

25. K. Strimmer, O. G. Pybus, *Mol. Biol. Evol.* **18**, 2298 (2001).  
 26. A. J. Drummond, G. K. Nicholls, A. G. Rodrigo, W. Solomon, *Genetics* **161**, 1307 (2002).  
 27. J. R. Pannell, *Evolution* **57**, 949 (2003).  
 28. P. M. Anderson, A. V. Lozhkin, *Quat. Sci. Rev.* **20**, 93 (2001).  
 29. I. Barnes, P. E. Matheus, B. Shapiro, D. Jensen, A. Cooper, *Science* **295**, 2267 (2002).  
 30. D. K. Grayson, D. J. Meltzer, *J. Archaeol. Sci.* **30**, 585 (2003).  
 31. R. E. Morlan, *Quat. Res.* **60**, 123 (2003).  
 32. We thank the museums and collections that donated

material and T. Higham, A. Beaudoin, K. Shepherd, R. D. Guthrie, B. Potter, C. Adkins, D. Gilchinsky, R. Gangloff, S. C. Gerlach, C. Li, N. K. Vereshchagin, T. Kuznetsova, G. Boeskorov, the Alaska Bureau of Land Management, and the Yukon Heritage Branch for samples, logistical support, and assistance with analyses. We thank D. Rubenstein, R. Fortey, and P. Harvey for comments on the manuscript; Balliol College; the Royal Society; the Natural Environment Research Council; the Biotechnology and Biological Sciences Research Council; Rhodes Trust; Wellcome and Leverhulme Trusts for financial support; and Oxford

Radiocarbon Dating Service and Lawrence Livermore National Laboratory for carbon dating.

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4 June 2004; accepted 4 October 2004

# Periodical Cicadas as Resource Pulses in North American Forests

Louie H. Yang

Resource pulses are occasional events of ephemeral resource superabundance that occur in many ecosystems. Aboveground consumers in diverse communities often respond strongly to resource pulses, but few studies have investigated the belowground consequences of resource pulses in natural ecosystems. This study shows that resource pulses of 17-year periodical cicadas (*Magicicada* spp.) directly increase microbial biomass and nitrogen availability in forest soils, with indirect effects on growth and reproduction in forest plants. These findings suggest that pulses of periodical cicadas create "bottom-up cascades," resulting in strong and reciprocal links between the aboveground and belowground components of a North American forest ecosystem.

Ecologists are increasingly investigating the effects of resource pulses in natural systems (1). Examples of resource pulses include mast years of unusually heavy seed production (2–4), eruptive plant growth after El Niño rainfalls (5–8), postspawning salmon mortality in riparian communities (9, 10), and large-scale insect outbreaks (3, 11–13). Despite great variation in the specific characteristics of these resource pulses, each represents a brief, infrequent event of high resource availability. Resource pulses are of broad interest because they provide extreme examples of the spatiotemporal variability inherent in all ecosystems. Recent theoretical efforts have suggested that many communities may be strongly influenced by transient dynamics after ecological perturbations (14, 15), and empirical studies in diverse systems have demonstrated that resource pulses are often substantial perturbations with strong effects on consumer populations, especially among opportunistic generalist species (1).

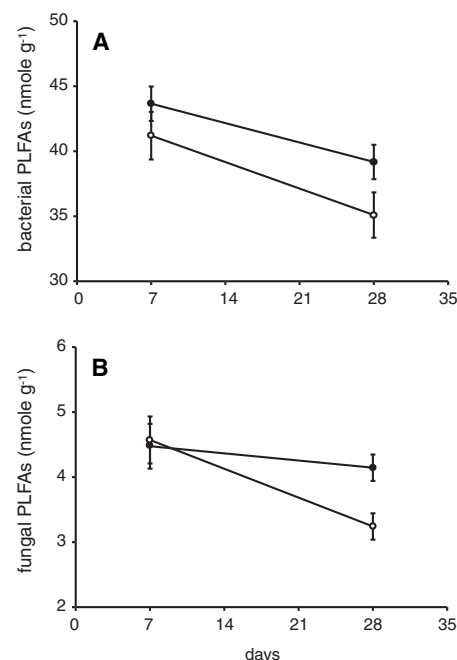
Resource pulses have well-documented effects on aboveground consumers, and they may also provide important inputs to belowground systems (1, 16). In many pulsed systems, only a small proportion of resource biomass is consumed aboveground (17–19), and aboveground predator satiation during re-

source pulses could allow large belowground inputs. Many belowground organisms are well-adapted to take advantage of resource pulses because of their high intrinsic rates of growth and rapid foraging responses (20, 21). Studies in natural systems support the idea that aboveground resource pulses may contribute to belowground systems. For example, mast events in boreal forests produce large inputs of rapidly decomposed spruce seeds that increase soil nitrogen availability (22), and large-scale gypsy moth outbreaks in temperate forests influence nutrient cycling through defoliation and frass deposition (11).

The role of arthropods in regulating plant inputs and facilitating decomposition is widely acknowledged (21), although most ecologists have assumed that arthropod bodies are an unimportant ecosystem biomass component (23). However, the unusual life history of periodical cicadas suggests that they may be a substantial, temporally stored resource pulse. Periodical cicadas are the most abundant herbivores in North American deciduous forests in both number and biomass (24), but their role in forest ecosystems is largely unrecognized because of their long belowground life history. Adult periodical cicadas emerge synchronously across large geographic areas, or "broods," often on a scale of  $10^5$  km<sup>2</sup>. The spatial distribution of cicadas is highly variable and dynamic on small scales (<1 km) and is influenced by fragmentation in forest habitats (17, 23–26). Yet, cicadas are broadly

distributed across a large and diverse area, with a cumulative range encompassing much of the eastern United States (fig. S1). Adult cicadas are aboveground for less than 6 weeks (26). Cicada emergence densities ranging from 3 to 350 cicadas m<sup>-2</sup> are well documented (26), and most cicadas escape predation at high densities (17, 18). Direct measures of cicada densities in 2002 and 2004 support previously reported density estimates (27). In dense populations, the cumulative biomass of periodical cicadas is among the greatest of any terrestrial animal (24) and represents a substantial flux of high-quality biomass (23, 28, 29). Little is known about the belowground effects of this resource pulse.

Here, I investigate the direct belowground and indirect aboveground effects of cicada litter inputs resulting from cicada resource pulses. I conducted field experiments during three con-

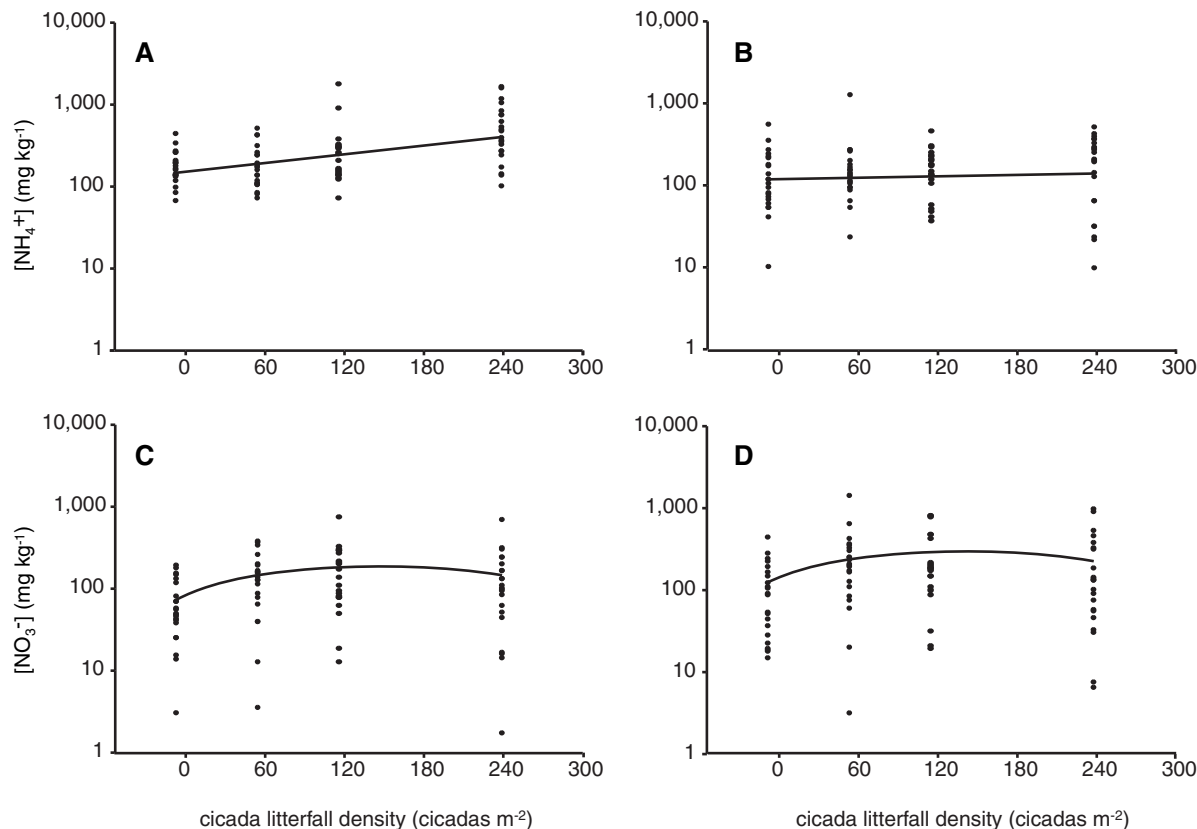


**Fig. 1.** Cicada litterfall increases soil bacterial and fungal PLFAs relative to those of controls, indicating increased microbial biomass. (A) Bacterial PLFAs in cicada-supplemented and control plots 7 and 28 days after experimental cicada pulse. (B) Fungal PLFAs in cicada-supplemented and control plots 7 and 28 days after experimental cicada pulse. Open circles represent control plots, and filled circles represent plots receiving 120 cicadas m<sup>-2</sup>. Error bars show mean  $\pm$  SE.

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**Fig. 2.** Cicada litterfall increases indices of soil nitrate and ammonium availability in forest soils. (A) Soil ammonium availability under experimentally controlled cicada litterfall densities in the first 30 days and (B) in days 31 to 100. (C) Soil nitrate availability under experimentally controlled cicada litterfall densities in the first 30 days and (D) in days 31 to 100. Fitted lines represent least-squares polynomial regressions.



secutive emergence years to examine the effects of cicada carcass deposition on soil microbial biomass, nitrogen availability, and the growth and reproduction of forest plants (27).

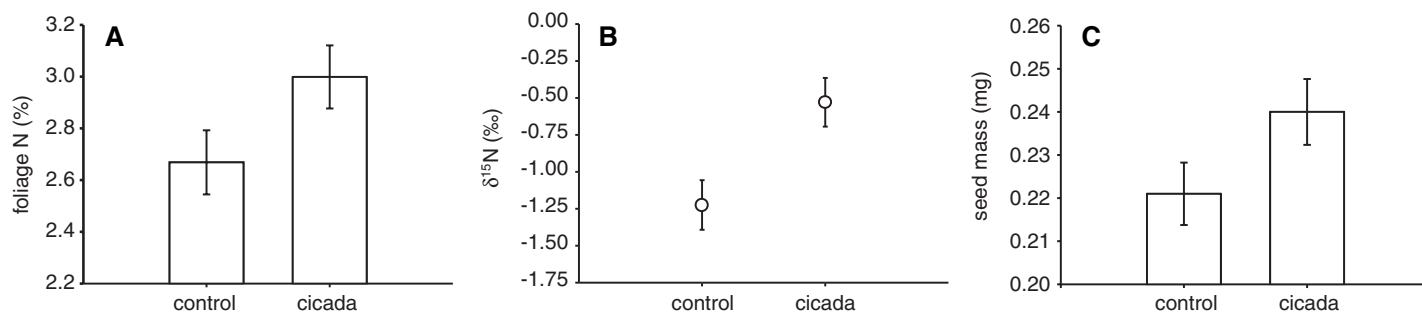
The role of soil microbes in mobilizing organic detritus in plant-available forms is well established (30), and many soil communities respond to detrital carbon inputs with rapid increases of bacterial and fungal biomass. To assess the phenology and magnitude of belowground cicada litterfall effects on microbial biomass, I conducted field experiments in which dead cicada carcasses were applied to replicate forest plots to simulate natural cicada litterfall densities. Differences in the abundance of microbial phospholipid fatty acids (PLFAs) between control (0 cicadas  $m^{-2}$ ) and treatment (120 cicadas  $m^{-2}$ ) plots were undetectable 7 days after the pulsed input (Fig. 1). However, 28 days after the cicada resource pulse, the abundance of bacterial PLFAs was 12% greater in cicada litterfall plots relative to control plots (Fig. 1A,  $P = 0.0383$ ), suggesting an increase in bacterial biomass. The abundance of fungal PLFAs in treatment plots increased by 28% (Fig. 1B,  $P = 0.0036$ ), indicating an increase in fungal biomass. There was little change in the microbial community composition: The fungal-to-bacterial ratio increased insignificantly in cicada-supplemented plots compared with that in control plots ( $P = 0.0918$ ) after 28 days. In contrast, the total abundance of microbial PLFAs was

12% greater in cicada-supplemented plots ( $P = 0.0280$ ). These results are consistent with expectations of broad, rapid microbial growth after a short lag in response to cicada litterfall.

Across the distribution of periodical cicadas, primary productivity is generally believed to be nitrogen limited (31), and mineralized soil nitrogen is the primary nitrogen pool for plant uptake in temperate forest systems (30). Pulsed inputs of nitrogen-rich detritus could be expected to cause an ephemeral acceleration of nitrogen mineralization (16), and cicada carcasses are relatively high-nitrogen inputs [N content = 10.4% (27)]. To assess the effect of cicada litterfall on plant-available soil nitrogen, I conducted field experiments in which cicada carcasses were applied at a range of naturally occurring densities to replicate forest plots during two consecutive cicada emergence years in distant locations. In 2002, cicada supplementation was positively correlated with indices of cumulative soil ammonium [adjusted  $R^2$  ( $R^2_{adj}$ ) = 0.21,  $P = 0.006$ ] and nitrate ( $R^2_{adj} = 0.11$ ,  $P = 0.037$ ) availability during the 100-day experiment (fig. S2). Mean indices of soil ammonium availability were 412% greater in maximally supplemented cicada plots (300 cicada  $m^{-2}$ ) compared with those of controls, and indices of soil nitrate were 199% greater in the same comparison. In 2003, I conducted a second, larger experiment to assess the relationship between cicada litterfall and mineralized soil

nitrogen, the phenology of this relationship, and the generality of previous results. The density of cicada supplementation was again positively correlated with indices of mineralized ammonium (Fig. 2A,  $R^2_{adj} = 0.25$ ,  $P < 0.0001$ ) and nitrate (Fig. 2C,  $R^2_{adj} = 0.06$ ,  $P = 0.027$ ) availability throughout the first 30 days of the experiment. Mean soil ammonium availability increased 306% in maximally supplemented plots (240 cicadas  $m^{-2}$ ) relative to that of controls (Fig. 2A), and mean nitrate availability increased by 249% relative to that of controls (Fig. 2C). A significant interaction effect of cicada litterfall density and sampling period on ammonium availability ( $P = 0.007$ ) suggests that this response was strongly pulsed in time, with larger effects during the first 30 days and no residual effect during the subsequent 70 days of this experiment (Fig. 2B,  $P = 0.522$ ). Conversely, the effect of cicada litterfall on soil nitrate availability was more persistent, showing a positive correlation with cicada litterfall density during the first 30 days, which continued during days 31 to 100 (Fig. 2D,  $R^2_{adj} = 0.06$ ,  $P = 0.029$ ). These results are consistent with expectations of net mineralization from the decomposition of a nitrogen-rich detritus pulse. Although immobilization, plant uptake, and other losses may reduce nitrogen availability over time, these findings suggest that some effects may be long-lasting.

A third field experiment investigated the effects of belowground enrichment from cica-



**Fig. 3.** Cicada litterfall increases (A) foliage nitrogen content, (B) foliage  $\delta^{15}\text{N}$ , and (C) seed size in cicada-supplemented American bellflowers relative to controls. Error bars show mean  $\pm$  SE.

da litterfall on growth and reproduction in a forest plant, the American bellflower (*Campylopus americanus*). This herbaceous annual/biennial forest understorey species is native throughout much of the geographic range of periodical cicadas, and previous studies with this species have suggested that the maternal nutrient environment can contribute to larger seed size (32), which influences germination (33) and seedling performance (34). Pulses of cicada litterfall provide a natural context to interpret plant responses to temporally variable nutrient conditions. This experiment tested the prediction that cicada litterfall increases foliage nitrogen content and seed size in American bellflowers.

In this experiment, cicada-supplemented bellflowers (140 cicadas  $\text{m}^{-2}$ ) from a natural field population produced foliage with 12% greater nitrogen content relative to controls (Fig. 3A,  $P = 0.031$ ), and an 11% decrease in the carbon-to-nitrogen ratio ( $P = 0.025$ ). Stable isotope analysis of bellflower foliage indicated higher  $\delta^{15}\text{N}$  in cicada-supplemented plants compared with that in controls [mean  $\delta^{15}\text{N}_{\text{treatment}} - \text{mean } \delta^{15}\text{N}_{\text{control}} = 0.695$  per mil (‰),  $P = 0.004$ , Fig. 3B]. Cicadas show enriched  $\delta^{15}\text{N}$  relative to their plant diet ( $\delta^{15}\text{N}_{\text{cicada}} = 1.56\%$ ), resulting from preferential retention of the heavier isotope in trophic consumers (27). The increased  $\delta^{15}\text{N}$  in cicada-supplemented plants suggests a mechanistic link between a cicada-derived nitrogen source and increased plant nitrogen assimilation. These experimental plants also produced seeds that were 9% larger than those of controls (Fig. 3C,  $P = 0.028$ ). These results suggest that the belowground effects of cicada pulses can be rapidly used in plant growth and reproduction during the emergence year and may influence aboveground plant processes. These plant responses indicate reciprocal links between aboveground and belowground communities: indirect aboveground enrichment from the belowground decomposition of an aboveground resource pulse that resulted from the life history of a belowground root-feeding herbivore.

Taken together, these results show that cicada litterfall during emergence years can

cause substantial pulsed enrichment of North American forest soils, with direct effects on belowground systems and indirect effects aboveground. These observations suggest that cicada resource pulses could influence forest dynamics over a landscape scale, and the patchiness of cicada distributions may contribute to spatial and temporal heterogeneity in these resource pulse effects. The costs of cicada herbivory and oviposition in plants are well documented, but these findings also suggest the potential for positive and partially compensatory effects on primary productivity due to pulsed fertilization. Indeed, the heretofore puzzling observation of greater wood accumulation in years following cicada emergence (35) may be related to this belowground resource pulse.

Although these belowground and aboveground consequences result from the unusual life history of a single insect genus, these findings may also illustrate a more general consequence of resource pulses for belowground systems. This study suggests a mechanism by which resource pulses may link aboveground and belowground components of other ecosystems. These findings contribute to an emerging body of theory and observations suggesting that rare perturbations may have large and lasting effects in diverse ecological systems.

**References and Notes**

- R. S. Ostfeld, F. Keesing, *Trends Ecol. Evol.* **15**, 232 (2000).
- W. J. McShea, *Ecology* **81**, 228 (2000).
- C. G. Jones, R. S. Ostfeld, M. P. Richard, E. M. Schaubert, J. O. Wolff, *Science* **279**, 1023 (1998).
- J. O. Wolff, *J. Mamm.* **77**, 850 (1996).
- P. Stapp, G. A. Polis, *Oikos* **102**, 111 (2003).
- M. Lima, P. A. Marquet, F. M. Jaksic, *Ecography* **22**, 213 (1999).
- S. J. Wright, C. Carrasco, O. Calderon, S. Paton, *Ecology* **80**, 1632 (1999).
- M. Holmgren, M. Scheffer, E. Ezcurra, J. R. Gutierrez, G. M. J. Mohren, *Trends Ecol. Evol.* **16**, 89 (2001).
- M. Ben-David, T. A. Hanley, D. M. Schell, *Oikos* **83**, 47 (1998).
- J. M. Helfield, R. J. Naiman, *Ecology* **82**, 2403 (2001).
- G. M. Lovett et al., *Bioscience* **52**, 335 (2002).
- J. Elkinton et al., *Ecology* **77**, 2332 (1996).
- S. C. Hahus, K. G. Smith, *J. Mamm.* **71**, 249 (1990).
- A. Hastings, *Ecol. Lett.* **4**, 215 (2001).
- X. Chen, J. E. Cohen, *Proc. R. Soc. London Ser. B.* **268**, 869 (2001).
- D. A. Wardle, *Communities and Ecosystems: Linking*

*the Aboveground and Belowground Components* (Princeton Univ. Press, Princeton, NJ, 2002).

- K. S. Williams, K. G. Smith, F. M. Stephen, *Ecology* **74**, 1143 (1993).
- R. Karban, *Ecology* **63**, 321 (1982).
- B. W. Sweeney, R. L. Vannote, *Evolution* **36**, 810 (1982).
- D. C. Coleman, in *Food Webs: Integration of Patterns and Dynamics*, G. Polis, K. Winemiller, Eds. (Chapman and Hall, London, 1996), chap. 3.
- J. C. Moore, D. E. Walter, H. W. Hunt, *Annu. Rev. Entomol.* **33**, 419 (1988).
- O. Zackrisson, M. C. Nilsson, A. Jaderlund, D. A. Wardle, *Oikos* **84**, 17 (1999).
- M. R. Whiles, M. A. Callahan, C. K. Meyer, B. L. Brock, R. E. Charlton, *Am. Midl. Nat.* **145**, 176 (2001).
- H. S. Dybas, D. D. Davis, *Ecology* **43**, 432 (1962).
- N. L. Rodenhouse, P. J. Bohlen, G. W. Barrett, *Am. Midl. Nat.* **137**, 124 (1997).
- K. S. Williams, C. Simon, *Annu. Rev. Entomol.* **40**, 269 (1995).
- Materials and methods are available as supporting material on Science Online.
- J. J. Brown, G. M. Chippendale, *J. Insect Physiol.* **19**, 607 (1973).
- G. L. Wheeler, K. S. Williams, K. G. Smith, *For. Ecol. Manage.* **51**, 339 (1992).
- J. P. Schimmel, J. Bennett, *Ecology* **85**, 591 (2004).
- C. A. Black, *Soil-Plant Relationships* (Wiley, New York, ed. 2, 1968).
- L. F. Galloway, *Am. J. Bot.* **88**, 832 (2001).
- L. F. Galloway, *Ecology* **82**, 2781 (2001).
- T. E. Richardson, A. G. Stephenson, *Evolution* **46**, 1731 (1992).
- W. D. Koenig, A. M. Liebhold, *Can. J. For. Res.* **33**, 1084 (2003).
- I thank R. Karban, J. Stamps, J. Rosenheim, T. Schoener, L. Galloway, K. Scow, R. Drenovsky, T. Bruce, T. Payne, G. Stauffer, J. Busch, M. Watnik, N. Willits, S. Strauss, K. Spence, J. Fordyce, A. Agrawal, M. Stanton, P. Lee, D. Spiller, A. McCall, V. Rudolf, and three anonymous reviewers for advice and assistance; the Division of Agriculture and Natural Resources Analytical Lab, the Scow Lab, and the University of California at Davis (UCD) Stable Isotope Facility for assistance with laboratory analyses; the University of Virginia's Mountain Lake Biological Station and Blandly Farm, the Stonebridge Farm, the Maryland Department of Forestry, the Wilderness Conservancy of Mountain Lake, the Powdermill Nature Reserve, and Concord College for field assistance. This research was supported by an NSF Graduate Research Fellowship grant, an NSF grant DEB-0121050 to R. Karban, the Mountain Lake Biological Station, Sigma Xi, and the Center for Population Biology, the Population Biology Graduate Group, the John Muir Institute of the Environment, the Department of Entomology, and the Section of Evolution and Ecology at UCD.

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22 July 2004; accepted 4 October 2004

PERSPECTIVES

clusters derived from gravitational lensing and x-ray data sometimes differ by up to a factor of 2 (17, 18), providing a further indication that our picture of these largest cosmological objects is not complete. Therefore, care should be taken before using the x-ray emission from the dark matter-dominated galaxy clusters to derive cosmological distances (19).

The astrophysical observations discussed here indicate that axions and neutralinos may have been abundantly produced in the early universe and/or inside stars. These two types of particles remain the favorite candidates for dark matter and other celestial phenomena. As ever more sensitive detectors are built, more defini-

tive evidence for or against neutralinos and axions should become available. Existence of one does not preclude existence of the other: The dark matter in the universe may contain both of these particles, as well as many other, as yet unforeseen ones.

References and Notes

1. P. Jean *et al.*, *Astron. Astrophys.* **407**, L55 (2003).
2. F. Aharonian *et al.*, *Astron. Astrophys.* **425**, L13 (2004).
3. R. Irion, *Science* **305**, 763 (2004).
4. R. D. Peccei, H. R. Quinn, *Phys. Rev. Lett.* **38**, 1440 (1977).
5. R. D. Peccei, H. R. Quinn, *Phys. Rev. D* **16**, 1791 (1977).
6. R. Bradley *et al.*, *Rev. Mod. Phys.* **75**, 777 (2003).
7. G. G. Raffelt, *Phys. Rep.* **333–334**, 593 (2000).
8. G. G. Raffelt, *Annu. Rev. Nucl. Part. Sci.* **49**, 163 (1999).
9. CERN Axion Solar Telescope (<http://cast.web.cern.ch/CAST>).

10. L. DiLella, A. Pilaftsis, G. Raffelt, K. Zioutas, *Phys. Rev. D* **62**, 125011 (2000).
11. L. DiLella, K. Zioutas, *Astropart. Phys.* **19**, 145 (2003).
12. K. Zioutas, K. Dennerl, L. DiLella, D. H. H. Hoffmann, Th. Papaevangelou, *Astrophys. J.* **607**, 575 (2004).
13. K. Ebisawa, Y. Maeda, H. Kaneda, S. Yamauchi, *Science* **293**, 1633 (2001).
14. M. P. Muno *et al.*, *Astrophys. J.* **613**, 326 (2004).
15. C. Day, *Phys. Today* **56**, 16 (March 2003).
16. S. Peng Oh, *Mon. Not. R. Astron. Soc.* **353**, 468 (2004).
17. I. G. McCarthy, A. Babul, G. P. Holder, M. L. Balogh, *Astrophys. J.* **591**, 515 (2003).
18. I. G. McCarthy, G. P. Holder, A. Babul, M. L. Balogh, *Astrophys. J.* **591**, 526 (2003).
19. A. Cho, *Science* **304**, 1092 (2004).
20. We thank Ch. Eleftheriadis, Y. Semertzidis, and S. Vascotto for their assistance. Supported by the Bundesministerium für Forschung und Technologie, the General Secretariat for Research and Technology (Greece), and CERN.

ECOLOGY

# Oh the Locusts Sang, Then They Dropped Dead

Richard S. Ostfeld and Felicia Keesing

The Bob Dylan song “Day of the Locusts” refers to the cacophony from the 1970 emergence of 17-year cicadas (*Magicalcada* spp.), which happened to coincide with his acceptance of an honorary degree from Princeton University. These cicadas, which dutifully reappeared aboveground

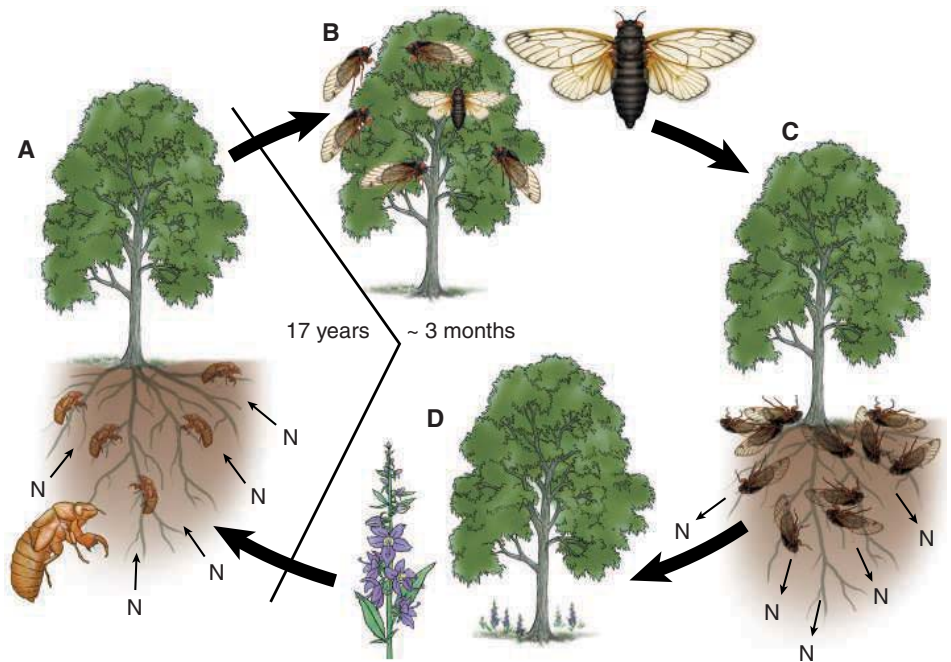
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in 1987 and then again this year, are a quintessential case of a resource pulse—a transient, multiannual episode of resource superabundance. On page 1565 of this issue, Yang (1) describes the ramifying impacts that massive pulses of cicada carcasses have on forest soils, microbial biomass, nitrogen availability, and reproductive success of understory plants.

Resource pulses typically are associated with reproductive events in plants, such as synchronized heavy seed production (mast-seeding) within populations of oaks or bamboos, and even more spectacularly, across dozens of genera of paleotropical dipterocarp trees (2). Plant populations that synchronize seed production achieve high reproductive success because seed predators can only consume a fraction of the hyperabundant resource (“predator satiation”) (3), and most of the escapees ger-

minate. Similarly, so many periodical cicadas are involved in the dissonant mating swarms that their predators—principally birds—can consume no more than 15% of the peak numbers (4). The remainder die after reproducing and drop to the forest floor.

Although much is known about the evolutionary causes of synchronized reproductive events, only recently have ecologists begun to analyze the consequences of resource pulses for ecosystems (5). The predominant type of resource pulse—mast seeding—occurs in grasses, annual forbs, shrubs, and trees, across at least four continents and from deserts to tropical rain forests. Generalist consumers—often rodents—are the most immediate beneficiary of this superabundant resource, and they respond with population outbreaks of their own. These rodent irruptions, in turn, result in severe impacts on their alternate prey, such as songbird eggs (6), their avian



**A 17-year pulse of nitrogen from cicada carcasses.** (A) For 17 years, cicada nymphs feed on tree xylem, slowly incorporating belowground nitrogen (N) absorbed by the tree’s roots. (B) Upon emergence, adult cicadas mate and lay eggs within a several-week period, and then die and drop to the forest floor. (C) The accumulated nitrogen in their carcasses is released after a burst of activity by microbial decomposers. (D) This spike of available soil nitrogen leads to increased nitrogen content and seed size of the American bellflower (*C. americanum*), an understory plant.

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and mammalian predators (7), and their parasites and pathogens (5, 8). In these cases, the pulsed resource is quickly converted into consumer biomass, and the direct and indirect consequences for ecosystems follow this consumer pathway.

The research by Yang demonstrates a new pathway by which resource pulses can affect ecosystems—through the action of decomposers (1). Unlike seeds, which germinate following escape from predation, periodical cicadas die and rot. These insects are a high-quality fertilizer indeed (about 10% nitrogen), delivered at a rate of up to 0.5 kg m<sup>-2</sup>. Within a month of a simulated cicada irruption, biomass of both fungal and bacterial decomposers in the soil increased dramatically, and this in turn resulted in a tripling of soil ammonium, and a more-than-doubling of soil nitrate concentration. As with other fertilizers, the cicada-induced flush of soil nutrients ultimately boosted nitrogen concentration and seed mass in the American bellflower (*Campanulastrum americanum*), an understory plant.

Periodical cicada nymphs spend 16-plus years attached to tree roots sucking on xylem (9), resulting in a persistent, long-term deflection of soil-derived nitrogen from leaves into insect biomass. Upon emergence, the cicadas then transport this stolen nitrogen aboveground. From there, a

little ends up in avian or mammalian consumer tissue, and another fraction goes to cicada egg production, but most becomes fertilizer, first for soil microbes and then for understory plants like bellflowers. Because the nitrogen-enriched bellflower tissues die and decompose themselves, the trees would seem to be the ultimate recipients of the prodigal nitrogen's return underground (see the figure).

Analyzing radial tree-ring growth of oaks within the geographic ranges of 13-year and 17-year cicadas, Koenig and Liebhold (10) found a ~4% decrease in tree growth during the year of emergence, which they attributed to the damage caused by oviposition wounds in twigs. However, some of Koenig and Liebhold's analyses also demonstrated a ~1% increase in tree radial growth during the first 4 years after emergence, for which they had no explanation. The fertilization effect of cicada carcasses reported by Yang might account for this apparently compensatory stimulation of growth after emergence.

Spectacular resource pulses like the emergence of periodical cicadas constitute one of the more obvious demonstrations that ecological systems rarely exist in equilibrium states, but instead are in constant flux. By tracing the responses of populations or entire trophic levels to resource pulses, ecologists can assess the extent to

which resources versus consumers control abundance or biomass—in other words, whether control is bottom-up or top-down. They can also determine the strength and nature of interconnections between species or trophic levels. A trophic cascade occurs when top-down effects permeate through three or more trophic levels (11), and we suggest that the cicada-decomposer-plant system, which represents the penetrance of bottom-up effects through three trophic levels, be considered a “trophic fountain.” The bottom-up metaphor, of course, refers to the effects of lower trophic levels on higher ones. In a more physical sense of the metaphor, Yang's work demonstrates how organisms and materials flow inexorably from bottom to top and back again.

#### References

1. L. H. Yang, *Science* **306**, 1565 (2004).
2. L. M. Curran, M. Leighton, *Ecol. Monogr.* **70**, 101 (2000).
3. D. H. Janzen, *Ann. Rev. Ecol. Syst.* **2**, 465 (1971).
4. K. S. Williams, K. G. Smith, F. M. Stephen, *Ecology* **74**, 1143 (1993).
5. R. S. Ostfeld, F. Keesing, *Trends Ecol. Evol.* **15**, 232 (2000).
6. K. A. Schmidt, R. S. Ostfeld, *Ecology* **84**, 406 (2003).
7. B. Jedrzejewska, W. Jedrzejewski, *Predation in Vertebrate Communities: The Białowieża Primeval Forest as a Case Study* (Springer, New York, 1998).
8. T. L. Yates *et al.*, *BioScience* **52**, 989 (2002).
9. J. White, C. E. Strehl, *Ecol. Entomol.* **3**, 323 (1978).
10. W. D. Koenig, A. M. Liebhold, *Can. J. For. Res.* **33**, 1084 (2003).
11. M. L. Pace, J. J. Cole, S. R. Carpenter, J. F. Kitchell, *Trends Ecol. Evol.* **14**, 483 (1999).

## PLANETARY SCIENCE

# Nothing Simple About Asteroids

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**T**welve years ago, scientists obtained the first close look at asteroids, when the Galileo mission en route to Jupiter acquired high-resolution images of Gaspra and Ida (1, 2). Since then, much has changed but little has solidified. Even following a year-long rendezvous by NASA's NEAR Shoemaker orbiter at asteroid Eros (see first and second figures) (3), asteroid science remains at a crossroads. The surface remote sensing and imaging techniques applied to date have yet to resolve a single fundamental question of asteroid geophysics or chemistry. A detailed new model for asteroid seismology, reported by Richardson *et al.* on page 1526 of this issue (4), shows how acoustic reverberations from impacts can cause asteroid topography to flatten, diffusing small-scale features and erasing small craters. Like other recent

models (5), this work also illustrates how seismological experiments—akin to those conducted by Apollo astronauts on the Moon—may soon reveal information about the structure and evolution of comets and asteroids.

Asteroids are famously menacing, and the movie script requires them to be tamed or destroyed. The hazard posed by asteroids has focused minds, but their essence is the more interesting question. Asteroids are not mere rocks; their own self-gravitation, however minuscule, is central to their evolution (6). Nor are they planets: Most asteroids are undifferentiated (never melted) precursors to planets, or fragments of these. Others are

fragments of differentiated planet precursors that were catastrophically disrupted long ago. Most are very porous, spin rapidly, and are irregular in shape, suggesting a tumultuous history. Contradictory attempts have been made to correlate their visible and infrared colors to the confusing taxonomy of meteorites.

As for asteroid geophysics, the most basic terminology is undecided. Conflicting definitions exist for terms such as regolith,



**Eros: the best studied asteroid.** This image of the 33 by 13 by 13 km near-Earth object, with dimensions of 33 by 13 by 13 km<sup>3</sup>, was taken on 28 January 2001 by the NEAR Shoemaker orbiter.

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