Deposition and decomposition of periodical cicadas (Homoptera: Cicadidae: *Magicicada*) in woodland aquatic ecosystems

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Abstract. Many freshwater ecosystems receive allochthonous resource subsidies from adjacent terrestrial environments. In eastern North American forests, geographic broods of periodical cicadas emerge every 13 to 17 y to breed, and local abundances can sometimes be >300 individuals/m^2. Most individuals avoid predation, senesce after breeding, and become a resource pulse for forest ecosystems; some cicada carcasses enter freshwater ecosystems where they represent a detrital resource pulse. Here, we present a 2-part study in which we examined the deposition of cicada detritus into woodland ponds and low-order streams in southwestern Ohio during the emergence of Brood X periodical cicadas. We compared the deposition of nutrients associated with periodical cicada detritus and terrestrial leaf litter into small woodland ponds and low-order streams. We used a laboratory experiment to compare patterns of decomposition and nutrient release of adult periodical cicada carcasses and sycamore leaf litter. Input of periodical cicada detritus to woodland streams and ponds was a function of local cicada emergence densities. Organic C loading to woodland aquatic ecosystems from cicada detritus was substantially less than that from terrestrial leaf litter; however, the higher mass-specific N and P content of cicada material made cicada detritus a relatively important nutrient input. N and P deposited in cicada detritus represented 0.2 to 61% of the N and 0.3 to 50% of the P deposited into woodland aquatic ecosystems via terrestrial leaf litter. Decomposition experiments indicated that cicada detritus was of much higher quality than was sycamore leaf litter; female and male cicada carcasses lost mass at significantly faster rates than sycamore leaves (female $k = -0.05$/d, male $k = -0.04$/d, sycamore leaf $k = -0.002$/d). Release rates of C, N, and P from cicada carcasses were 4, 39, and 150× greater, respectively, than release rates from sycamore leaves. Our study indicates that periodical cicada detritus can represent a substantial allochthonous resource pulse to forested aquatic ecosystems and that cicada detritus is of substantially higher quality than is terrestrial leaf litter. These results suggest that deposition and decomposition of periodical cicada detritus can affect the productivity and dynamics of woodland aquatic ecosystems and that the role of animal-derived resource pulses to ecosystems requires further exploration.

Key words: allochthonous subsidy, resource pulse, decomposition, stoichiometry, periodical cicada, nutrient recycling, leaf litter.

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Virtually all freshwater ecosystems, including streams, rivers, wetlands, and lakes, receive prey, nutrients, and energy from the terrestrial environment (Wallace et al. 1997, Wipfli 1997, Pace et al. 2004, Mehner et al. 2005, Graham et al. 2006). Terrestrially derived (allochthonous) resource subsidies can profoundly affect foodweb structure, productivity, and

stability of aquatic ecosystems (Wallace et al. 1997, Huxel and McCann 1998, Huxel et al. 2002, Takimoto et al. 2002, Nowlin et al. 2007). Many terrestrial resource subsidies occur as pulsed inputs, either seasonally (i.e., deposition of terrestrial insects or autumnal leaf litter) or coincident with large perturbation events (i.e., large storm event and watershed runoff; Nowlin et al. 2008). Small-sized aquatic ecosystems, such as low-order streams and woodland ponds, are closely tied to the terrestrial landscape and receive pulses of terrestrial organic matter that affect community and ecosystem structure and function (Wallace et al. 1997, Rubbo and Kiesecker 2004, Rubbo et al. 2006, Nowlin et al. 2007, 2008). In particular, ponds and headwater streams in forested areas receive considerable inputs of detritus, such as leaf litter and woody debris, from terrestrial primary producers. These inputs serve as the principal energy and nutrient source for their food webs (Wallace 1997, Johnson and Wallace 2005, Rubbo et al. 2006).

In eastern North American forests, periodical cicadas (Homoptera:Cicadidae:*Magicicada*) synchronously emerge from below ground in early to midsummer every 13 to 17 y, and local abundances vary between 60 and 300 individuals/m² (Dybas and Davis 1962, Rodenhouse et al. 1997, Yang 2004). The highest emergence densities typically occur along forest edges or in lowland riparian areas (Dybas and Davis 1962, Williams et al. 1993, Rodenhouse et al. 1997). The synchronous emergence of large numbers of individuals satiates predators, so only a fraction of an emergent cicada brood falls victim to predation. Most individuals reproduce, die, and become deposited as detritus on the landscape (Williams et al. 1993). These carcasses are a large resource pulse for habitats in forest ecosystems (Yang 2004, 2006, Nowlin et al. 2007, Menninger et al. in press).

Periodical cicada carcasses potentially are a high-quality detritus source, and contain relatively large amounts of N, protein, and lipids (Brown and Chippendale 1973). Thus, mass deposition of periodical cicada carcasses during an emergence event represents a high-quality resource pulse for terrestrial forest communities, and affects soil microorganisms, herbaceous vegetation, arthropods, birds, and rodents (Hahus and Smith 1990, Krohne et al. 1991, Yang 2004, 2006, Koenig and Liebhold 2005). A portion of the emergent biomass also is deposited in small woodland aquatic habitats, where it might be consumed by larger aquatic organisms (Williams and Simon 1995, Vokoun 2000). Deposition of periodical cicada detritus in aquatic systems releases substantial amounts of dissolved nutrients that elicit rapid population responses from bacteria, algae, and invertebrates (Now-

lin et al. 2007) and stimulate community metabolism (Menninger et al. in press). Despite the implications of this large and infrequent resource pulse to the productivity and dynamics of woodland aquatic systems, little is known about its importance relative to other resource inputs, such as terrestrial leaf litter.

Terrestrial primary producer detritus is often the dominant energy and nutrient source in forest ponds and streams, but differences in the seasonal timing and quality of terrestrial primary producer litter and cicada detritus might lead to substantially divergent community and ecosystem responses to these resource pulses. Leaf litter typically is imported to forest aquatic ecosystems during a cool period of the year (autumn and early winter) when microbial decomposers and invertebrate consumers have low metabolic and feeding rates. Furthermore, much of the energy in leaf litter is bound into recalcitrant polyphenolic compounds, such as lignin (Chapin et al. 2002). Given the recalcitrant nature of this resource, it can persist for relatively long periods of time and provide extended support for food webs. Inputs of terrestrial detritus can support aquatic food webs for years (Wallace et al. 1997, Hall et al. 2000). In contrast, periodical cicada carcasses are a labile nutrient and energy source that is deposited in aquatic systems during summer. Therefore, when periodical cicadas die and fall into woodland aquatic habitats, they might decompose quickly and potentially could release significant amounts of C, N, and P, which can stimulate heterotrophic bacteria and algae (Nowlin et al. 2007). The initial quality of leaf litter and cicada carcasses undoubtedly differs when they enter stream and pond habitats, but how the stoichiometry and nutrient release rates of these organic matter sources differ during the decomposition process is yet to be determined.

We examined nutrient dynamics associated with the deposition and decomposition of periodical cicadas in forested aquatic habitats. We had 2 goals: 1) to compare deposition of nutrients and organic matter associated with periodical cicada detritus and terrestrial leaf litter in small woodland ponds and low-order streams, and 2) to determine patterns of decomposition, nutrient stoichiometry, and nutrient release rates of periodical cicada carcasses and terrestrial leaf litter in aquatic systems. To address the 1st question, we examined the inputs of cicada litter into forest aquatic habitats during the summer of an emergence event and estimated loading of P, N, and C from cicada detritus. We then contrasted these loadings to inputs of terrestrial leaf litter in autumn of the same year. We addressed the 2nd question by conducting a replicated laboratory microcosm experiment in which we examined the decom-
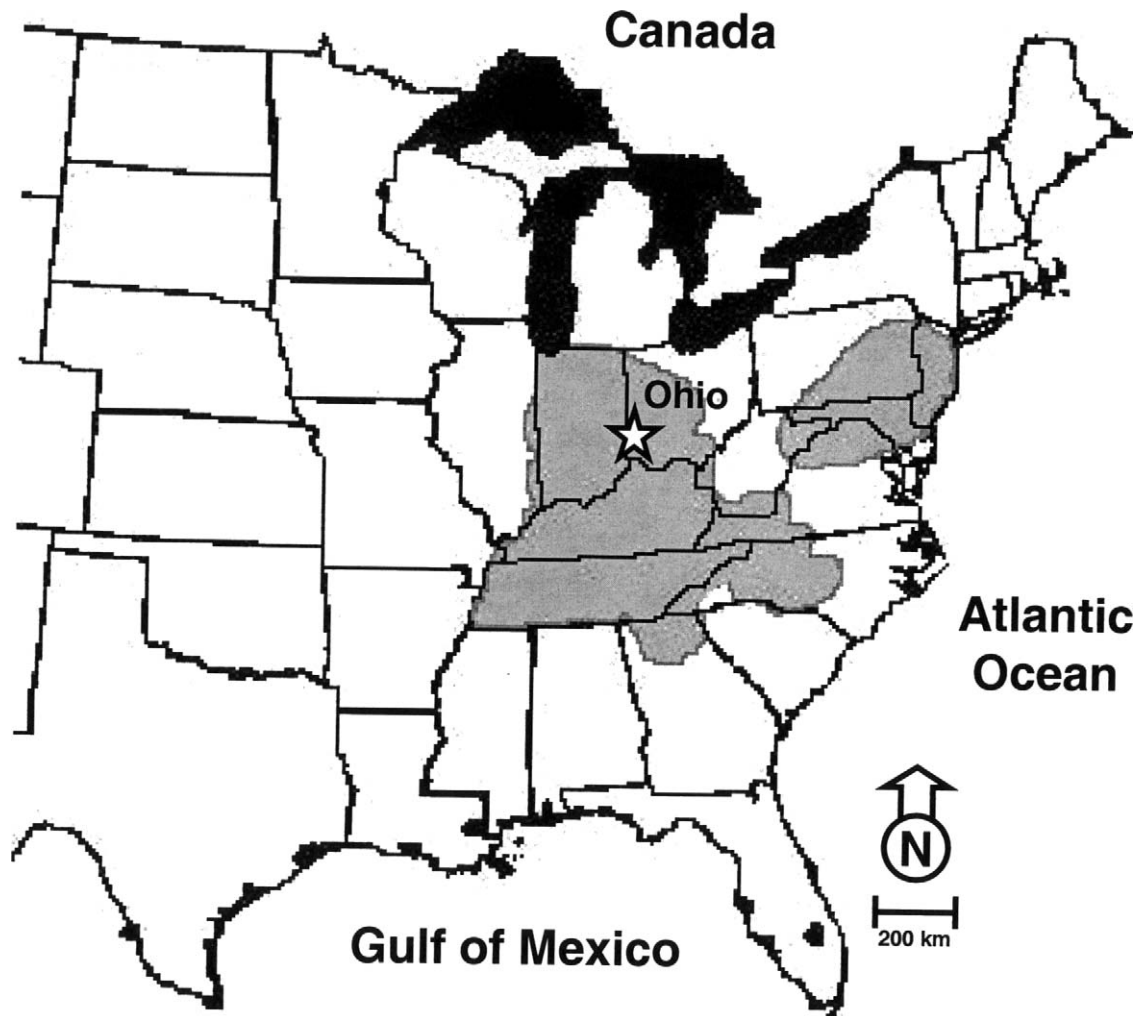
FIG. 1.   Geographic distribution of Brood X periodical cicadas that emerged in summer 2004. The shaded grey area is the geographic distribution of Brood X cicadas. The location of the study area within the state of Ohio is indicated with a star.

position rates of periodical cicada carcasses and terrestrial leaf litter under controlled conditions.

Methods

Our study was conducted in southwestern Ohio (USA) in summer 2004. Starting in mid-May 2004, periodical cicadas emerged over much of Ohio as part of the Brood X emergence (Fig. 1). Brood X cicadas emerge in the midwestern and eastern US over an area of 15 states (Marshall 2001). Cicadas emerging at our study sites were composed of 3 species: *Magicicada cassini*, *Magicicada septendecim*, and *Magicicada septendecula*.

Deposition of cicada detritus and leaf litter

To estimate the deposition of periodical cicada litter into woodland aquatic habitats, we studied 10 temporary and semipermanent woodland ponds and six 30-m stream segments within 10 km of Oxford, Ohio. We chose all pond and stream sites before the Brood X cicada emergence period began. We chose sites that were in lowland areas with abundant woody vegetation. Detailed descriptions of pond and stream sites and the sampling design used to collect cicada litter are presented in Nowlin et al. (2007). Briefly, we used plastic litterfall baskets to estimate loadings of cicada detritus during the emergence period. We collected all cicada-derived litter from baskets every 3 to 5 d and sorted it into 5 specific types: whole nymphs, molted nymph exoskeletons, whole adults, severed adult heads with attached wings, and severed wings (Williams et al. 1993). We determined dry mass deposition (g/m^2) for each basket, and we estimated areal nutrient loading $(mmol/m^2$ of C, N, and P) in each individual basket during the emergence period by multiplying the total mass of each litter type

deposited in a basket over the emergence period by the amount of C, N, and P in each litter type (see below). Detailed methods used to measure nutrient content in each cicada litter type are presented in Nowlin et al. (2007). We determined ecosystem-level areal loadings of cicada litter in individual ponds and stream reaches from the mean deposition of cicada matter and nutrients in all baskets within each pond or stream reach. Open litterfall baskets are used commonly for estimating deposition of organic matter (OM) into aquatic systems; however, it is likely that our measurements of cicada OM and nutrient deposition are underestimates because of losses to scavenging birds and mammals (Yang 2004, WHN, personal observation).

We replaced litter baskets in the same locations at all sites in early September 2004 to estimate deposition of terrestrial leaf litter into the same ponds and streams. From late September until early December, we removed all leaf litter material collected in baskets every 3 to 4 wk and brought it to the laboratory, where we dried it at 60°C for 48 to 72 h and determined dry mass (g). The dominant tree species and their relative abundances varied among all sites, but several tree species, including sycamore (*Platanus occidentalis*), red maple (*Acer rubrum*), hickory (*Carya tomentosa*), beech (*Fagus* spp.), tulip tree (*Liriodendron tulipifera*), and white oak (*Quercus alba*), were common at most sites.

Leaf litter collected in baskets was composed of leaves from multiple species, and many leaves were fragmented and difficult to identify. We used the nutrient content of sycamore to estimate nutrient loading associated with leaf litter deposition. Sycamore is an abundant tree species in riparian zones in Ohio (Kupfer 1996, Vadas and Sanger 1997). We collected sycamore leaf litter from a riparian area in January 2004, dried 6 batches of 5 to 7 individual leaves at 60°C for 48 h, and homogenized each batch. We analyzed C, N, and P content of batch samples. We measured C and N of leaf material with a Perkin Elmer 2400 Series II CHN analyzer (Perkin Elmer, Boston, Massachusetts). We digested samples with HCl and measured PO_4^{3-} on a Lachat QuikChem® FIA+ 8000 Series autoanalyzer (Lachat Instruments, Loveland, Colorado). For comparison purposes, we also obtained %N and %P (by mass) of senesced leaf litter from Killingbeck's (1996) review. We calculated the average %N and %P of senesced leaves of red maple, hickory, beech, tulip tree, and white oak from table 1 in Killingback (1996). The %C values for these litter types were not reported in Killingbeck (1996).

Our analyses of sycamore leaves indicated that C, N, and P were 46.90, 1.01, and 0.04% of sycamore litter dry mass, respectively. These values are similar to those of Killingbeck (1996), who reported %N and %P values for senesced red maple, hickory, beech, tulip tree, and white oak leaves that were 0.83 ± 0.24% and 0.05 ± 0.02% (mean ± 1 SD), respectively. Therefore, we calculated mean values for mass-specific leaf nutrient content from Killingbeck's (1996) values and our analyses (C: 46.90%, N: 0.877%, P: 0.045%). We used these percentages and the dry mass deposition of leaf litter (g/m²) into each basket to estimate nutrient (C, N, and P) loading from leaf litter into baskets at pond and stream sites. We determined leaf litter loading into each individual basket (mg dry mass/ m² and mmol/m² of C, N, and P from late September to early December) and estimated ecosystem-level areal loadings of leaf litter into individual ponds and stream reaches by calculating the mean amount of leaf matter and nutrients deposited in all baskets within an individual pond or stream reach.

Cicada emergence densities

We also wanted to know whether cicada deposition rates into woodland ponds and low-order streams were related to local cicada emergence densities. We estimated cicada emergence densities around woodland ponds and streams by counting cicada emergence holes in the ground (Williams et al. 1993, Rodenhouse et al. 1997, Whiles et al. 2001). We estimated emergence densities in the areas immediately adjacent to all ponds and stream sites ~2 to 3 wk after the onset of the Brood X emergence (Williams et al. 1993). Detailed description of the rationale and methods used to determine cicada emergence densities are presented in appendix A in Nowlin et al. (2007). Briefly, at pond sites, we counted cicada emergence holes along transects radiating out in 3 randomly selected compass directions from the edge of a pond. At stream sites, we estimated cicada emergence densities along 2 transects that were parallel to the stream banks. We calculated average local cicada emergence density (number/m²) at each site as the mean emergence density of all quadrat counts taken at a site.

Decomposition and nutrient release of cicada detritus and leaf litter

We examined patterns of decomposition and nutrient release in cicada detritus and terrestrial leaf litter in laboratory experiments. Use of a laboratory setting to examine decomposition and nutrient release eliminates factors that can affect OM decomposition, such as water movement (Hoover et al. 2006) and the presence of detritivorous metazoans (Cummins et al. 1989, Dangles and Guerold 2001). Thus, our laboratory experiments provide insight into the relative quality of

periodical cicadas and leaf litter as detritus sources and the potential input of nutrients from both OM types to the nutrient cycles of woodland aquatic ecosystems.

We collected live male and female adult cicadas from the Miami University campus (Oxford, Ohio) during the peak of the emergence period. We examined decomposition of male and female cicadas separately because males and females are likely to differ in their nutrient content and biochemical composition; male bodies have a large resonance chamber that is used for calling, and female bodies are full of eggs and reproductive organs. We used *M. cassini* adults for cicada decomposition experiments because this species was the most abundant species at most field locations (WHN, personal observation).

We used essentially the same protocol to examine decomposition of cicada adults and terrestrial leaf litter. We placed 2 male or 2 female adult *M. cassini* cicadas into individual 125-mL high-density polyethylene (HDPE) bottles (18 replicate bottles/gender treatment) and ~1 g of an intact piece of dry sycamore leaf litter into 18 individual 125-mL HDPE bottles. We collected water from a nearby pond (Miami University Ecological Research Center) in a large plastic carboy, screened it through 63-μm Nitex mesh to remove macroinvertebrates, and added 125 mL of the screened water to each bottle. We used this water source because decomposition experiments were conducted in conjunction with an outdoor pond mesocosm experiment that used this water source (Nowlin et al. 2007). We inserted foam stoppers loosely into the bottle tops and incubated bottles in a walk-in environmental chamber at 21°C under constant full-spectrum fluorescent illumination (~100 μmol quanta m^{-2} s^{-1}). We removed 3 replicate bottles containing male and female cicadas from the environmental chamber on days 5, 6, 8, 12, 18, and 20, and 3 replicate bottles containing sycamore leaf material on days 3, 8, 10, 12, and 20. On each sampling day, we removed all remaining cicada or leaf material from each bottle and dried it at 60°C for 48 h to determine dry mass. We homogenized dried material from each bottle and analyzed C, N, and P content of the material.

We estimated mass loss rates of cicada and sycamore leaf material during decomposition experiments from plots of the % initial dry mass remaining as a function of time (days). We could not directly determine the initial dry mass of the pairs of male and female cicadas placed in bottles, so we measured the dry mass of additional pairs of male and female adult *M. cassini* ($n = 8$ for male and female pairs). Mean (±1 SD) dry masses (g) of female and male *M. cassini* pairs were 0.554 ± 0.07 and 0.336 ± 0.05, respectively. Variation among pairs of males and females was small, so we used these values as estimates of initial dry mass of cicada carcasses.

Data analysis

We compared loadings of cicada matter, leaf litter, and associated nutrients between ponds ($n = 10$) and streams ($n = 6$) with 1-way analysis of variance (ANOVA). We plotted loadings of cicada detritus and associated nutrients to sites as a function of the local cicada emergence density, and used ordinary least-squares (OLS) linear regression to examine the relationship between deposition and the local emergence density of periodical cicadas. We inferred significance at $\alpha \leq 0.05$.

To assess potential differences in decomposition of the 3 detritus types in the laboratory experiments, we plotted % initial dry mass remaining of each detritus type (adult female cicada carcasses, adult male cicada carcasses, and sycamore leaf litter) as a function of time (d) and fitted an exponential decay model to the data to produce a decay constant (k) for each detritus type. To determine whether mass loss rates differed between detritus types, we regressed $\ln(x)$-transformed % initial mass remaining of each detritus type as a function of day, and compared slopes of these relationships with analysis of covariance (ANCOVA). Percent initial mass remaining was the dependent variable, detritus type was the independent (categorical) variable, and day was the covariate. We used a sequential Bonferroni procedure to adjust α (Rice 1989, Moran 2003) for multiple comparisons (females vs males, females vs leaves, and males vs leaves). We ranked response-variable p-values from least to greatest and compared the lowest p-value to α/j, where j is the number of comparisons ($\alpha = 0.05/3 = 0.017$). We inferred significance if the p-value of a response variable was lower than the adjusted α. We compared greater p-values progressively to $j - 1$, $j - 2$, etc., until the p-value of a response variable exceeded the adjusted α.

We examined changes in nutrient content of the 3 detritus types during the decomposition experiment by plotting molar nutrient ratios (C:N, C:P, and N:P) as functions of day and analyzing with OLS regression. We compared rates of change in nutrient ratios of the 3 detritus types over the course of the experiment (slopes of the OLS regressions) with ANCOVA. Molar nutrient ratio was the dependent variable, detritus type was the independent (categorical) variable, and day was the covariate. We log(x)-transformed data before analyses to meet assumptions of linearity and homogeneity of variances associated with ANCOVA.

TABLE 1. Nutrient content (mmol/g dry mass) of types of periodical cicada detritus and leaf litter. Sycamore leaf litter values are based on our analyses. The composite leaf values are mean C, N, and P content from our sycamore leaf analyses and data for 6 tree species commonly found in Ohio riparian forests (Killingbeck 1996).

Detritus type	C content (mmol/g dry mass)	N content (mmol/g dry mass)	P content (mmol/g dry mass)
Nymph	42.92	6.61	0.17
Exuvium	37.32	6.46	0.02
Adult female body	44.31	8.42	0.25
Adult male body	47.50	7.23	0.22
Head and wing pair	42.17	8.34	0.22
Wing	41.04	8.99	0.07
Sycamore leaf	39.08	0.72	0.001
Composite leaf	39.08	0.63	0.02

We used a sequential Bonferroni procedure to adjust α for multiple comparisons.

We used changes in mass and nutrient content of each detritus type during decomposition experiments to compare short-term nutrient release rates of each detritus type. We calculated release rate (RR; μmol/d) of C, N, and P from each detritus type as:

$$RR(\mu mol/d) = ([DM_0 Nut_0] - [DM_{20} Nut_{20}])/20$$

where DM is the dry mass (mg) of items at day 0 and day 20 and Nut is the proportional nutrient content (C, N, or P mg/mg dry mass) on days 0 and 20 of the experiment. We could not determine the initial nutrient content of the leaf and cicada material placed into bottles. Therefore, we used the nutrient content of 30 female and 30 male adult cicadas and 6 homogenized batches of 5 to 7 sycamore leaves (see above) and assumed that initial content of female adult cicadas was 50.83% C, 11.78% N, and 0.77% P; initial content of adult male cicadas was 52.26% C, 10.12% N, and 0.69% P; and initial content of sycamore leaves was 46.90% C, 1.01% N, and 0.04% P. We determined the initial dry mass of sycamore leaf litter before incubation, but we could not do this for female and male cicadas. Therefore, we assumed that the initial dry mass of a pair of female cicadas was 554 mg and a pair of male cicadas was 336 mg on the basis of prior analyses ($n = 8$ for both male and female pairs; see above). We compared release rates of C, N, and P for each detritus type with 1-way ANOVA ($n = 3$ for each detritus type). If we detected a significant treatment effect, we determined homogenous groups with post hoc Tukey honestly significant difference (HSD) tests. We compared molar ratios of nutrients released from cicada carcasses and sycamore leaf litter (C:P, N:P, and C:N) over the experimental period with 1-way ANOVA ($n = 3$ for each type). If we detected a significant treatment effect, we determined homogenous groups with post hoc Tukey HSD tests. We set $\alpha \leq 0.05$ and used a sequential Bonferroni procedure to adjust α for multiple comparisons.

Results

Deposition of cicada detritus and leaf litter

All types of cicada detritus and sycamore leaf litter had similar mass-specific amounts of C (~40 mmol C/g; Table 1). Cicada detritus had high amounts of N (mean = 7.70 mmol/g; Table 1). Most types of cicada detritus had ~0.20 mmol/g P. N and P content were lower in composite leaf litter (0.63 mmol/g N, 0.02 mmol/g P) than in cicada detritus.

All pond and all stream sites received inputs of cicada detritus during the emergence of Brood X periodical cicadas; however, the amount of cicada detritus deposited varied among sites. Aquatic ecosystems received 0.03 to 16.99 g/m² (3.27 ± 4.66 g/m²; x̄ ± 1 SD) of cicada detritus dry mass. Stream sites received significantly larger cicada detritus inputs than did pond sites (ANOVA, $F_{1,15} = 22.55$, $p < 0.001$; Fig. 2). Across all sites, whole adult cicadas and nymphal exuviae were the most common cicada detritus type deposited (Fig. 2); the combination of these detritus types made up 72% and 98% of dry mass deposition in pond and stream ecosystems, respectively. Males and females were deposited in a ~1:1 ratio (WHN, unpublished data).
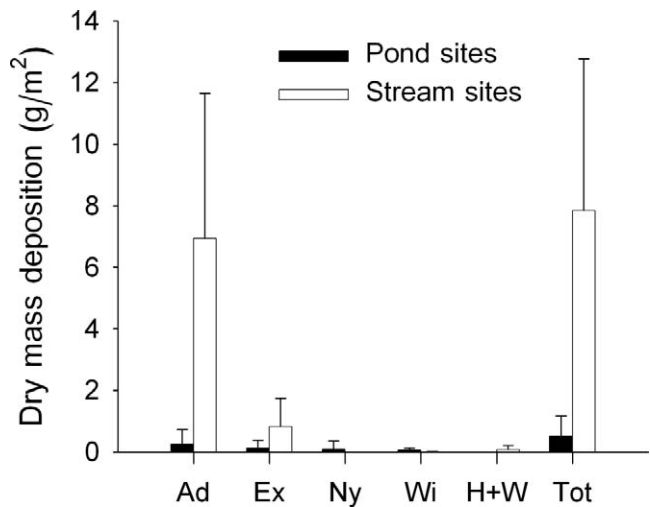

FIG. 2. Mean (+1 SD) dry mass deposition (g/m²) of periodical cicada detritus in woodland pond and headwater stream sites. Ad = adult cicadas, Ex = nymphal exuviae, Ny = whole nymphs, Wi = wings only, H+W = severed heads with wings attached, Tot = total cicada material.

TABLE 2. Means (±1 SD) and ranges of dry mass (g/m²) and nutrient loading (mmol/m²) of leaf litter and periodical cicada detritus to woodland aquatic ecosystems within 10 km of Oxford, Ohio, USA.

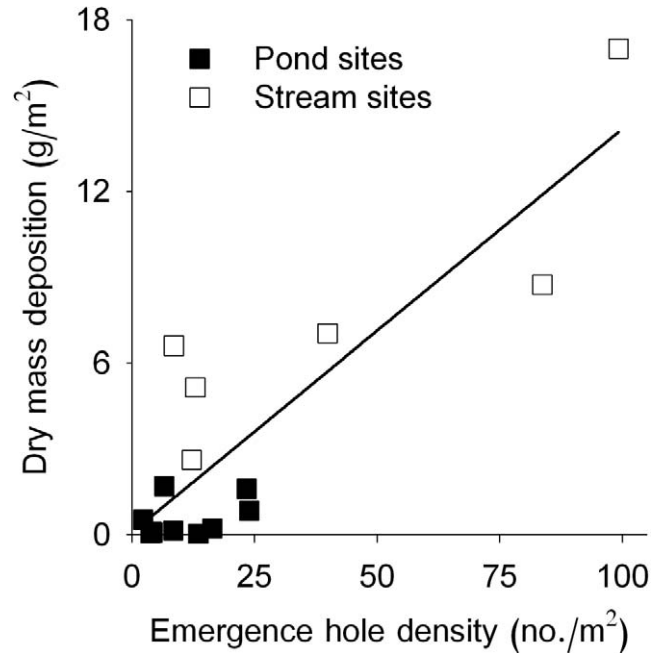| Sites	Leaf litter				Cicada detritus			
	Dry mass (g/m²)	C (mmol/m²)	N (mmol/m²)	P (mmol/m²)	Dry mass (g/m²)	C (mmol/m²)	N (mmol/m²)	P (mmol/m²)
Pond	300.00 ± 106.41 169.25–447.34	11724.10 ± 4158.38 6614.22–17482.02	189.00 ± 67.04 106.63–281.82	6.00 ± 2.13 3.38–8.95	0.53 ± 0.64 0.03–1.69	22.99 ± 29.04 1.43–77.53	3.77 ± 4.46 0.31–12.02	0.08 ± 0.13 0.002–0.32
Stream	288.76 ± 105.12 129.80–409.62	11284.70 ± 4108.04 5072.46–16007.84	181.92 ± 66.22 81.77–258.06	5.78 ± 2.10 2.60–8.19	7.85 ± 4.92 2.61–16.99	364.04 ± 230.79 123.30–798.26	56.23 ± 35.34 18.88–122.14	1.58 ±1.04 0.56–3.60
All	295.79 ± 102.51 129.80–447.34	11559.32 ± 4006.10 5072.46–17482.02	186.35 ± 64.58 81.77–281.82	5.92 ± 2.05 2.60–8.95	3.27 ± 4.66 0.03–16.99	150.89 ± 217.58 1.43–798.26	23.44 ± 33.41 0.31–122.14	0.64 ± 0.97 0.002–3.60

FIG. 3. Relationship between local emergence density of periodical cicadas (estimated from emergence holes) and dry mass deposition of periodical cicada detritus in woodland aquatic ecosystems. The regression line was generated using all sites. See Results for the separate results of ordinary least-squares regressions for pond sites and stream sites.

Loadings of C, N, and P from cicada detritus into aquatic habitats followed the same pattern as dry mass deposition. On average, stream sites received significantly greater loadings of C, N, and P from cicada detritus than did pond sites (C: $F_{1,15} = 22.23$, $p < 0.001$; N: $F_{1,15} = 22.50$, $p < 0.001$; P: $F_{1,15} = 21.01$, $p < 0.001$; Table 2). Across all pond and stream sites, the C, N, and P loadings from cicada detritus were 150.89 mmol/m², 23.44 mmol/m², and 0.64 mmol/m², respectively (Table 2).

Differences in cicada detritus dry mass, C, N, and P loadings between stream and pond sites were associated with differences in the local emergence density of periodical cicadas at the 2 site types. Dry mass deposition of cicada detritus was a positive function of local emergence density in the immediate area around aquatic habitats ($y = 0.141x + 0.073$, $r^2 = 0.75$, $F_{1,15} = 42.51$, $p < 0.001$; Fig. 3). Stream sites typically had higher emergence densities (42.75 ± 39.67) than did pond sites (10.66 ± 8.19). When pond sites were considered alone, the relationship between emergence density and cicada litter deposition was not significant ($F_{1,9} = 1.71$, $p = 0.228$). However, when stream sites were considered alone, the relationship between emergence density and cicada litter deposition was significant ($F_{1,5} = 11.19$, $p = 0.029$).

Deposition of leaf litter did not differ significantly between pond and stream sites ($F_{1,15} = 0.32$, $p = 0.581$; Table 2). Dry mass deposition of leaf litter in ponds and streams ranged from 129.80 to 447.34 g/m². Leaf litter inputs provided substantial C loadings (5072.46–17,482.02 mmol/m²), but loadings of N and P associated with leaf litter were considerably smaller and ranged from 81.77 to 281.82 mmol/m² N and 2.60 to 8.95 mmol/m² P. Even though the dry mass and C loading of terrestrial leaf litter were much larger than those of cicada detritus (cicada litter dry mass represented 0.01–5.42% of the dry mass deposition of leaf litter), the much higher mass-specific N and P content of cicada detritus made it a relatively important nutrient input in some forest aquatic ecosystems, especially stream sites. On the basis of deposition data presented in Table 2, N and P deposited into ponds via cicada litter represented 0.16 to 6.89% of the N ($\bar{x} = 2.23\%$) and 0.3 to 5.76 % of the P ($\bar{x} = 1.35\%$) deposited in autumnal leaf litter. In contrast, in streams, N and P deposited in cicada litter represented 10.94 to 61.18% ($\bar{x} = 33.40$) of the N and 10.26 to 50.36% ($\bar{x} = 29.05\%$) of the P deposited in autumnal leaf litter.

Decomposition and nutrient release of cicada detritus and leaf litter

Adult female and male cicada carcasses lost mass quickly during decomposition experiments, and the relationships between time and % inital mass remaining were best described by exponential decay functions (Fig. 4). Mass loss rates did not differ significantly between male and female cicada carcasses (female: $k = -0.051$, male: $k = -0.037$; ANCOVA: $F_{1,41} = 1.58$, $p = 0.216$). Mass loss rates for female (ANCOVA: $F_{1,38} = 57.59$, $p < 0.001$) and male (ANCOVA: $F_{1,38} = 61.80$, $p < 0.001$) cicada carcasses were significantly greater than those for sycamore leaf litter (sycamore leaf: $k = -0.002$).

C:N, C:P, and N:P of adult male and female cicada carcasses and sycamore leaf litter changed significantly (except C:P of sycamore leaf litter) as they decomposed (Fig. 5A–C; Table 3). C:N increased faster in female than in male cicada carcasses (ANCOVA: $F_{1,41} = 34.28$, $p < 0.001$; Fig. 5A). Patterns of change in C:N of both female (ANCOVA: $F_{1,41} = 569.82$, $p < 0.001$) and male (ANCOVA: $F_{1,41} = 1050.59$, $p < 0.001$) cicada carcasses were dramatically different from patterns of change in C:N of sycamore leaf litter (Fig. 5A). The slope of the relationship between sycamore leaf litter C:N and day was negative, indicating a decrease in C:N with time, whereas the slope of this relationship was positive for both female and male cicada carcasses (Table 3). C:P increased faster in female than in male cicada carcasses
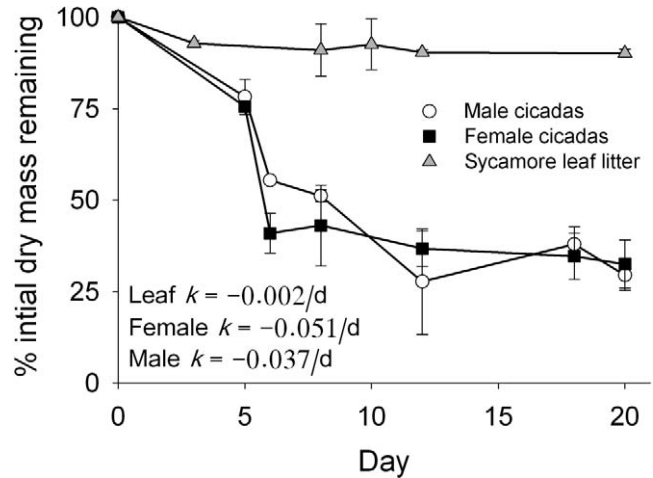

FIG. 4. Mean (±1 SE) % initial dry mass remaining of adult male and female periodical cicada carcasses and sycamore leaf litter in laboratory decomposition experiments. See Methods for calculation of decomposition constants (*k*) for each detritus type.

(ANCOVA: $F_{1,41} = 15.75$, $p < 0.001$), but C:P of both female (ANCOVA: $F_{1,41} = 351.77$, $p < 0.001$) and male (ANCOVA: $F_{1,41} = 554.81$, $p < 0.001$) cicada carcasses changed more slowly than did C:P of sycamore leaf litter (Fig. 5B). N:P of all detritus types increased markedly as decomposition progressed (Fig. 5C). Rates of N:P change did not differ significantly between male and female cicada carcasses (ANCOVA: $F_{1,41} = 0.77$, $p = 0.385$), but N:P of both female (ANCOVA: $F_{1,41} = 40.83$, $p < 0.001$) and male (ANCOVA: $F_{1,41} = 45.88$, $p < 0.001$) cicada carcasses changed faster than did N:P of sycamore leaf litter.

Differences in rates of mass loss and nutrient stoichiometry among detritus types during decomposition led to contrasting nutrient release rates (Fig. 6A–C). Female and male cicada carcasses released significantly greater amounts of C, N, and P than did sycamore leaf litter (ANOVA: C: $F_{1,8} = 6.96$, $p = 0.027$; N: $F_{1,8} = 28.67$, $p = 0.001$; P: $F_{1,8} = 44.98$, $p < 0.001$). Release rates of C, N, and P were 4, 39, and 150× greater, respectively, from cicada carcasses than from sycamore leaf litter. In fact, the negative N release rate of sycamore leaf litter (Fig. 6B) indicated that N was taken up during the experiment. In general, nutrient release rates of female cicada carcasses were greater than those of males, but this difference was significant only for P (Fig. 6C). On the basis of nutrient content of cicada carcasses and nutrient release rates observed in decomposition experiments, female and male cicada carcasses released 64%, 73%, and 91% of the C, N, and P they contained over the 20-d period. In contrast,
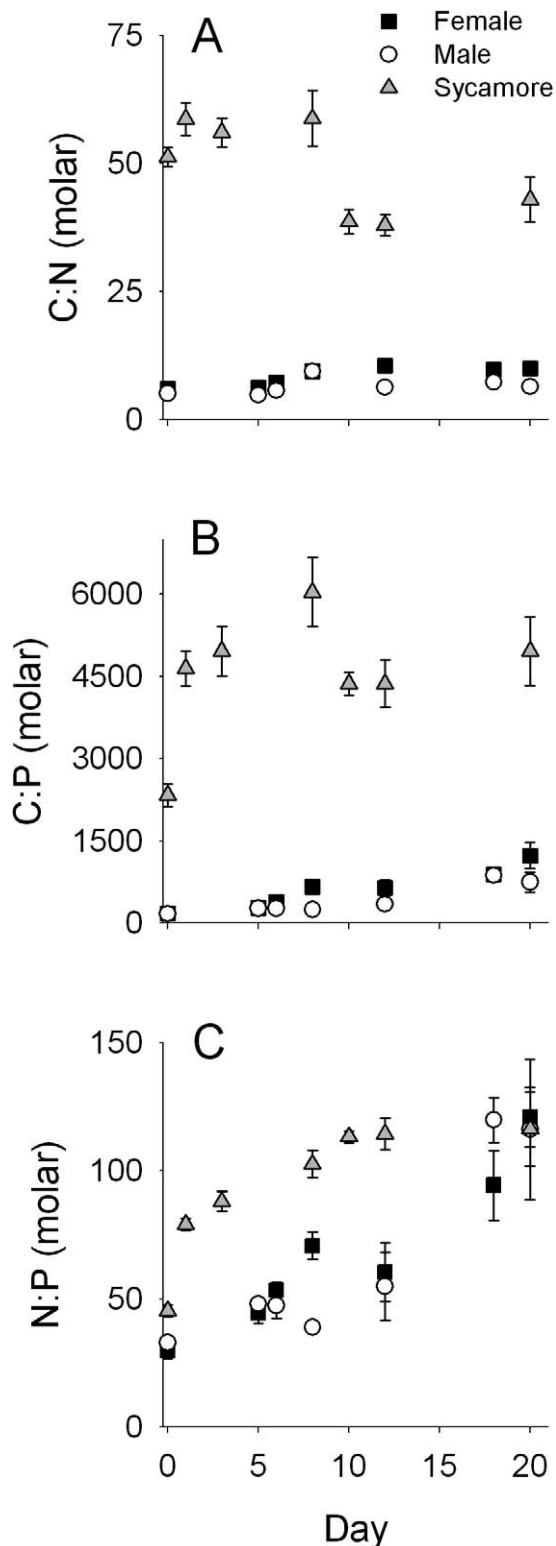
FIG. 5.   Mean (± 1 SE) molar C:N (A), C:P (B), and N:P (C) of adult female and male periodical cicada carcasses and sycamore leaf litter during laboratory decomposition experiments. Results of ordinary least-squares (OLS) regression analyses are presented in Table 3. Data presented here are

sycamore leaf litter released 7%, -16%, and 54% of the C, N, and P it contained over the 20-d period.

C:P of nutrients released by female and male cicada carcasses did not differ significantly ($p = 0.999$), but C:P of nutrients released by male and female cicada carcasses was significantly lower (47:1) than that of nutrients released by sycamore leaf litter (1717:1) (ANOVA: $F_{2,8} = 26.78$, $p = 0.001$; female cicada vs male cicada: $p < 0.999$; female cicada vs sycamore: $p = 0.002$; male cicada vs sycamore: $p = 0.002$; Fig. 6D). Sycamore leaf litter showed a net increase in N content (e.g., a negative N release rate); thus C:N and N:P ratios for released nutrients were not calculated for sycamore leaf litter because the values would be negative. The C:N and N:P ratios for nutrients released by female and male cicada carcasses were not significantly different (ANOVA: C:N: $F_{1,5} = 0.93$, $p = 0.776$; N:P: $F_{1,5} = 0.92$, $p = 0.776$; Fig. 6E, F).

We used our estimates of nutrient loss from cicada carcasses and sycamore leaf litter to calculate short-term C, N, and P release by these detritus sources in woodland aquatic ecosystems. We assumed that all types of cicada material (i.e., bodies, exuvia, head/wing pairs) had the same patterns of % nutrient release as adult cicada carcasses and that all types of terrestrial leaf litter had the same % nutrient release as sycamore leaf litter over a 20-d period (i.e., same percentage of total C, N, and P contained in detritus was released over 20 d). We coupled these nutrient release estimates with measurements of C, N, and P deposition of cicada and leaf detritus into woodland ponds and streams (Table 2) to determine the amount of C, N, and P released in woodland ponds and streams during a 20-d period. These nutrient release estimates represent the amount of nutrients released by cicada detritus and leaf litter into the surrounding water across the range of cicada detritus and leaf litter observed in woodland ponds and streams. Across all pond and stream ecosystems, cicada litter released 96.57 mmol C (range = 0.92–510.89 mmol), 17.70 mmol N (range = 0.23–92.22 mmol), and 0.60 mmol P (range = 0.002–3.32 mmol). In these same ecosystems, terrestrial leaf litter released 809.15 mmol C (range = 355.04–1223.74 mmol) and 3.16 mmol P (range = 1.40–4.83 mmol). We estimate that leaf litter would absorb 29.82 mmol N (range = 13.08–45.00 mmol) over a 20-d period. Thus, the potential importance of periodical cicada detritus as a source of N and P to aquatic communities is more apparent when field OM deposition and laboratory decomposition data are coupled.

$\leftarrow$

untransformed, whereas the OLS regression analyses in Table 3 were generated with log(x)-transformed data.

TABLE 3. Results of ordinary least-squares regression analyses for changes in nutrient ratios of adult female and male cicada carcasses and sycamore leaf litter during laboratory decomposition experiments. Analyses presented here were generated with $\log(x)$-transformed data. Untransformed data are presented in Fig. 5.

Nutrient ratio (molar)	Detritus type	Equation	r^2	$F_{1,20}$	p
C:N	Female cicada carcass	$y = 0.012x + 0.80$	0.70	18.09	<0.001
	Male cicada carcass	$y = 0.006x + 0.74$	0.20	9.64	0.006
	Sycamore leaves	$y = -0.008x + 1.75$	0.43	8.68	0.008
C:P	Female cicada carcass	$y = 0.039x + 2.33$	0.90	72.54	<0.001
	Male cicada carcass	$y = 0.035x + 2.20$	0.92	66.10	<0.001
	Sycamore leaves	$y = 0.0079x + 3.58$	0.19	3.20	0.089
N:P	Female cicada carcass	$y = 0.029x + 1.48$	0.89	62.45	<0.001
	Male cicada carcass	$y = 0.027x + 1.53$	0.91	47.92	<0.001
	Sycamore leaves	$y = 0.016x + 1.83$	0.59	21.66	<0.001

Discussion

Deposition of cicada detritus and terrestrial leaf litter

Detritus generated from the emergence of Brood X periodical cicadas provided a substantial pulse of allochthonous resources to aquatic ecosystems in forested areas. Both woodland ponds and low-order streams received a pulse of periodical cicada detritus; however, the size of this input was a function of the local emergence density of the cicadas. The range in local emergence densities across all woodland aquatic habitats spanned almost 2 orders of magnitude (2–99 individuals/m^2), but stream sites had significantly higher emergence densities than did pond sites. Periodical cicada emergence densities around our woodland aquatic systems are within the range of those values reported by others (from 2 to >350 individuals/m^2) (Dybas and Davis 1962, Williams et al. 1993, Rodenhouse et al. 1997, Whiles et al. 2001, Yang 2004).

The systematic differences between stream and pond sites in periodical cicada emergence densities and deposition rates might be related to habitat preferences of breeding and ovipositing periodical cicadas. In our study, average emergence densities were ~4× higher at stream sites than at the pond sites. Cicadas might prefer lowland riparian habitats to upland forests (Dybas and Davis 1962, Williams et al. 1993, Whiles et al. 2001), and cicadas prefer forest edges to interiors (Lloyd and White 1976, Lloyd and Karban 1983, Rodenhouse et al. 1997). Many of the forest pond sites in our study were in the interior of wood lots and had almost complete canopy cover over pond surfaces. In contrast, all stream sites had open canopy over portions of the streambed and were entirely within lowland habitats. Indeed, stream banks represent edge habitat that periodical cicadas might select when breeding and ovipositing. In addition, all stream sites were within public natural lands, whereas the pond sites were in wood lots adjacent to agricultural fields. Disturbance regimes of these respective environments might affect the number of cicadas emerging from each environment and the number of cicadas selecting these sites for oviposition.

Dry mass deposition of periodical cicada detritus in summer represented a fraction of the dry mass loading of terrestrial leaf litter into aquatic systems in autumn (~1.23% of dry mass deposition of leaf litter). Likewise, loading of C from periodical cicadas was 1.44% of loading of C from leaf litter. Leaf litter and cicada litter contained approximately the same amount of C per unit mass (~40 mmol/g dry mass), but the greater total mass deposition of leaf litter resulted in much greater C loadings associated with leaf litter than with cicada litter. To examine these allochthonous C inputs in the context of autochthonous C production in woodland aquatic ecosystems, we compared C loadings (mmol C m^{-2} d^{-1}) from leaf litter and periodical cicada litter to in situ measurements of primary production in woodland aquatic habitats. Roberts et al. (2007) estimated that the daily gross primary production in Walker's Branch, a forested headwater stream in Tennessee, was ~43 mmol C m^{-2} d^{-1} (i.e., annual total production divided by 365 d). Daily allochthonous leaf litter input to our forested streams in Ohio was 30.92 mmol C m^{-2} d^{-1}, and annual cicada input was 1.0 mmol C m^{-2} d^{-1} (i.e., C loading from each detritus type in Table 2 divided by 365 d). Thus, in some woodland aquatic systems, allochthonous C inputs from leaf litter is of similar magnitude to autochthonous primary production, but C inputs via cicada detritus is a fraction of both leaf litter and in situ primary production.

In contrast to the relatively small C inputs associated with cicada detritus, its higher N and P content made cicada detritus a sizable N and P pulse in some aquatic habitats, particularly stream ecosystems with high cicada emergence densities. At stream sites, the
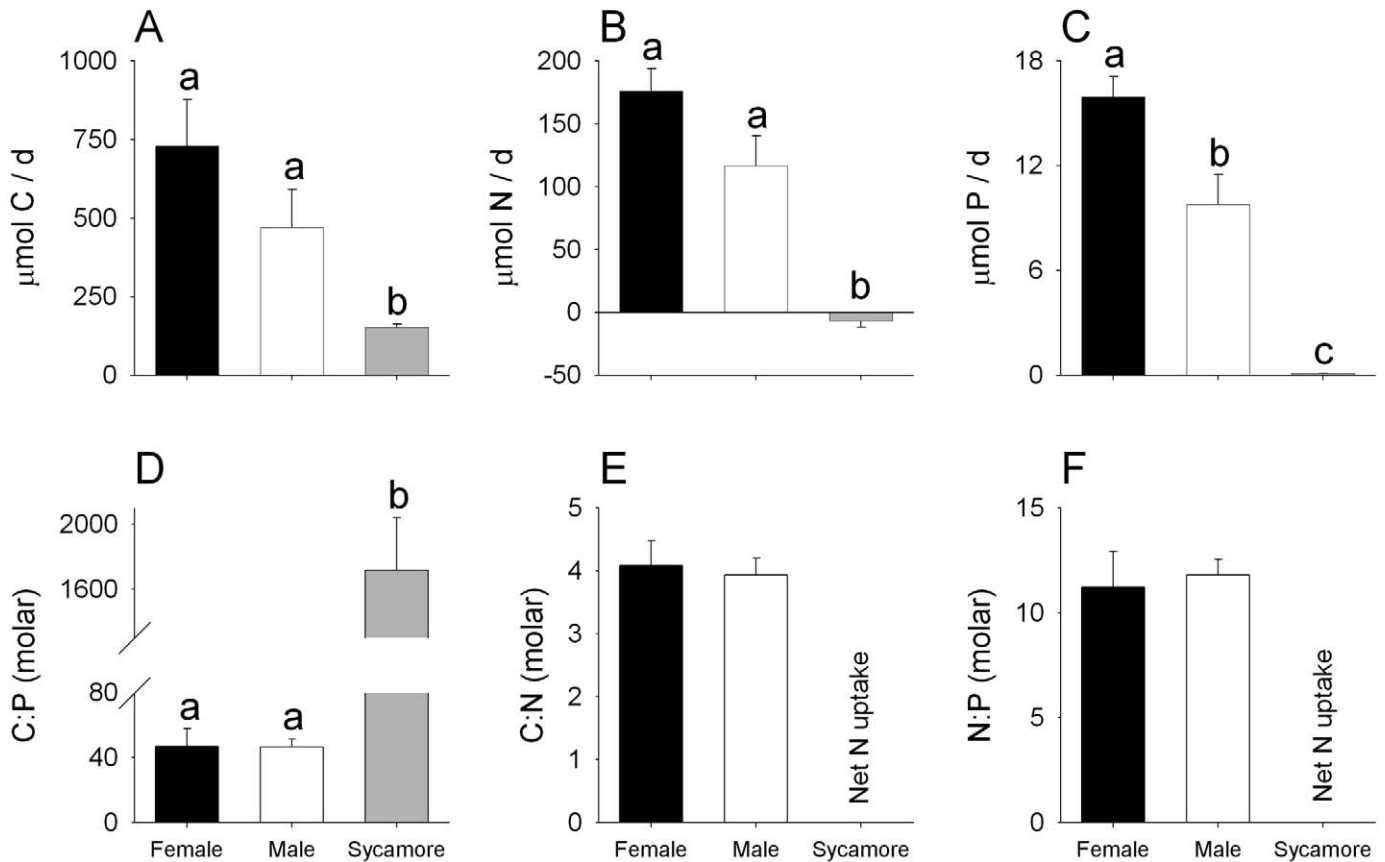
FIG. 6.   Mean (+1 SE) release rates (μmol/d) of C (A), N (B), and P (C) and the molar C:P (D), C:N (E), and N:P (F) of nutrients released from adult female and male periodical cicada carcasses and sycamore leaf litter during laboratory decomposition experiments. Homogeneous treatment groups (Tukey tests) share a letter.

maximum observed amount of N and P deposited in cicada detritus represented 61% of the N and 50% of the P associated with the deposition of terrestrial leaf litter. We also compared nutrient loading from cicada detritus to loadings from other outside sources that can contribute substantial amounts of nutrients to woodland aquatic ecosystems. Atmospheric deposition of N into aquatic ecosystems is of concern in many parts of eastern North America, including southwestern Ohio (Fenn et al. 1998). We obtained data for atmospheric deposition of inorganic N from the National Atmospheric Deposition Program (NADP) website (http://nadp.sws.uiuc.edu/) for a site at the Miami University Ecology Research Center, Oxford, Ohio (NADP monitoring location OH09; also designated by the US Environmental Protection Agency as Clean Air Status and Trends Network site OXF 122). Annual atmospheric deposition of inorganic N from 1985 to 2005 in our study area ranged from 29.21 to 55.57 mmol m^{-2} y^{-1}, with a mean annual deposition of 40.44 mmol m^{-2} y^{-1}. During summer 2004, cicada detritus N loading into woodland ponds

and streams in the same area ranged from 0.31 to 122.14 mmol m^{-2} y^{-1} ($\bar{x} = 23.44$ mmol m^{-2} y^{-1}). These data indicate that the short-term pulsed input of N from cicada detritus is of similar magnitude to the annual atmospheric inorganic N load to these ecosystems (e.g., cicada N deposition was 1–220% of annual atmospheric N deposition).

Small woodland ponds and streams are highly subsidized by allochthonous leaf litter. However, our data indicate that N and P associated with periodical cicada detritus can become a sizeable pulse (e.g., >10% of the N and P associated with autumnal leaf litter deposition) when local emergence densities exceed ~12 individuals/m^2 (Table 2, Fig. 3). Deposition of periodical cicada carcasses on the forest floor represented <1% of the nutrient flux associated with annual leaf litter deposition in an Arkansas forest with relatively low periodical cicada emergence densities (~6 individuals/m^2) (Wheeler et al. 1992). Emergence densities did not exceed 99 individuals/m^2 in our study, but others have reported much greater emergence densities (>350 individuals/m^2) (Dybas and

Davis 1962, Yang 2004). Therefore, N and P loading from deposition of periodical cicada detritus probably exceeds N and P loading from terrestrial leaf litter in some systems.

Decomposition and nutrient release of cicada detritus and leaf litter

Nutrient ratios indicated that cicada detritus (C:N = 6:1, C:P = 173:1) was a much higher-quality resource than was sycamore leaf litter (C:N = 51:1, C:P = 2332:1) to aquatic microbes and metazoan detritivores (Sterner and Elser 2002, Cross et al. 2005). Potential differences in quality and lability were reflected in mass loss in decomposition experiments. Cicada carcasses decomposed at a significantly faster rate than did leaf litter (~30% of cicada carcass initial mass remaining at the end of the experiment vs ~90% of initial sycamore leaf litter mass remaining). In leaf litter, C associated with lignin and cellulose is slow to be released because these molecules yield little net energy gain for microbes during decomposition (Chapin et al. 2002). C contained in cicada carcasses is in the form of soluble proteins, triglycerides, and chitin (Brown and Chippendale 1973), and these labile fractions are quickly leached out of cicada bodies.

Patterns of nutrient stoichiometry and nutrient release during decomposition differed substantially between cicada carcasses and sycamore leaf litter. Release rates of C, N, and P were considerably greater from cicada carcasses than from sycamore leaf litter. Thus, C:N, C:P, and N:P of cicada carcasses increased significantly as decomposition progressed. In contrast, C:N of sycamore leaf litter decreased during decomposition as leaf litter gained N content. The net gain of N content was probably a consequence of microbial colonization and increasing biomass on leaf surfaces during the experimental period (Cross et al. 2005) and indicates that the microbial communities on leaf litter surfaces took up dissolved N from the external environment. Cicada carcasses released nutrient at much lower C:P (47:1) than did sycamore leaf litter (1717:1). These differences in the ratios at which nutrients were released from cicada carcasses and leaf litter indicate the higher quality of cicada carcasses as a source of OM.

The most striking contrasts observed in our decomposition experiments were the differences between cicada carcasses and leaf litter, but the nutrient dynamics of decomposing male and female cicada carcasses also differed. C:N and C:P increased faster in female than in male carcasses during decomposition because of generally faster female nutrient release rates. Faster nutrient release rates by female cicadas

might have been caused by differences in the biochemical composition of male and female cicadas. Male and female cicadas have approximately the same mass-specific C, N, and P content (Table 1), but female cicadas contain roughly 2× as much soluble protein and 3× as much lipid as males (Brown and Chippendale 1973). Female cicada carcasses might have faster nutrient release rates than males because their greater protein and lipid content is more readily released as they decompose.

Implications of periodical cicada detritus for woodland aquatic ecosystems

Our data indicate that the amount of N and P entering woodland streams and ponds via cicada detritus in years of emergence (every 17 y) can be a sizable pulsed input when compared with other allochthonous resource subsidies that occur within the same year (i.e., leaf litter and atmospheric deposition). Given the relative size, quality, and lability of periodical cicada detritus, it is likely that this resource pulse can have large effects on ecosystem productivity and community dynamics of forest aquatic ecosystems. Indeed, deposition of periodical cicada carcasses into small-order streams can lead to rapid, short-term increases in daily whole-stream respiration rates (Menninger et al., in press). Deposition of periodical cicada carcasses to woodland pond mesocosms at a range of commonly observed emergence densities leads to rapid increases in total and dissolved nutrients that quickly led to increases in biomass of bacteria, phytoplankton, zooplankton, periphyton, and snails (Nowlin et al. 2007).

The amount of cicada detritus entering an individual forest aquatic ecosystem and the magnitude of effects on community and ecosystem processes is a function of the local cicada emergence density (Nowlin et al. 2007, Menninger et al., in press; this study). In addition, environmental conditions in local ecosystems have the potential to affect adjacent or downstream aquatic systems, so that habitats with low emergence densities might be affected by the deposition of large amounts of periodical cicada detritus in another system. Individual reaches can retain a large fraction of deposited cicada detritus (Menninger et al., in press), but streams export a substantial proportion of energy and nutrients from animal-derived resource pulses to downstream systems because of water movement (e.g., Mitchell and Lamberti 2005). A large proportion of the nutrients released by cicada pulses might be exported downstream and used in reaches with low local densities of emergent cicadas. Thus, deposition of periodical cicada detritus into aquatic

systems in forested landscapes can be extremely patchy, but the effects might be far reaching because of rapid decomposition of cicada detritus and distribution of nutrients by flow in these ecosystems.

The effects of deposition of leaf litter in forested aquatic ecosystems probably are less spatially variable than are the effects of deposition of cicada carcasses. Deposition of leaf litter ranged from 129.8 to 447.3 g/m^2 (3× range), whereas deposition of periodical cicada detritus ranged from 0.03 to 17.0 g/m^2 (570× range) at our study sites. Deposited leaf litter can be retained in stream reaches (Brookshire and Dwire 2003), but smaller spatial variation in leaf litter inputs, relatively lower nutrient content of leaves, and slow decomposition rates of leaf material suggests that the effects of leaf litter inputs within an ecosystem should be more spatially homogeneous than those of cicada detritus and that local effects are less likely to propagate to other habitats.

Rapid decomposition of periodical cicada detritus and subsequent nutrient release produce rapid responses in aquatic ecosystems, and both community- (Nowlin et al. 2007) and ecosystem-level (Menninger et al., in press) processes respond within days of deposition of periodical cicada detritus. However, the long-term implications of this resource pulse remain unknown. In southwestern Ohio forests, cicada detritus is deposited into aquatic ecosystems every 17 y and community- and ecosystem-level effects are unlikely to span this time interval. However, if populations of long-lived consumers (i.e, those that live for >1 y) or organisms that produce persistent resting stages or seeds respond to pulses of periodical cicada detritus, then the effects of an emergence event might persist for longer than a single growing season. In contrast, leaf litter is deposited every year, slow to decompose, and can support aquatic food webs for extended periods (Wallace et al. 1997). Thus, cicada detritus is a much more pulsed allochthonous resource input than is terrestrial leaf litter (Nowlin et al. 2008).

Allochthonous resource subsidies can influence the productivity and stability of ecosystems (Polis et al. 1997, Huxel and McCann 1998, Huxel et al. 2002), and the quality of these allochthonous resource subsidies can have fundamental influences on ecological dynamics (Huxel 1999, Rubbo and Kiesecker 2004). Deposition of periodical cicada carcasses into woodland aquatic systems is an allochthonous resource pulse that can have profound effects on the productivity and dynamics of woodland aquatic ecosystems. Indeed, allochthonous subsidies of carcasses from many animal taxa (i.e., ants, salamanders, and fish) are resource pulses that influence ecological dynamics (Carlton and Goldman 1984, Helfield and Naiman

2001, Naiman et al. 2002, Regester and Whiles 2006). Resource pulses generated from animal material in aquatic ecosystems have received less attention from ecologists than have pulses of plant material, but our study and others indicate that animal-derived allochthonous subsidies can be critical resource pulses that can alter the dynamics of communities and ecosystems.

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