belowground Communities. Ecology
493 84:2258–2268.
- 494Bezemer, T. M., R. Wagensaar, N. M. Van Dam, and F. L. Wackers. 2003.
495 Interactions Between Above- and Belowground Insect Herbivores as
496 Mediated by the Plant Defense System. Oikos 101:555–562.
- 497Blossey, B., and T. R. Hunt-Joshi. 2003. Belowground Herbivory by Insects:
498 Influence on Plants and Aboveground Herbivores. Annual Review of
499 Entomology 48:521–547.

500Cho, H.-C., and S. Abe. 2013. Is two-tailed testing for directional research
 501 hypotheses tests legitimate? *Journal of Business Research* 66:1261–
 502 1266.

503Cook, W. M., and R. D. Holt. 2002. Periodical cicada (*Magicicada cassini*)
 504 oviposition damage: visually impressive yet dynamically irrelevant.
 505 *American Midland Naturalist* 147:214–224.

506Cyr, H., and M. L. Pace. 1993. Magnitude and patterns of herbivory in aquatic
 507 and terrestrial ecosystems. *Nature* 361:148–150.

508Dybas, H. S., and D. D. Davis. 1962. A population census of seventeen-year
 509 periodical cicadas (Homoptera: Cicadidae: *Magicicada*). *Ecology*
 510 43:432–444.

511Fitch, H. S., and R. L. McGregor. 1956. The forest habitat of the University of
 512 Kansas Natural History Reservation. University of Kansas Publications,
 513 Museum of Natural History 10:77–127.

514Flory, S., and W. Mattingly. 2008. Response of host plants to periodical
 515 cicada oviposition damage. *Oecologia* 156:649–656.

516Gratton, C., J. Donaldson, and M. J. V. Zanden. 2008. Ecosystem linkages
 517 between lakes and the surrounding terrestrial landscape in northeast
 518 Iceland. *Ecosystems* 11:764–774.

519Hawkes, C. V., and J. J. Sullivan. 2001. The Impact of Herbivory on Plants in
 520 Different Resource Conditions: A Meta-Analysis. *Ecology* 82:2045–2058.

521Hunt, R. 1982. Plant growth curves. The functional approach to plant growth
 522 analysis. Edward Arnold Ltd.

523 Jackman, S. 2017. pscl: Classes and Methods for R Developed in the Political
 524 Science Computational Laboratory. United States Studies Centre,
 525 University of Sydney, Sydney, New South Wales, Australia.
 526 Karban, R. 1980. Periodical cicada nymphs impose periodical oak tree wood
 527 accumulation. *Nature* 287:326–327.
 528 Karban, R. 1982a. Increased reproductive success at high densities and
 529 predator satiation for periodical cicadas. *Ecology* 63:321–328.
 530 Karban, R. 1982b. Experimental removal of 17-year cicada nymphs and
 531 growth of apple trees. *Journal of the New York Entomological Society*
 532 90:74–81.
 533 Karban, R. 1985. Addition of periodical cicada (*Magicicada* spp.) nymphs to
 534 an oak (*Quercus ilicifolia*) forest: Effects on cicada density, acorn
 535 production and rootlet density. *Journal of the Kansas Entomological*
 536 *Society* 58:269–276.
 537 Karban, R. 2014. Transient habitats limit development time for periodical
 538 cicadas. *Ecology* 95:3–8.
 539 Koenig, W. D., and A. M. Liebhold. 2003. Regional impacts of periodical
 540 cicadas on oak radial increment. *Canadian Journal of Forest Research*
 541 33:1084–1089.
 542 Lloyd, M., and H. S. Dybas. 1966. The periodical cicada problem I. Population
 543 ecology. *Evolution* 20:133–149.

544Maier, C. T. 1980. A moleseye view of 17-year periodical cicada nymphs,
 545 *Magicicada septendecim* (Hemiptera, Homoptera, Cicadidae). *Annals of*
 546 the Entomological Society of America 73:147–152.
 547Marlatt, C. L. 1907. The periodical cicada. *Bulletin of the USDA Bureau of*
 548 Entomology 71:1–181.
 549Masters, G. J., V. K. Brown, and A. C. Gange. 1993. Plant Mediated
 550 Interactions between Above- and Below-Ground Insect Herbivores.
 551 *Oikos* 66:148–151.
 552Mueller, R. C., B. D. Wade, C. A. Gehring, and T. G. Whitham. 2005. Chronic
 553 herbivory negatively impacts cone and seed production, seed quality
 554 and seedling growth of susceptible pinyon pines. *Oecologia* 143:558–
 555 565.
 556Potter, D. A., and D. W. Held. 2002. Biology and Management of the Japanese
 557 Beetle. *Annual Review of Entomology* 47:175–205.
 558R Core Team. 2018. R: A Language and Environment for Statistical
 559 Computing. R Foundation for Statistical Computing, Vienna, Austria.
 560RStudio Team. 2016. RStudio: Integrated Development Environment for R.
 561 RStudio, Inc., Boston, MA.
 562Schowalter, T. D., and D. A. Crossley. 1983. Forest canopy arthropods as
 563 sodium, potassium, magnesium and calcium pools in forests. *Forest*
 564 Ecology and Management 7:143–148.
 565Weiner, J. 1990. Asymmetric competition in plant-populations. *Trends in*
 566 Ecology & Evolution 5:360–364.

567Whiles, M. R., M. A. Callaham, C. K. Meyer, B. L. Brock, and R. E. Charlton.
568 2001. Emergence of periodical cicadas (*Magicicada cassini*) from a
569 Kansas riparian forest: densities, biomass and nitrogen flux. *American*
570 *Midland Naturalist* 145:176–187.

571White, J. 1980. Resource partitioning by ovipositing cicadas. *American*
572 *Naturalist* 115:1–28.

573White, J. 1981. Flagging - hosts defenses versus oviposition strategies in
574 periodical cicadas (*Magicicada* spp., Cicadidae, Homoptera). *Canadian*
575 *Entomologist* 113:727–738.

576White, J., and M. Lloyd. 1975. Growth-rates of 17-year and 13-year periodical
577 cicadas. *American Midland Naturalist* 94:127–143.

578White, J., M. Lloyd, and J. H. Zar. 1979. Faulty eclosion in crowded suburban
579 periodical cicadas - populations out of control. *Ecology* 60:305–315.

580White, J., and C. E. Strehl. 1978. Xylem feeding by periodical cicada nymphs
581 on tree roots. *Ecological Entomology* 3:323–327.

582Williams, K. S., and C. Simon. 1995. The ecology, behavior, and evolution of
583 periodical cicadas. *Annual Review of Entomology* 40:269–295.

584Williams, K. S., K. G. Smith, and F. M. Stephen. 1993. Emergence of 13-yr
585 periodical cicadas (Cicadidae, *Magicicada*) - phenology, mortality, and
586 predator satiation. *Ecology* 74:1143–1152.

587Yang, L. 2013. Resource pulses of dead periodical cicadas increase the
588 growth of American bellflower rosettes under competitive and non-
589 competitive conditions. *Arthropod-Plant Interactions* 7:1–6.

590 Yang, L. H. 2004. Periodical cicadas as resource pulses in North American
 591 forests. *Science* 306:1565–1567.

592 Yang, L. H. 2006a. Interactions between a detrital resource pulse and a
 593 detritivore community. *Oecologia* 147:522–532.

594 Yang, L. H. 2006b. Periodical cicadas use light for oviposition site selection.
 595 Proceedings of the Royal Society of London Series B-Biological
 596 Sciences 273:2993–3000.

597 Yang, L. H. 2008. Pulses of dead periodical cicadas increase herbivory of
 598 American bellflowers. *Ecology* 89:1497–1502.

599 Yang, L. H., K. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O.
 600 Spence. 2010. A meta-analysis of resource pulse-consumer
 601 interactions. *Ecological Monographs* 80:125–151.

602 Yang, L. H., and C. Gratton. 2014. Insects as drivers of ecosystem processes.
 603 *Current Opinion in Insect Science* 2:26–32.

604 Yang, L. H., and R. Karban. 2009. Long-term habitat selection and chronic
 605 root herbivory: explaining the relationship between periodical cicada
 606 density and tree growth. *American Naturalist* 173:105–112.

607 Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression models for count
 608 data in R. *Journal of Statistical Software* 27:1–25.

609 Zvereva, E. L., V. Zverev, and M. V. Kozlov. 2012. Little strokes fell great
 610 oaks: minor but chronic herbivory substantially reduces birch growth.
 611 *Oikos* 121:2036–2043.

612Figure 1. a) Dead cicada carcasses can represent a significant pulsed detrital
613subsidy. b) Cicadas oviposit into egg nest incision in woody branches. c)
614Experimental trees in May 2015. d) The same trees in July 2017.

615Figure 2. Fertilization with dead cicada carcasses increased a) tree height
616and b) trunk diameter. The fertilization effect is shown as the difference
617between blue and red lines, especially when comparing within herbivory
618treatments. This effect persisted for two years after the emergence year,
619caused by a transient increase in the growth rate of trees in the first year (c-
620f). We did not detect any significant effect of cicada herbivory on tree
621growth. Data represent means $\pm$ 95% CL.

622Figure 3. a) Fewer bagworms were observed on trees with cicadas present.
623b) More bagworms were observed on trees that received cicada subsidies. c)
624Trees with cicadas present also had less foliar damage by Japanese beetles
625compared with control trees. All data represent back-transformed means $\pm$
626SE.

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630Figure 1

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633Figure 2

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636Figure 3

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