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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9**Abstract**

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

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34

35 Introduction

36 Both resource limitation and herbivory can limit plant growth (e.g., Hawkes 37 and Sullivan 2001). While many studies have documented these effects, 38 most studies investigate systems in which herbivory is pulsed (episodic) and 39 resource availability is pressed (continuous). Experimental studies often 40 manipulate herbivory in episodic bouts that mimic herbivore damage 41 consistent with population outbreaks, seasonal dynamics or other transient 42 phenomena (Zvereva et al. 2012) while assuming that nutrient availability is 43 a relatively constant characteristic determined by edaphic factors, and 44 unlikely to change on an experimental timescale. While the paradigm of 45 pulsed herbivory and pressed nutrient resources is common, examples of the 46 converse - chronic herbivory and pulsed resources - are also widespread. 47 Terrestrial plants are actually more likely to experience low levels of chronic 48 herbivory as opposed to episodic bouts of severe herbivory (Cyr and Pace 49 1993), and even low levels of background herbivory can strongly affect plant 50 growth (Zvereva et al. 2012) and reproduction (Mueller et al. 2005) over 51 longer timescales. Likewise, the belowground nutrient resources available to 52 plants are often highly dynamic on multiple timescales (Bardgett et al. 53 2005), and often show episodic pulses as a result of inputs from the 54 aboveground community or changing abiotic conditions (Yang et al. 2010). 55 However, few studies have experimentally examined the combined 56 consequences of pulsed resources and pressed herbivory on plant growth.

57Periodical cicadas present a natural context in which to examine questions

58about pulsed resources and chronic herbivory. Periodical cicadas are among

59the most abundant herbivores of deciduous trees in North America both in

60terms of numbers and biomass, with emergence densities as high as 372

61cicadas per m^2 in continuous floodplain forests and 579 cicadas per m^2 in

62fertilized landscapes (Dybas and Davis 1962, Karban 2014). The species

63with more northern ranges develop belowground for 17 years before their

64emergence, while the species with more southern ranges develop for 13

65years prior to emergence (Marlatt 1907, Williams and Simon 1995). During

66this prolonged development, cicada nymphs actively feed on xylem fluid

67from plant roots (White and Strehl 1978). After emergence, the adult stage

68lasts only 2-4 weeks (Marlatt 1907), and this ephemeral abundance of

69cicadas effectively satiates their potential predators in the aboveground

70community (Lloyd and Dybas 1966, Karban 1982a, Williams et al. 1993). As

71a consequence, most adult cicadas are not killed or consumed; instead, dead

72adults accumulate on the forest floor where their nutrients return to the

73rhizosphere as a detrital subsidy (Whiles et al. 2001, Yang 2004, 2006a)(Fig.

741a). In the late summer of the emergence year, the next generation of first

75instar cicadas hatches from eggs laid in trees (Fig. 1b), falls to the ground

76and begins digging to find suitable roots. Although this unusual natural

77history has been well-documented, the relationship between periodical

78cicadas and their host trees as herbivores and as resource pulses is not well-

79understood.

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 (Karban 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 (Karban 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

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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. Moveover, 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.

171Methods

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 m^2 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. Eggnests 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

221eggnests 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 eggnests at each tree;

228each eggnest 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 (Karban

2361984, 1985, Clay et al. 2009), suggesting that nymphal densities are likely to 237be limited by other factors.

238We measured the height of each tree on 28 May 2015, 7 August 2015, 30 239May 2016, and 12 July 2017. We measured the trunk diameter at 50 cm 240above ground at each of those dates using dial calipers. In each year, 4-6 241trees had multiple trunks; in these cases, we measured the height and 242diameter of each trunk, and used the maximum of each measurement to 243represent the tree. We observed qualitatively identical results if these trees 244were excluded. We quantified tree growth in height and diameter using 245absolute growth rates (AGR) and relative growth rates (RGR). Absolute 246growth rates reflect growth in measurement units per day (cm day^{-1} for 247height, and mm day^{-1} for diameter), while relative growth rates reflect 248proportional growth per day (cm cm^{-1} day^{-1} for height, and mm mm^{-1} day^{-1} for 249diameter). Both metrics were calculated using standard formulae (e.g., Hunt 2501982), assessed independently for each measurement interval (28 May 2015 251to 7 August 2015; 7 August 2015 to 30 May 2016; 30 May 2016 to 12 July 2522017). Because plant size was measured non-destructively at each 253observation, this procedure allowed a separate measurement of each growth 254rate (AGR and RGR) for each measurement (height and diameter) for each 255tree in each measurement interval.

256We constructed two sets of linear models in order to evaluate the effects of 257herbivory, 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 × 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.

303For all analyses, effect sizes were calculated based on model coefficients to

304account for differences in initial measurements, and reported relative to

305control means. Because the analysis of main effects in these models

306evaluate directional *a priori* hypotheses, we assessed their significance using

307one-tailed tests accounting for the direction of observed and predicted

308effects (Cho and Abe 2013). All analyses were conducted in R version 3.5.1

309(R Core Team 2018) using the Rmarkdown format in Rstudio version 1.1.456

310(RStudio Team 2016).

311Results

312Trees that received cicada carcass fertilization showed tree heights (Fig. 2a)

313and trunk diameters (Fig. 2b) that were greater than those of unfertilized

314trees in each year of this study (*2015*: 5.2% greater height, t_{97}=3.87, $p<$

3150.0001; 13.8% larger diameter, t_{97}=4.13, $p<0.0001$; *2016*: 5.0% greater

316height, t_{97}=3.51, $p=$ 0.0003; 7.4% larger diameter, t_{97}=2.84, $p=$ 0.0028;

317*2017*: 5.4% greater height, t_{97}=1.94, $p=$ 0.028; 9.7% larger diameter,

318t_{97}=2.2, $p=$ 0.015).

319The addition of live cicada nymphs (herbivory) did not have a significant

320effect on tree heights (Fig. 2a) and trunk diameters (Fig. 2b) in any year of

321this study (*2015*: 0.13% greater height, t_{97}=-0.095, $p=0.54$; 2.4% larger

322diameter, t_{97}= -0.0001, $p=0.50$; *2016*: 0.19% greater height, t_{97}= -0.47,

323$p=0.68$; 1.8% smaller diameter, t_{97}= 0.081, $p=0.47$; *2017*: 4.0% greater

324height, t_{97}= -1.33, p=0.91; 0.32% larger diameter, t_{97}= -0.38, p=0.65). There

325were no significant herbivory × 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)

327or 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

329emergence year caused measurable increases in tree size that persisted

330throughout the following three years.

331The effect of fertilization on tree height and trunk diameter growth rates (Fig.

3322c-f) varied by year (tree height AGR: fertilization × date, p=0.063; tree

333height RGR: fertilization × date, p=0.036; trunk diameter AGR: fertilization ×

334date, p=0.00097; trunk diameter RGR: fertilization × date, p=0.0001).

335Fertilization 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

337subsequent years (*2016*: 6.3% higher AGR, t_{98}=1.4, *p*=0.09; *2017*: 1.3%

338higher AGR, t_{98}=0.24, *p*=0.41). A similar pattern was observed for the AGR of

339trunk diameter (*2015*: 38.3% higher AGR, t_{98}=4.03, *p*<0.0001; *2016*: 2.4%

340higher AGR, t_{98}= 0.39, *p*=0.35; *2017*: 8.4% higher AGR, t_{98}=0.46, *p*=0.32).

341Analyses 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

343RGR, t_{98}=0.023, *p*=0.49) and trunk diameter (*2015*: 40.7% higher RGR,

344t_{98}=4.55, *p*<0.0001; *2016*: 0.8% smaller RGR, t_{98}= -0.18, *p*=0.57; *2017*: 2.2%

345smaller RGR, t_{98}= -0.32, *p*=0.63) showed the same pattern. In all growth rate

346analyses, 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,

353t_{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,

355t_{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;

358*2017*: 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;

360*2017*: 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 × fertilization, *z*=0.205, *p*=0.84). However, the analysis of

366non-zero counts suggested a significant herbivory × 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

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369bagworm counts (Fig. 3a, z=-2.7, p=0.003), while trees receiving cicada

370fertilization had 15% higher non-zero bagworm counts (Fig. 3b, z=1.9,

371p=0.03), though these differences were strongly affected by a single tree

372with high bagworm densities. However, we observed a similar pattern with

373foliar damage by Japanese beetles. Trees with cicada nymphs added showed

374less Japanese beetle damage than trees with nymphs absent (Fig. 3c, 23.7%

375damage with nymphs present, compared with 30.5% damage with nymphs

376absent; t_{98}=1.9, p=0.03). Beetle damage was not affected by cicada

377fertilization (27.9% damage with subsidy absent, compared with 26.3%

378damage with subsidy present; t_{98}=-0.32, p=0.63) or the herbivory ×

379fertilization interaction ($F_{1,97}$=0.005, p=0.94).

380**Discussion**

381Our findings show that subsidies of dead periodical cicadas increased tree

382growth in the year of emergence, creating significant differences in tree size

383that persisted throughout this study. These observed differences in tree size

384were observed over multiple years, but emerged from a transient period of

385significantly increased growth occurring only in the emergence year,

386immediately following cicada deposition and decomposition. Thus, although

387these changes in tree growth rate were ephemeral, they created differences

388in tree height and trunk diameter that persisted through multiple growing

389seasons. 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 (Karban 1980, 1982b,

403Koenig and Liebhold 2003), other studies did not observe evidence for

404cicada-mediated reductions in tree growth during this early period (Karban

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.

413 The responses of aboveground herbivores suggest that chronic belowground

414 herbivory may reduce the likelihood or intensity of subsequent aboveground

415 herbivory two years after the emergence year. This pattern could result from

416 induced plant defenses, differential host plant selection, competition, or

417 other mechanisms that have previously been shown to influence the

418 interactions between belowground and aboveground herbivores (Masters et

419 al. 1993, Bardgett and Wardle 2003, Blossey and Hunt-Joshi 2003, Bezemer

420 et al. 2003). Japanese beetles also feed on root tissue as larvae, and could

421 plausibly compete directly with periodical cicada nymphs, though are

422 generally described as feeding on relatively shallower and non-woody roots

423 (Potter and Held 2002). A similar pattern was observed in bagworms, which

424 do not compete with periodical cicadas for access to plant roots, suggesting

425 that direct competition for root feeding resource is unlikely to explain this

426 pattern. While belowground herbivores can have large effects on

427 aboveground herbivores in some systems mediated by changes in plant

428 quality or quantity, future studies will be necessary to identify the

429 mechanisms of observed effects in this system.

430 Cicada fertilization also increased the density of bagworms when present.

431 This result is consistent with previous studies suggesting that fertilization by

432 cicadas increase the nutrient quality of plant tissue, making it more

433 attractive to selectively feeding herbivores (Yang 2004, 2008). However,

434 cicada 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.

484**Acknowledgements**

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612Figure 1. a) Dead cicada carcasses can represent a significant pulsed detrital

613subsidy. b) Cicadas oviposit into eggnest 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 ± 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 ±
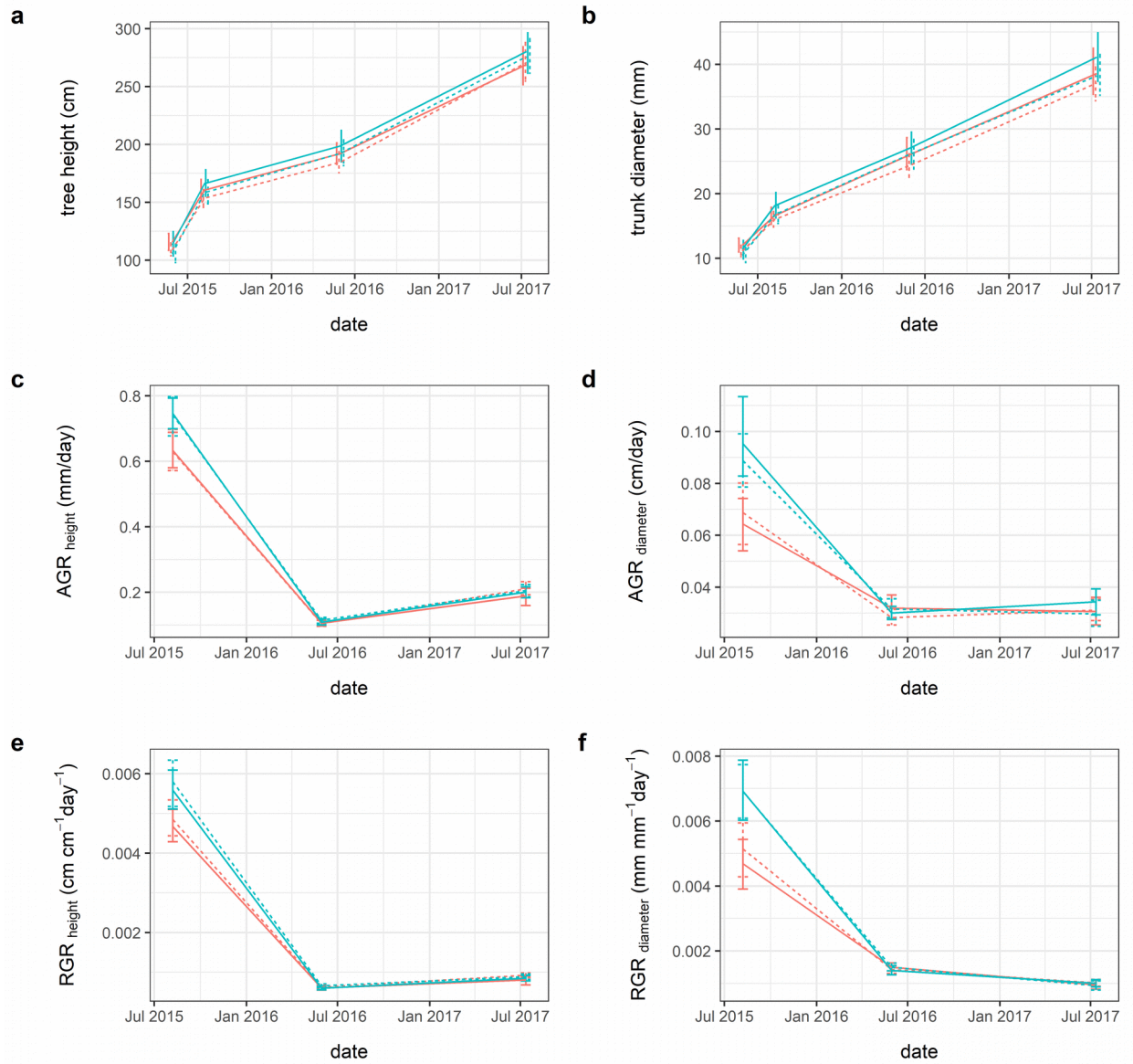
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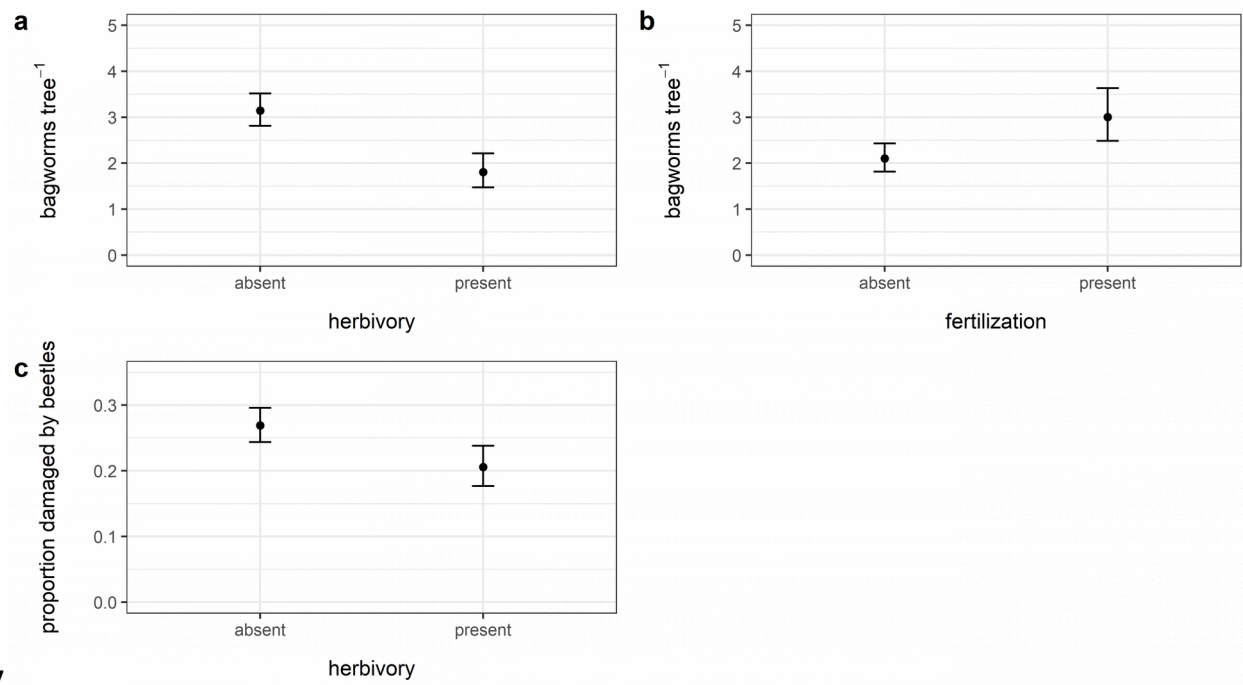
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630 Figure 1

a

b

c

d

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633Figure 2

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636Figure 3