

# Resource pulses of dead periodical cicadas increase the growth of American bellflower rosettes under competitive and non-competitive conditions

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**Abstract** This experiment investigates how pulsed nutrient resources interact with intraspecific competition to influence biomass production and nutrient use efficiency in the American bellflower (*Campanulastrum americanum*). The competitive environment of these plants was manipulated by growing plants alone or with neighboring conspecifics, and the occurrence of pulsed nutrient resources was manipulated through the addition of 17-year periodical cicada (*Magicicada septendecim*) carcasses in order to simulate naturally occurring pulsed resources in this system. The addition of cicada carcasses increased mean plant biomass by 61 % compared to non-supplemented plants, while competition decreased mean plant biomass by 44 % compared to plants grown without competition; these effects were additive. In comparison, nutrient use efficiency decreased in fertilized plants (cicada-supplemented plants showed 20 % greater foliage nitrogen concentrations compared to non-supplemented plants), but was not significantly affected by the plant's competitive environment. In addition, cicada supplementation did not significantly increase the biomass asymmetry in competing pairs of plants. These results suggest that these plants increased their total nutrient uptake at a timescale commensurate with the pulsed increase in nutrient availability due to cicada carcass decomposition.

**Keywords** Resource pulses · Competition · Nutrient use efficiency · Foliage nitrogen · Periodical cicadas

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(*Magicicada septendecim*) · American bellflowers  
(*Campanulastrum americanum*)

## Introduction

Resource pulses are widespread and diverse phenomena characterized by relatively infrequent, large magnitude and short duration periods of increased resource availability (Ostfeld and Keesing 2000; Yang et al. 2008). Several studies have recently begun to illuminate how these events influence species interactions in both the aboveground and belowground components of terrestrial ecosystems in a multitude of habitats (e.g., Chen and Wise 1999; Gratton and Denno 2003; Hoekman et al. 2011; Yang et al. 2010). While it seems clear that pulsed resources can have strong direct effects on consumer dynamics, relatively few studies have examined how resource pulses affect competitive interactions between consumers (but see Boutin et al. 2006; Gebauer et al. 2002; Jankju-Borzelabad and Griffiths 2006). In this experiment, I investigate how a pulsed detrital resource interacts with intraspecific competition to influence plant biomass production and nutrient use efficiency. In this interaction, nutrients from the decomposition of insect bodies provide the pulsed resource, and the plant is the consumer of these nutrients. I use the term “consumer” in the broad sense (i.e., not limited to heterotrophic consumers) to be consistent with the general framework of pulsed resource–consumer theory (Holt 2008; Yang et al. 2010, 2008).

The interactions between American bellflowers (*Campanulastrum americanum*) and pulses of periodical cicada (*Magicicada* spp.) carcasses provide an excellent system to investigate the combined effects of pulsed resources and competition. High densities of 17-year periodical cicada

carcasses commonly fall to the ground in a pulsed fashion during cicada emergence years, and these events have been shown to have strong effects on the belowground components of ecosystems, including effects on detritivore arthropods, soil microbes, soil nitrogen, plant nutrient uptake, seed production and herbivory (Whiles et al. 2001; Yang 2008, 2006, 2004). However, previous studies have not documented effects of cicada–detrital supplementation on plant biomass accumulation. One possible explanation is that these experiments have been conducted with natural field populations of American bellflowers during the bolting and flowering phase of their life history, when resources are likely to be allocated to reproduction over growth. However, American bellflower can express either an annual or biennial life history, depending on the timing of seed germination. Seeds that germinate in the spring (as opposed to the fall) show a strict biennial life history with rosette growth during their first growing season, followed by bolting and flowering in their second year. Thus, investigating a spring-germinating cohort in their first year would allow one to examine the effects of a cicada resource pulse on rosette growth without concurrent allocations to reproduction.

This system also provides a context to investigate how the deposition of dead periodical cicadas could influence intraspecific competition for belowground resources. While many relatively isolated bellflowers can be found, these plants can also commonly be found growing in close proximity to conspecifics, where two or more plants develop in the same microsite with overlapping root zones (*personal observation*). The discrete nature of individual cicada carcasses combined with the microtopography of the soil means that deposition events are likely to contribute to a mosaic of fertilized and unfertilized patches at the scale of plant microsites. Thus, individual American bellflowers within the range of a cicada emergence event can commonly be found growing in all combinations of competition and cicada presence: with or without intraspecific competition, and with or without cicada fertilization. Moreover, cicada carcass deposition generally peaks during the early summer (Williams et al. 1993; Yang 2004), a period of rapid growth for American bellflowers.

Relatively little is known about the combined effects of resource pulses and intraspecific competition. On the one hand, resources pulses could be expected to reduce competition by lifting some aspects of resource limitation. Alternatively, consumer responses to resource pulses could lead to increased resource demand (due to increases in consumer biomass or density, or decreases in resource use efficiency), ultimately leading to stronger resource competition. The effects of resource pulses on competitive interactions are likely to result from the interplay of resource and consumer dynamics; understanding how

resource pulses interact with competition is important for understanding the dynamics of resource pulses more generally.

In this study, I ask two specific questions: (1) How do inputs of periodical cicada carcasses influence plant growth and nutrient uptake? and (2) How do inputs of periodical cicada carcasses affect the strength of intraspecific root competition? In order to investigate these questions, I conducted a factorial greenhouse experiment to examine the effects of competition in the presence and absence of a cicada-derived nutrient pulse.

## Materials and methods

Periodical cicadas are common herbivores in eastern North American deciduous forests in terms of both number and cumulative biomass (Dybas and Davis 1962). These insects feed on plants roots belowground for 13 or 17 years during development before emerging synchronously over a large but patchy geographic area (often on the order of  $10^5$  km<sup>2</sup>), at densities of 0–350 cicadas m<sup>-2</sup> (Williams and Simon 1995). Although many aboveground consumers feed on periodical cicadas, a very small proportion of cicada biomass is consumed by aboveground predators (Karban 1984; Williams et al. 1993), and the vast majority of cicada carcasses decompose on the forest floor, creating a substantial pulse of plant-available soil nitrogen (Yang 2006, 2004).

I collected seeds from 74 American bellflower plants in a natural population of bellflowers at the Mountain Lake Biological Station (37°21.287'N, 80°32.606'W, Pembroke, VA, University of Virginia) on September 8, 2003. These seeds were individually germinated on 5-mm filter paper disks in 96-well cell culture trays under 12:12 h and 15:25 °C light:dark conditions with approximately 20 µL of water seed<sup>-1</sup> week<sup>-1</sup> in a controlled-environment chamber beginning on March 9, 2004. These plants were germinated under cool conditions to simulate spring germination (Baskin and Baskin 1984; Galloway 2001a). These conditions result in a biennial life history, yielding a single measure of summer vegetative growth. On May 22, 2004, I transferred plants at the cotyledon stage to moistened, individual peat pellets (Jiffy-7, Jiffy Products, 3.8 cm diameter × 3.8 cm height) in a greenhouse at the University of Virginia's Blandy Experimental Farm (39°3.838'N, 78°3.846'W, Boyce, VA).

On June 25, 2004, I randomly assigned 102 plants to 68 pots (17 cm diameter × 20 cm height filled with approximately 2 L of Professional Growing Media III; Wetsel Seed Company, Inc., Harrisonburg, Virginia, USA) in one of the four treatment groups ( $N = 17$ ) in a 2 × 2 factorial design: grown alone without cicada carcasses (“control”),

grown alone with cicada carcasses (“cicada”), grown in a pair without cicada carcasses (“competition”), and grown in a pair with cicada carcasses (“competition and cicada”). This experimental design varies the density of plants in the presence and absence of a constant cicada input in order to manipulate the intensity of resource competition. This soil substrate for these experiments contains approximately 55 % peat, 35 % fine pine bark, and 10 % perlite and provides minimal nutrient availability (% total  $N = 0.65$ ,  $C:N = 50$ ). Natural populations of American bellflowers commonly grow in thin, shale-dominated soils and may commonly experience similarly low background nutrient availabilities.

Cicadas were *M. septendecim* adults in an approximately 1:1 sex ratio collected from concurrent natural populations of Brood X periodical cicadas at the Blandy Experimental Farm. Cicadas were collected by hand, frozen within 1 h of collection, and used in these experiments less than 7 days after collection. Cicada carcasses contain approximately 10.4 % nitrogen (Yang 2004). Six cicadas were placed in each experimentally fertilized pot, approximately equivalent to a carcass deposition density of 260 cicadas  $m^{-2}$ . The magnitude of this experimental pulse represents a high density within the range of documented cicada deposition densities from natural emergence events (Williams and Simon 1995; Yang 2004). These cicadas were coarsely fragmented with scissors to mimic the shredding activities of natural detritivore communities (Yang 2006). These plants were watered with daily drip irrigation to a bottom tray, and natural light was supplemented with sodium vapor lamps during daylight hours. All plants were harvested on September 6, 2004, 74 days after the establishment of treatments. The root biomass of these plants was extremely fine and dense and could not be reliably extricated from the soil. Aboveground biomass (hereafter, *biomass*) of each plant was dried at 50 °C for 48 h to achieve constant dry weights.

I conducted a two-way ANOVA to investigate the effects of competition, cicada fertilization, and the competition  $\times$  fertilization interaction on the surviving biomass of American bellflowers. The biomass of plants in each competition replicate was analyzed as the mean of the surviving plant biomasses; in competition replicates ( $N = 6$ ) where one plant died, the dead plants were assumed to have a biomass of zero. Identical conclusions emerged from analyses in which the biomass of the surviving plant was used to represent the pair. These data were log transformed prior to analysis to meet assumptions of residual normality and equality of variances, although analyses with untransformed data yielded identical qualitative results. Normality and homoscedasticity assumptions were confirmed with Shapiro–Wilk’s tests, quantile–quantile plots and Levene’s tests.

All analyses were implemented in R 2.14.1 (R Development Core Team 2011).

I used elemental analyses of foliage to examine how competition and cicada fertilization affects plant nitrogen use efficiency. Two- to three-milligram samples (representing four to ten 3-mm leaf disk subsamples) were collected from each plant, and a homogenized sample of foliage biomass from each pot was analyzed at the University of California at Davis Stable Isotope Facility using continuous-flow isotope mass spectrometry. These analyses yielded data about foliage nitrogen content ( $g\ N\ g^{-1}$  total dry biomass), where nitrogen use efficiency is defined as the reciprocal of foliage nitrogen content (Berendse and Aerts 1987; Shaver and Melillo 1984). I investigated the effects of competition, cicada fertilization and the competition  $\times$  fertilization interaction on foliage nitrogen content using a two-way analysis of variance (ANOVA). These data met normality and homoscedasticity assumptions without transformation.

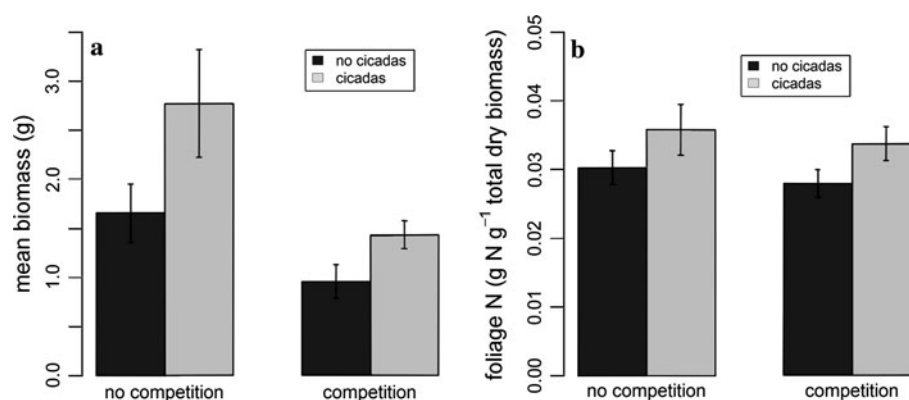
Within the competition replicates, I used a one-tailed Wilcoxon rank sum test to evaluate the specific hypothesis that cicada fertilization would increase biomass asymmetry for plant pairs grown in competition treatments with and without cicada fertilization. A non-parametric test was appropriate due to the non-normality of residuals in this analysis. I used the absolute biomass difference between individuals in the pair, the coefficient of variation, and the Gini coefficient as measures of asymmetry (Weiner and Solbrig 1984). All analyses yielded identical conclusions, and only results for absolute biomass differences are presented here.

## Results

Competition with a neighboring individual decreased the mean biomass of surviving bellflowers by 44 % compared to plants grown alone (Fig. 1a,  $F_{1,53} = 10.06$ ,  $p = 0.003$ ). Conversely, cicada fertilization increased the mean biomass of bellflowers by 61 % compared to unfertilized plants (Fig. 1a,  $F_{1,53} = 9.50$ ,  $p = 0.003$ ). The interaction effect was not significant in this analysis (Fig. 1a,  $F_{1,53} = 0.31$ ,  $p = 0.58$ ), suggesting that the proportional effects of competition on biomass accumulation did not vary due to cicada addition. The mean biomass of plants grown in competitive environments with cicada carcasses was similar to the mean biomass of plants grown alone without cicada fertilization (competition with cicadas present =  $1.44\ g \pm 0.14\ SE$ ; no competition with cicadas absent =  $1.66\ g \pm 0.29\ SE$ ).

Cicada fertilization increased the nitrogen concentration of plant foliage by 20 % compared to unfertilized controls, across competition treatments (Fig. 1b,  $F_{1,53} = 4.53$ ,

**Fig. 1 a** Intraspecific competition between neighboring bellflower rosettes decreased plant biomass, while fertilization with dead cicada carcasses increased bellflower biomass. **b** Cicada fertilization increased foliage nitrogen concentration (i.e., decreased nitrogen use efficiency). The effect of competition on foliage nitrogen concentration was not significant



$p = 0.038$ ). Competition did not affect foliage nitrogen concentrations (Fig. 1b,  $F_{1,53} = 0.40$ ,  $p = 0.53$ ). These experiments were unable to detect any effect of cicada fertilization on the biomass asymmetry of bellflower pairs when grown in competition ( $p = 0.38$ ).

## Discussion

In this experiment, the addition of cicada carcasses substantially increased plant biomass, while competition decreased plant biomass. The positive effects of fertilization on plant biomass were counterbalanced by the negative effects of intraspecific competition in an additive manner. This suggests that the addition of cicada carcasses increased plant growth, but did not change the proportional effects of competition. In addition, cicada supplementation increased foliage nitrogen concentrations in both competitive and non-competitive environments. This result corresponds to a pattern of decreased nitrogen use efficiency under cicada fertilization.

The observation that competition was not significantly altered by cicada resources suggests at least two possibilities. First, this pattern could result if the observed increases in plant resource consumption (due to increased growth and reduced nitrogen use efficiency) occurred at a timescale commensurate with the timescale of cicada-detrital decomposition. If this were the case, then cicada fertilization (while pulsed relative to the entire biennial life history of the plant) did not present nutrient resources in excess of consumer demand at the timescale of this experiment. This study did not attempt to determine whether there may have been a transient period during which nutrient supply temporarily exceeded consumer demand, or whether plant requirements that increased under pulsed conditions (due to increased biomass or reduced nutrient use efficiency) would ultimately have contributed to more intense competition as the availability of resources

declined. Future studies should aim to examine the effects of pulsed resources on competition using longitudinal designs that quantify consumer responses through time.

The second possibility is that the competitive interactions among conspecifics could have been undiminished even if belowground resources were supplied in excess of demand, if competition shifted toward some other limiting resource. In general, if specific resources are supplied in excess of demand, competitive interactions are generally expected to shift to other niche dimensions (e.g., Harpole and Tilman 2007). For example, strong resource enrichment in the belowground environment commonly increases aboveground competition for light (Weiner 1986; Wilson and Tilman 1993). In this experiment, the cumulative effects of intraspecific competition could have been undiminished if reduced nutrient limitations belowground resulted in increased light limitations aboveground. However, competition for light is often considered to be fundamentally asymmetric (Weiner 1990), such that increased light competition would be associated with increased biomass asymmetry between competing plants in the cicada-fertilized group. This biomass asymmetry is generally expected to be self-reinforcing because larger plants shade smaller plants, and greater exposure to light allows more biomass accumulation, as has been shown for bellflower rosettes (Galloway and Etterson 2009). However, these current analyses did not find a significant increase in the biomass asymmetry of competing plants in the cicada fertilization treatment, suggesting that belowground fertilization may not have caused a significant shift toward increased competition for light, or that the high light conditions of the experiment may have reduced the importance of light competition.

Taken together, these results suggest that the consumers in this system (American bellflowers) responded to the pulsed increase in belowground resources (decomposing cicada carcasses) with relatively rapid increases in nutrient uptake through both increased growth and reduced nutrient

use efficiency. Similar increases in the biomass and seed size of American bellflowers have been documented in response to inorganic fertilization, with effects on the timing of germination (Galloway 2001a, b). These studies extend previous results by investigating biomass responses to a naturally occurring resource pulse, and examining the effects of this pulse on competitive interactions. These results also contribute to a growing understanding of the direct and indirect effects of cicada-derived pulsed resources in this system and provide experimental evidence that cicada pulses can increase plant growth in terrestrial systems. These results are consistent with previous studies in this system that have documented increases in nutrient uptake and seed mass (Yang 2004), increases in mammalian and insect herbivory (Yang 2008), increases in the growth of phytoplankton in aquatic systems (Nowlin et al. 2007), and possible increases in the wood accumulation of trees (Koenig and Liebhold 2003; Yang and Karban 2009) that may be associated with cicada fertilization. The results of this experiment are also generally consistent with previous studies of plant responses to diverse resource pulses in other systems. Plants commonly respond to increased resource availability with rapidly increased resource uptake via physiological or morphological plasticity (Hodge 2004; Miao and Bazzaz 1990; Peek and Forseth 2003), including increased growth and reduced nutrient use efficiency (Birk and Vitousek 1986; e.g., Chapin 1980; Shaver and Melillo 1984; Yang et al. 2010).

The results of this experiment suggest some of the ways in which these insects continue to affect plant interactions after their death. Because the deposition of dead cicada bodies in North American forests following periodical cicada emergence events is likely to create small, patchy zones of fertilized soil at the scale of plant microsites, the deposition of cicada detritus could increase the growth of bellflower rosettes growing alone, while nearby plants remain unfertilized. For plants growing in close competition with conspecifics, the deposition of cicada detritus could increase rosette growth to be comparable to plants that are growing in the absence of competition without cicada fertilization.

More generally, these results contribute to a growing number of studies that investigate the effects of pulsed resources on species interactions (e.g., Yang et al. 2010). While future studies will be necessary to examine how pulsed resources affect competitive interactions over shorter and longer timescales, these results suggest that pulsed resources are unlikely to reduce resource limitations in a simple or persistent sense, especially in systems where consumer responses are relatively rapid.

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## References

- Baskin JM, Baskin CC (1984) The ecological life-cycle of *Campanula americana* in north central Kentucky. *Bull Torrey Bot Club* 111: 329–337
- Berendse F, Aerts R (1987) Nitrogen-use-efficiency: a biologically meaningful definition? *Funct Ecol* 1:293–296
- Birk EM, Vitousek PM (1986) Nitrogen availability and nitrogen use efficiency in loblolly pine stands. *Ecology* 67:69–79
- Boutin S, Wauters LA, McAdam AG et al (2006) Anticipatory reproduction and population growth in seed predators. *Science* 314:1928–1930
- Chapin FS (1980) The mineral nutrition of wild plants. *Annu Rev Ecol Syst* 11:233–260
- Chen B, Wise DH (1999) Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 80: 761–772
- Dybas HS, Davis DD (1962) A population census of seventeen-year periodical cicadas (Homoptera: Cicadidae: Magicicada). *Ecology* 43:432–444
- Galloway LF (2001a) The effect of maternal and paternal environments on seed characters in the herbaceous plant *Campanula americana* (Campanulaceae). *Am J Bot* 88:832–840
- Galloway LF (2001b) Parental environmental effects on life history in the herbaceous plant *Campanula americana*. *Ecology* 82:2781–2789
- Galloway LF, Etterson JR (2009) Plasticity to canopy shade in a monocarpic herb: within- and between-generation effects. *New Phytol* 182:1003–1012. doi:10.1111/j.1469-8137.2009.02803.x
- Gebauer R, Schwinning S, Ehleringer J (2002) Interspecific competition and resource pulse utilization in a cold desert community. *Ecology* 83:2602–2616
- Gratton C, Denno RF (2003) Inter-year carryover effects of a nutrient pulse on *Spartina* plants, herbivores, and natural enemies. *Ecology* 84:2692–2707
- Harpole WS, Tilman D (2007) Grassland species loss resulting from reduced niche dimension. *Nature* 446:791–793
- Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytol* 162:9–24
- Hoekman D, Dreyer J, Jackson RD et al (2011) Lake to land subsidies: experimental addition of aquatic insects increases terrestrial arthropod densities. *Ecology* 92:2063–2072. doi:10.1890/11-0160.1
- Holt RD (2008) Theoretical perspectives on resource pulses. *Ecology* 89:671–681
- Jankju-Borzelabad M, Griffiths H (2006) Competition for pulsed resources: an experimental study of establishment and coexistence for an arid-land grass. *Oecologia* 148:555–563. doi:10.1007/s00442-006-0408-1
- Karban R (1984) Opposite density effects of nymphal and adult mortality for periodical cicadas. *Ecology* 65:1656–1661
- Koenig WD, Liebhold AM (2003) Regional impacts of periodical cicadas on oak radial increment. *Can J for Res* 33:1084–1089
- Miao SL, Bazzaz FA (1990) Responses to nutrient pulses of two colonizers requiring different disturbance frequencies. *Ecology* 71:2166–2178

- Nowlin WH, González MJ, Vanni MJ et al (2007) Allochthonous subsidy of periodical cicadas affects the dynamics and stability of pond communities. *Ecology* 88:2174–2186
- Ostfeld RS, Keesing F (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol Evol* 15:232–237
- Peek MS, Forseth IN (2003) Microhabitat dependent responses to resource pulses in the arid land perennial, *Cryptantha flava*. *J Ecol* 91:457–466
- R Development Core Team (2011) R: a language and environment for statistical computing. Austria, Vienna
- Shaver GR, Melillo JM (1984) Nutrient budgets of marsh plants—efficiency concepts and relation to availability. *Ecology* 65:1491–1510
- Weiner J (1986) How competition for light and nutrients affects size variability in *Ipomoea tricolor* populations. *Ecology* 67:1425–1427
- Weiner J (1990) Asymmetric competition in plant-populations. *Trends Ecol Evol* 5:360–364
- Weiner J, Solbrig OT (1984) The meaning and measurement of size hierarchies in plant populations. *Oecologia* 61:334–336
- Whiles MR, Callahan MA, Meyer CK et al (2001) Emergence of periodical cicadas (*Magicicada cassini*) from a Kansas riparian forest: densities, biomass and nitrogen flux. *Am Midl Nat* 145:176–187
- Williams KS, Simon C (1995) The ecology, behavior, and evolution of periodical cicadas. *Annu Rev Entomol* 40:269–295
- Williams KS, Smith KG, Stephen FM (1993) Emergence of 13-year periodical cicadas (Cicadidae, Magicicada)—phenology, mortality, and predator satiation. *Ecology* 74:1143–1152
- Wilson SD, Tilman D (1993) Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74:599–611
- Yang LH (2004) Periodical cicadas as resource pulses in North American forests. *Science* 306:1565–1567
- Yang LH (2006) Interactions between a detrital resource pulse and a detritivore community. *Oecologia* 147:522–532
- Yang LH (2008) Pulses of dead periodical cicadas increase herbivory of American bellflowers. *Ecology* 89:1497–1502
- Yang LH, Karban R (2009) Long-term habitat selection and chronic root herbivory: explaining the relationship between periodical cicada density and tree growth. *Am Nat* 173:105–112
- Yang LH, Bastow JL, Spence KO, Wright AN (2008) What can we learn from resource pulses? *Ecology* 89:621–634
- Yang LH, Edwards K, Byrnes JE et al (2010) A meta-analysis of resource pulse–consumer interactions. *Ecol Monogr* 80:125–151