

PULSES OF DEAD PERIODICAL CICADAS INCREASE HERBIVORY OF AMERICAN BELLFLOWERS

LOUIE H. YANG¹

Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106-9610 USA

Abstract. Resource pulses can have both direct bottom-up and indirect top-down effects on their consumers, but comparatively few studies have investigated the top-down effects of naturally occurring resource pulses on plants. This study describes two years of field experiments conducted to determine the indirect effects of 17-year periodical cicadas (*Magicicada* spp.) on herbivory in American bellflowers (*Campanulastrum americanum*). In 2004, the area of damaged leaves on cicada-supplemented plants was 78% greater than the area of damaged leaves on control plants. In 2005, cicada-supplemented plants were more likely to experience herbivory by mammalian herbivores than control plants. When large herbivores were excluded, similar patterns of leaf herbivory were observed, but these differences were not statistically significant. These results suggest that the pulsed input of dead periodical cicada bodies increased rates of herbivory on bellflowers, and that this effect was largely mediated by the selective foraging of large mammalian herbivores. More broadly, this study suggests that pulses of limiting resources can have both positive direct effects on plants and negative indirect effects due to selective herbivory, and that the net effects of pulsed resources on plants may depend on the composition and behavior of the surrounding herbivore community.

Key words: bottom-up effects; *Campanulastrum americanum*; fertilization; foliar nitrogen; *Magicicada* spp.; periodic cicada; pulsed resources; resource pulses; satiation; selective herbivory; top-down effects; white-tailed deer.

INTRODUCTION

Resource pulses are large, infrequent, and brief episodes of increased resource availability. Many consumers in a wide range of natural systems respond to resource pulses with increased growth at the population or individual level. While these bottom-up effects of resource pulses are well documented, an increasing number of studies have suggested that resource pulses may also create indirect top-down effects on consumers mediated by higher trophic levels (Ostfeld and Keesing 2000, Yang et al. 2008). These top-down effects occur when higher trophic levels respond to pulse-driven increases in the availability or quality of their prey or hosts. For example, El Niño rainfalls in semiarid Chile create resource pulses for herbivorous and granivorous rodents, and the predators of these small mammals (hawks and owls) respond to increasing rodent populations with lagged top-down effects on their prey populations (Jaksic et al. 1997, Lima et al. 2002). Investigating both the direct bottom-up and indirect top-down effects of resource pulses is important for understanding the consequences of these large perturbations. Although top-down effects from resource pulses have been observed in a handful of systems, these

few studies probably do not adequately reflect the diversity of such phenomena in nature. In particular, most previous studies have focused on multitrophic systems of animal consumers, where top-down effects are mediated by the behavioral or numerical responses of vertebrate predators to resource pulse-driven increases in the densities of their prey (Ostfeld and Keesing 2000, Yang et al. 2008). In comparison, the indirect top-down (i.e., herbivore-mediated) effects of naturally occurring resource pulses on plants have received considerably less attention.

However, several observations suggest that pulses of increased resource availability may also have top-down effects on plants (Fig. 1). For example, the addition of artificial fertilizers to woody plants has been shown to increase foliar nutrient quality, leading to increased herbivory by insect and mammalian herbivores (Kyto et al. 1996, Herms 2002, Tripler et al. 2002), and patchy pulses of simulated cattle urine increase herbivory of grasses by rabbits (Denyer et al. 2007). These studies suggest that similar processes may operate in systems that experience naturally-occurring detrital resource pulses. For example, the frass and greenfall from insect outbreaks (Risley and Crossley 1988), and inputs of decomposing seeds associated with mast seeding events (Zackrisson et al. 1999) may commonly provide substantial pulses of nutrients to plants. Do such naturally occurring resource pulses also cause top-down, herbivore-mediated effects on plants?

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¹ E-mail: lyang@lifesci.ucsb.edu

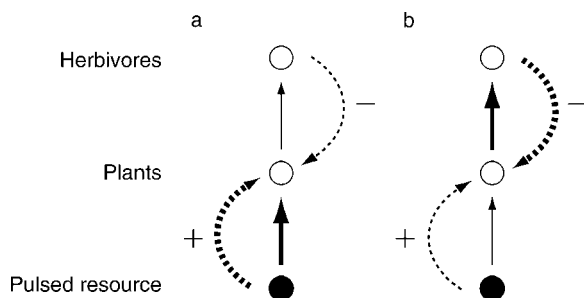


FIG. 1. Direct bottom-up and indirect top-down effects on plants resulting from resource pulses. Solid circles represent pulsed resources. Solid arrows represent fluxes of nutrients, water, or biomass; dotted arrows represent species interaction effects. The width of lines represents the intensity of interactions. (a) Resource pulses may have direct bottom-up effects on plants and (b) indirect top-down effects on plants mediated by changes in the density or behavior of herbivores. These two effects may occur sequentially or simultaneously.

Here, I investigate how detrital inputs associated with the emergence of 17-year periodical cicadas affect rates of herbivory on American bellflowers (*Campanulastrum americanum*). Periodical cicadas are long-lived, root-feeding, insect herbivores that emerge synchronously from belowground in cohorts that extend across large geographic areas, and at densities sometimes exceeding 350 cicadas/m² (Williams and Simon 1995). Previous studies have demonstrated that the dead bodies of periodical cicadas represent a substantial nutrient flux that occurs at 13- or 17-year intervals in many forest systems (Wheeler et al. 1992, Yang 2004). This biomass creates an infrequent but large pulse of mineralized nitrogen for plant uptake as the cicada bodies are decomposed (Yang 2004). Periodical cicada depositions are highly variable over both small (<1 m) and large (>1 km) spatial scales (Yang 2004), with synchronous emergence broods comprised of many patchy populations (usually on the scale of hectares) extending over cumulative geographic brood ranges on the order of 10⁵ km². As a result of small-scale patchiness, individual plants in the same population can receive widely different cicada inputs. American bellflowers are a native annual or biennial woodland species found throughout the range of periodical cicadas, commonly growing on thin, shale-derived, high-slope soils. Previous field and greenhouse studies suggest that bellflowers increase foliage nitrogen concentrations in response to pulses of cicada detrital biomass (Yang 2004; L Yang, unpublished manuscript). Combined with the patchiness of cicada deposition, these observations suggest that herbivores may commonly be choosing among plants that have experienced widely different local resource regimes.

I conducted field experiments over two years to investigate the following specific questions: (1) How do pulses of dead periodical cicadas affect herbivory by mammals? and (2) How do these pulses affect herbivory

by non-mammalian herbivores, particularly insects and gastropods?

MATERIALS AND METHODS

2004

On 10 June 2004, 100 small American bellflowers (mean initial height \pm SD, 42.0 \pm 10.9 cm; mean initial stem diameter \pm SD, 4.9 \pm 1.4 mm) from a natural population in an approximately 0.5-ha forested area of the University of Virginia's Mountain Lake Biological Station and the Wilderness Conservancy of Mountain Lake (Giles County, Virginia, USA; 37°20'50.98" N, 80°32'38.81" W) were randomly assigned to receive either 0 or 10 cicadas placed by hand on the soil surface immediately below each plant. This site is within the range of periodical cicadas, but did not experience local cicada emergences in 2004 or 2005. Cicadas were *Magicicada septendecim* individuals collected in an approximately 1:1 sex ratio from populations of Brood X periodical cicadas at the University of Virginia's Blandy Experimental Farm, the Stonebridge Farm near Millwood, Virginia, and the Green Ridge State Forest in Maryland. Cicadas were frozen within 6 hours after collection, and used in experiments 1–14 days later. This treatment density corresponds to approximately 140 cicadas/m² in the area immediately around each plant. Observations suggest that the high slope of the site, heavy rains, and aggressive scavenging by arthropods and small mammals in the absence of local cicada populations during the experiment caused substantial, but not complete, carcass loss within 24–48 h after supplementation. Because of these factors, the stated treatment density likely overestimates the effective supplementation, resulting in a conservative assessment of cicada pulse effects. The treatment density is well within the range of observed cicada densities: most well-documented emergence densities range between 0 and 350 cicadas/m² over landscape (>1 ha) scales (Williams and Simon 1995), with many observations of cicada densities exceeding 150 cicadas/m² in local areas (Cory and Knight 1937, Graham and Cochran 1954, Dybas and Davis 1962, White et al. 1979, Whiles et al. 2001). At typical densities, the vast majority of adult cicadas escape direct predation (Karban 1982, Williams et al. 1993), and observed emergence densities are probably good predictors of carcass deposition densities. Two recent studies that directly measured the density of cicada carcass deposition reported similarly broad, right-skewed, leptokurtic distributions of deposition densities, with many observations exceeding 150 cicadas/m² (Yang 2004, Nowlin et al. 2007). For example, a field survey of carcass deposition densities across a 120-km range of Brood X in 2004 indicated a mean (\pm SD) carcass deposition density of 56.94 \pm 134.63 cicadas/m², with a range of 0 to 1848 cicadas/m² (Yang 2004). Taken together, these data indicate that cicada deposition densities are highly patchy over small scales, and that both control and treatment deposition densities

employed here fall within the range of commonly encountered natural variation.

I quantified herbivory in two ways: by summing the fraction of leaf area removed by herbivores over all damaged leaves and counting the total number of damaged leaves on each surviving plant ($N = 42$ control plants and $N = 44$ cicada-supplemented plants) on 16 July 2004. I used Wilcoxon rank sum tests to evaluate the hypothesis that cicada detrital inputs increased the area and frequency of damaged leaves on plants. This nonparametric test was appropriate due to the persistent non-normality of residuals in parametric analyses.

2005

Expanded experiments were conducted in 2005 using similar methods as in 2004 in order to investigate the effects of cicada detrital inputs on herbivory in the presence and absence of large mammalian herbivores. Both experiments in 2005 were conducted in a single natural population of bellflowers at the University of Virginia's Mountain Lake Biological Station and the Wilderness Conservancy of Mountain Lake. This population (Giles County, Virginia, 37°21'15.43" N, 80°33'5.76" W) was located in an approximately 0.75-ha area of steep forested ridgeline approximately 1 km from the population studied in 2004. These experiments aimed to present foraging herbivores with neighboring supplemented and control plants, as in a choice experiment. In both years, bellflowers showed a patchy spatial distribution, with nearest neighbor interplant distances ranging from a few centimeters to approximately 10 m. The mean nearest neighbor interplant distance for the 2005 bellflower population was estimated to be approximately 2 m (SD = 1 m) based on subsequent image analysis of hand-drawn maps.

In the first experiment, I investigated the effects of dead cicadas on herbivory in a group of 60 American bellflowers exposed to large mammalian herbivores, including the white-tailed deer (*Odocoileus virginianus*). Experimental plants were randomly assigned to receive either 0 ($N = 30$ plants) or 10 cicadas ($N = 30$ plants) placed by hand on the soil surface immediately below each plant. All plants were initially caged with 122 cm tall, 30 cm diameter cylinders of 2.5-cm grid plastic netting in order to exclude large mammalian herbivores during early establishment; these enclosures were removed on 2 July 2005 to allow large mammalian herbivory during the majority of the growing season.

A second experiment was used to determine the effects of cicada detritus on herbivory in the absence of mammalian herbivores. A group of 100 American bellflowers was randomly assigned to receive either 0 or 10 dead cicadas, and was caged with cylinders of plastic netting throughout the experiment. These enclosures prevented herbivory by deer, but did not prevent herbivory by smaller mammals, arthropods or gastropods.

In both experiments, dead cicada carcasses were provided to small, bolting plants on 7 June 2005 from frozen stores of *Magicicada septendecim* collected in 2004. Cicada losses due to scavenging and surface runoff appeared to be similar to 2004. I measured the initial height (38.8 ± 12.3 cm [mean \pm SD]) and stem diameter (5.0 ± 1.7 mm) of each plant at the beginning of these experiments, and repeated these measurements on 16 August 2005 after most growth and seed set was completed. The relative growth rate of plants in the herbivore enclosure experiment was calculated as $(\ln H_2 - \ln H_1)/(t_2 - t_1)$, where H_x represents plant height at time x , and $t_2 - t_1$ represents the elapsed time in days between successive measurements.

I collected leaf samples at multiple intervals during these experiments in order to determine the effect of cicada detrital inputs on elemental foliar composition. On 27 June 2005, I collected the fifth most apical leaf from each plant; these leaves were dried to constant mass at 50°C and analyzed to determine their nitrogen fractions using a continuous-flow mass spectrometer at the University of California, Davis Stable Isotope Facility. Immediately prior to the harvest on 16 August 2005, I collected three to four terminal leaves from surviving plants in the herbivore enclosure experiment, and scanned leaves from a haphazard subsample of these plants ($N = 37$ control plants and $N = 36$ cicada-supplemented plants) to determine specific leaf area (leaf area/dry leaf mass) as a measure of leaf biomass allocation. The remaining leaf material ($N = 10$ control plants and $N = 7$ cicada-supplemented plants) was analyzed to determine potassium and phosphorus concentrations using microwave acid digestion, atomic absorption spectrometry and inductively coupled plasma atomic emission spectrometry at the University of California Davis Agriculture and Natural Resources Analytical Laboratory. I tested the effect of cicada supplementation on elemental foliar concentrations, specific leaf area and relative growth rates using analysis of variance; in all cases, assumptions of residual normality and homoscedasticity were met.

I quantified two types of plant damage in order to investigate the effect of cicada detrital inputs on mammalian and insect herbivory. In both experiments, I used the number of damaged (or missing) leaves per plant and the number of damaged (or missing) leaves per unit of plant height as general indices of herbivory. Missing leaves were counted if the entire leaf was removed, leaving a visible petiole attachment. These measurements included damage by a wide range of mammalian, arthropod, and gastropod herbivores. In the herbivore-open experiment, several plants were coarsely clipped mid-stem, with the apical portion of the plant wholly removed. For plants at this field site, this type of damage is characteristic of large mammalian herbivory, and I recorded the presence or absence of this stem clipping as a binary response. Because stem clipping reduces the number of observable leaves on

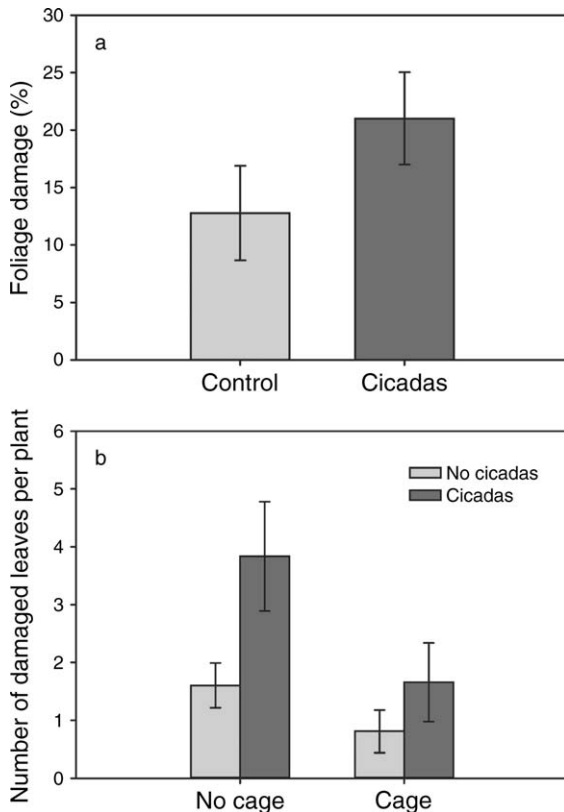


FIG. 2. (a) In 2004, cicada-carcass-supplemented bellflowers experienced greater leaf damage than unsupplemented control plants. Bars represent mean and SE. (b) In 2005 in the open (no cage) experiment, bellflowers that received cicada carcass litterfall experienced greater leaf damage than unsupplemented controls. When deer were excluded (cage), no significant effect of cicada supplementation was observed. Bars represent mean and SE.

the plant, leaf damage measures for these plants were based on remaining leaves. As such, estimates of leaf damage per plant probably represent conservative underestimates of the actual herbivore damage experienced by the plant. Several direct observations of deer herbivory, the height of many clipped stems and the observation that none of the caged plants experienced this kind of stem clipping damage, despite a sufficient gap at the base of the cages to allow browsing by smaller mammals, indicate that this type of damage was mostly or entirely caused by deer browsing.

Several deer were observed at each of these field sites in 2004 and 2005, and county-level harvest data suggests that these nonhunting field sites likely supported a relatively dense deer population, (Knox 1997, Virginia Department of Game and Inland Fisheries 2007). North American white-tailed deer densities have increased substantially over the past century (Knox 1997), although current densities appear to be comparable to or even lower than pre-European settlement densities (McCabe and McCabe 1997). However, because it was not possible to know the actual number of deer that

traversed these field sites over the course of these experiments, one cannot eliminate the possibility that the observed plant damage was caused by a small number of individual deer in each experiment. This would potentially reduce the generality of these experiments, but would also suggest that observed patterns of herbivory are more likely to represent direct comparisons between neighboring plants.

In the open experiment, I investigated whether the addition of dead cicada carcasses increased the proportion of plants receiving mammalian clipping damage using a logistic regression model that included initial plant height and stem diameter as covariates. In both the open and enclosure experiment, I analyzed whether cicada detrital input increased the number and frequency of damaged leaves using an analysis of covariance (ANCOVA) with initial plant height and stem diameter as covariates. In 2005, I used one-tailed tests to evaluate the hypothesis that herbivore damage was greater on cicada-supplemented plants compared to control plants, as observed in 2004. One-tailed tests are appropriate when a testing a specific, directional hypothesis (Zar 1999), though the conclusions of these analyses would be unchanged if evaluated with two-tailed test at $\alpha = 0.05$ in four of five cases. Nonsignificant interaction effects between treatment groups and covariates confirmed the assumption of homogeneous slopes, however these data showed persistent non-normality of residuals in analyses of both response variables and significantly heteroscedastic variances in the open experiment. In order to test the significance of observed patterns in the absence of normality assumptions, I generated empirical distributions of the F statistic using 9999 sets of bootstrapped residuals (Manly 2007). The conclusions of all bootstrap analyses were consistent with results obtained using standard ANCOVA under the assumption of residual normality and Welch's analysis of variance allowing for unequal variances.

RESULTS

In 2004, supplemented cicada detritus was associated with increased herbivory. The area of damaged leaves on cicada-supplemented plants was 78% greater than the area of damaged leaves on control plants (Wilcoxon rank sum test, $P = 0.030$; Fig. 2a), and the proportion of damaged leaves on each plant was 64% greater in the same comparison (Wilcoxon rank sum test, $P = 0.046$).

In the 2005 herbivore-open experiment, 14 of 29 cicada-supplemented plants and nine of 30 control plants were clipped mid-stem during the course of this experiment. A logistic ANCOVA indicated that cicada-supplemented plants were more likely to be clipped than control plants (one-tailed likelihood ratio test, $P = 0.027$). Additionally, cicada-supplemented plants had more damaged leaves per unit of plant height compared to control plants (one-tailed bootstrap ANCOVA, $P = 0.022$), and more damaged leaves on a per plant basis

than control plants (one-tailed bootstrap ANCOVA, $P = 0.011$; Fig. 2b).

In the deer-exclosure experiment, cicada-supplemented plants did not experience greater leaf damage compared to control plants (number of damaged leaves per unit plant height, one-tailed bootstrap ANCOVA, $P = 0.356$; number of damaged leaves, one-tailed bootstrap ANCOVA, $P = 0.318$; Fig. 2b).

Foliar elemental concentrations did not differ between cicada-supplemented and control plants in either open (nitrogen, $P = 0.743$) or deer-exclosure experiments (nitrogen, $P = 0.691$; phosphorus, $P = 0.274$; potassium, $P = 0.286$). Similarly, cicada-supplemented and control plants did not vary in their relative growth rates ($P = 0.339$) or specific leaf area ($P = 0.963$).

DISCUSSION

These results indicate that the pulsed inputs of dead periodical cicada bodies can increase rates of herbivory on fertilized bellflower plants, and that this effect probably results largely from selective herbivory by white-tailed deer. Because of the patchiness of periodical cicada deposition (Whiles et al. 2001, Yang 2004, Nowlin et al. 2007), the bottom-up effects of this resource pulse are likely to be heterogeneous in space; plants receiving substantial detrital inputs are commonly interspersed with plants that receive little or no fertilization, and selective herbivores encounter both fertilized and unfertilized plants. In contrast, invertebrate herbivores showed a pattern of increased herbivory on cicada-supplemented plants, but this difference was not statistically significant. This may have been due to the potentially smaller foraging range of invertebrates and high variability within the invertebrate leaf-chewing guild.

The observation of increased herbivory on cicada-supplemented plants combined with previous observations of foliar nitrogen enrichment suggests that dead cicada bodies may affect aboveground herbivores via a belowground fertilization pathway. If so, these effects would occur only after cicada bodies have been comminuted by macrodetritivores and decomposed by microbes, and after cicada-derived nutrients are assimilated by plants (Yang 2004, 2006). In turn, cicada-supplemented plants may experience both transiently increased bottom-up effects (fertilization) and top-down effects (herbivory) resulting from this resource pulse. These current findings extend previous results from this system by demonstrating a potential bottom-up pathway of resource pulse effects on herbivores and reciprocal top-down effects of herbivores on plants.

The effects of deer herbivory on plant populations appear to be both substantial and highly selective across a wide range of ecosystems (Russell et al. 2001). Previous studies suggest that deer are able to distinguish among plants that vary subtly in their nutritional quality. For example, experimental fertilization of sapling trees with urea has been shown to increase rates

of herbivory by deer, possibly mediated by the "luxury consumption" of nitrogen (Tripler et al. 2002). These current findings suggest that the pulsed input of dead cicada biomass may be a naturally occurring phenomenon that promotes similar herbivore responses.

The specific mechanisms behind these observed effects remain uncertain. Two separate, previous field and greenhouse studies observed increased foliar nitrogen in cicada-supplemented plants, suggesting that increased foliar nitrogen is a plausible explanation for these results (Yang 2004; L. Yang, *unpublished manuscript*). However, these effects were not assayed in the 2004 study, and were not detected in 2005 lab analyses. One possible explanation for this result is that magnitude of fertilization effects may have been reduced in this 2005 field experiment due to the rapid consumption of cicada carcasses by scavengers (Yang 2006), especially in the absence of satiation effects. In comparison, natural cicada emergences occurring over much larger spatial scales than these experimental manipulations would likely lead to proportionally reduced cicada consumption, with corresponding increases in the magnitude of the belowground resource pulse effect per cicada. The observation that increased herbivory persisted in the 2005 experiment despite the lack of a detectable effect on elemental foliar concentrations suggests the possibility that deer and other herbivores may be able to discern subtle or short-lived differences in leaf composition that were not detected in elemental laboratory analyses. Alternative hypotheses to explain the observed pattern of herbivory include fertilization-mediated changes in flowering phenology, growth rates, or secondary chemistry, though evaluating these alternative hypotheses is beyond the scope of available data.

More broadly, this study suggests that pulses of limiting resources can have both positive direct effects on plants and negative indirect effects due to selective herbivory. These findings contribute to general questions in the ecology of resource pulses concerning the indirect effects of resource pulses (Ostfeld and Keesing 2000, Schmidt and Ostfeld 2008, Yang et al. 2008). This study demonstrates that while the bottom-up effects of pulsed detrital fertilization can extend to herbivores, the top-down effects of these same consumers may reduce the positive effects of detrital fertilization for plants. The observation of linked positive direct and negative indirect effects from a single resource pulse raises the question as to whether the combined effects of fertilization and herbivory result in a net gain or loss from the plant perspective. Although general predictions about the effects of resource pulses remain elusive, these results suggest that the effects of pulsed resources on plants may depend on the scale and heterogeneity of pulsed resources, as well as the composition and behavior of the surrounding herbivore community. Increased top-down effects on plants following a resource pulse may be especially likely in systems where the effects of pulsed resources are patchy relative to the

scale of selective foraging by herbivores. These findings underscore the importance of integrating both bottom-up and top-down processes when evaluating the cumulative effects of resource pulses for consumers.

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LITERATURE CITED

- Cory, E. N., and P. Knight. 1937. Observations on Brood X of the periodical cicada in Maryland. *Journal of Economic Entomology* 30:287–294.
- Denyer, J. L., S. E. Hartley, and E. A. John. 2007. Small mammalian herbivore determines vegetation response to patch nutrient inputs. *Oikos* 116:1186–1192.
- Dybas, H. S., and D. D. Davis. 1962. A population census of seventeen-year periodical cicadas (Homoptera: Cicadidae: *Magicicada*). *Ecology* 43:432–444.
- Graham, C., and A. B. Cochran. 1954. The periodical cicada in Maryland in 1953. *Journal of Economic Entomology* 47: 242–244.
- Herms, D. A. 2002. Effects of fertilization on insect resistance of woody ornamental plants: reassessing an entrenched paradigm. *Environmental Entomology* 31:923–933.
- Jaksic, F. M., S. I. Silva, P. L. Meserve, and J. R. Gutierrez. 1997. A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. *Oikos* 78:341–354.
- Karban, R. 1982. Increased reproductive success at high densities and predator satiation for periodical cicadas. *Ecology* 63:321–328.
- Knox, W. M. 1997. Historical changes in the abundance and distribution of deer in Virginia. Pages 27–36 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Institution, Washington, D.C., USA.
- Kyto, M., P. Niemela, and S. Larsson. 1996. Insects on trees: population and individual response to fertilization. *Oikos* 75: 148–159.
- Lima, M., N. C. Stenseth, and F. M. Jaksic. 2002. Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. *Ecology Letters* 5:273–284.
- Manly, B. F. J. 2007. *Randomization, bootstrap, and Monte Carlo methods in biology*. Third edition. Chapman and Hall, Boca Raton, Florida, USA.
- McCabe, T. R., and R. E. McCabe. 1997. Recounting whitetails past. Pages 11–26 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. *The science of overabundance: deer ecology and population management*. Smithsonian Institution, Washington, D.C., USA.
- Nowlin, W. H., M. J. González, M. J. Vanni, M. H. Stevens, M. W. Fields, and J. J. Valente. 2007. Allochthonous subsidy of periodical cicadas affects the dynamics and stability of pond communities. *Ecology* 88:2174–2186.
- Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* 15:232–237.
- Risley, L. S., and D. A. Crossley. 1988. Herbivore-caused greenfall in the southern Appalachians. *Ecology* 69:1118–1127.
- Russell, F. L., D. B. Zippen, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist* 146:1–26.
- Schmidt, K., and R. Ostfeld. 2008. Numerical and behavioral effects within a pulse-driven system: consequences for shared prey. *Ecology* 89:635–646.
- Tripler, C., C. Canham, R. Inouye, and J. Schnurr. 2002. Soil nitrogen availability, plant luxury consumption, and herbivory by white-tailed deer. *Oecologia* 133:517–524.
- Virginia Department of Game and Inland Fisheries. 2007. Virginia deer management plan 2006–2015. Wildlife Information Publication. Virginia Department of Game and Inland Fisheries, Richmond, Virginia, USA.
- Wheeler, G. L., K. S. Williams, and K. G. Smith. 1992. Role of periodical cicadas (Homoptera: Cicadidae: *Magicicada*) in forest nutrient cycles. *Forest Ecology and Management* 51: 339–346.
- Whiles, M. R., M. A. Callahan, C. K. Meyer, B. L. Brock, and R. E. Charlton. 2001. Emergence of periodical cicadas (*Magicicada cassini*) from a Kansas riparian forest: densities, biomass and nitrogen flux. *American Midland Naturalist* 145:176–187.
- White, J., M. Lloyd, and J. H. Zar. 1979. Faulty eclosion in crowded suburban periodical cicadas: populations out of control. *Ecology* 60:305–315.
- Williams, K. S., and C. Simon. 1995. The ecology, behavior, and evolution of periodical cicadas. *Annual Review of Entomology* 40:269–295.
- Williams, K. S., K. G. Smith, and F. M. Stephen. 1993. Emergence of 13-yr periodical cicadas (Cicadidae, *Magicicada*): phenology, mortality, and predator satiation. *Ecology* 74:1143–1152.
- Yang, L. H. 2004. Periodical cicadas as resource pulses in North American forests. *Science* 306:1565–1567.
- Yang, L. H. 2006. Interactions between a detrital resource pulse and a detritivore community. *Oecologia* 147:522–532.
- Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? *Ecology* 89: 621–634.
- Zackrisson, O., M. C. Nilsson, A. Jaderlund, and D. A. Wardle. 1999. Nutritional effects of seed fall during mast years in boreal forest. *Oikos* 84:17–26.
- Zar, J. H. 1999. *Biostatistical Analysis*. Fourth edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.