

# Terrestrial Subsidies of Organic Carbon Support Net Ecosystem Production in Temporary Forest Ponds: Evidence from an Ecosystem Experiment

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## ABSTRACT

Recent research suggests that secondary production in aquatic systems can be driven by inputs of energy from terrestrial sources. Temporary forest ponds appear to be unproductive ecosystems that are reliant upon allochthonous inputs of energy to support secondary production, but the functioning of these systems has not been well quantified. To assess the metabolic state of this type of ecosystem as well as to quantify the importance of terrestrial subsidies of carbon to ecosystem function, we conducted an experiment in which we manipulated the amount of leaf litter in ponds. Litter was either removed or removed and replaced (that is, control) from the dry basins of ponds immediately after leaf abscission. Once the ponds filled, we monitored net ecosystem production (NEP) on a biweekly basis from 9 April to 27 May 2002. All

ponds were consistently net heterotrophic; however, NEP was significantly less negative in removal ponds. Furthermore, removal ponds also had lower levels of respiration (R) and higher dissolved oxygen levels than control ponds. The removal of litter had no effect on gross primary production, indicating that the difference in NEP between treatments was driven by the change in R. Therefore, it appears that terrestrial inputs of organic carbon support heterotrophic respiration in these ponds, and that the endogenous production of carbon is insufficient to support secondary production.

**Key words:** respiration; net ecosystem production; temporary pond; ecosystem experiment; heterotrophy.

## INTRODUCTION

Traditional food web theory maintains that food webs are supported primarily by the endogenous production of organic carbon (Hairston and others 1960; Polis and Strong 1996). However, in many

ecosystems, the autochthonous production of organic carbon is not sufficient to support the food web; thus, production must be either enhanced or subsidized to maintain secondary production (Polis and others 1997; Pace and others 2004). Inputs of nutrients (that is, nitrogen, phosphorous) can elevate autochthonous production in some aquatic ecosystems (Elser and others 1990; Carpenter and others 2001), whereas allochthonous inputs of prey or detritus have been shown to initiate numerical

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responses in consumers (Polis and others 1997; Wallace and others 1999; Nakano and Murakami 2001). Therefore, food webs can be maintained in unproductive ecosystems through a variety of pathways.

Aquatic ecosystems are frequently net heterotrophic; respiration exceeds primary production, indicating that the food web is supported by external inputs of energy (Cole and others 1994; del Giorgio and Peters 1994; Duarte and Agusti 1998). Allochthonous inputs of energy to unproductive aquatic systems are typically provided by inputs of dissolved and particulate organic carbon from the surrounding watershed (Wallace and others 1999; Caraco and Cole 2004). This carbon has traditionally been considered to be refractory in nature, but there is recent evidence to show that it can support bacterial production (Tranvik 1992; Kritzberg and others 2004). Bacteria may then transfer this carbon to higher trophic levels by serving as prey for consumers (Meyer 1994; Hall and Meyer 1998; Pace and others 2004). This microbially-mediated conversion of exogenous organic carbon, and subsequent transfer to higher trophic levels, has been shown to support food webs in lakes (Pace and others 2004) and streams (Hall and Meyer 1998; Wallace and others 1999).

Temporary forest ponds also appear to rely on allochthonous inputs of carbon (Rubbo and Kiesecker 2004). The food web of this system has served as a model for studies in community ecology (Wilbur 1997), but the manner in which energy flows through this ecosystem has not been identified. Temporary ponds are hydrologically isolated; thus, allochthonous inputs of energy to this system are principally leaf litter from overstory vegetation. Moreover, the environment of these ponds does not appear conducive to photosynthesis due to low light levels resulting from high levels of canopy coverage (Skelly and others 2002) and high levels of dissolved organic carbon (DOC) in the water (Bonner and others 1997). High DOC levels tend to minimize primary production by absorbing light, thereby darkening the water column. This absorption also warms the surface layers, which reduces the area available for photosynthesis (Carpenter and others 1998).

Because the food web of these ponds appears to rely on external subsidies of carbon to support secondary production, we were interested in quantifying the contributions of autochthonous versus allochthonous production to the functioning of this system. To accomplish this, we monitored net ecosystem production (NEP) in ponds. We chose to monitor NEP because it describes the

metabolic state of the entire ecosystem and because gross primary production (GPP) and respiration (R) can be derived from its measurement (Cole and others 2000). Net ecosystem production is defined as the difference between GPP and the sum of autotrophic ( $R_A$ ) and heterotrophic respiration ( $R_H$ ) (Cole and others 2000; Randerson and others 2002). It can be either positive or negative. Positive values of NEP indicate that the system is net autotrophic (that is, production exceeds respiration). Negative values indicate that the system is net heterotrophic (that is, respiration exceeds production), and that the food web must be subsidized with carbon from external sources (Cole and others 2000). We hypothesized that the ponds would be net heterotrophic systems. Moreover, to assess the contribution of allochthonous inputs to the functioning of this system, we excluded inputs of leaf litter. We hypothesized that eliminating litter inputs would decrease the amount of DOC in ponds, causing NEP to become less negative through a decrease in respiration and/or an increase in primary production.

## MATERIAL AND METHODS

### Study System

In this experiment, we used eight temporary woodland ponds in the State Game Lands 176, Centre County, Pennsylvania, USA. Temporary woodland ponds are small, hydrologically isolated systems that are fairly common in the forests of the northeastern United States. These ponds typically fill with snowmelt and rainwater in late winter/early spring (that is, February–March) and dry out by late summer (that is, June–July). The food web of this ecosystem type is dominated by invertebrates and larval amphibians. The ponds used in this study all lacked vegetation in their basins, had similar hydroperiods, and ranged in size from 51–132 m<sup>2</sup>, in maximum depth from 0.75 to 1.10 m, and in overhead canopy cover from 48% to 62%.

### Litter Manipulation

Immediately after litterfall (that is, late November) in 2001, we removed all of the freshly deposited litter from the dry basins of the ponds. The litter was removed by gently raking only the top layer of freshly deposited litter. We did not remove partially decomposed litter from previous years. Fresh litter was easily discernable from old litter because the old litter was dark black in color. We chose to remove only the fresh litter because leaf litter

quickly leaches all soluble compounds; therefore, the old litter was primarily refractory in nature. Moreover, this type of manipulation more closely resembled a realistic scenario (for example, defoliation event). Litter was raked onto plastic tarps and weighed. It was then brought back to a central location and thoroughly mixed to ensure homogeneity. We then returned the same approximate mass of litter that was removed per individual pond to the control ponds ( $n = 4$ ). We did not return litter to the removal ponds ( $n = 4$ ). Treatments (that is, removal, control) were randomly assigned to ponds. The ponds filled naturally in late March 2002.

### Amphibian Stocking

These ponds are used for breeding primarily by spotted salamanders (*Ambystoma maculatum*), Jefferson's salamanders (*A. jeffersonianum*), and wood frogs (*Rana sylvatica*). To help minimize potential variation among replicates, we stocked the ponds with an equivalent number of amphibian embryos per unit area. Amphibian embryos were then stocked in the ponds on an areal basis. This method ensured that the ponds all started out with an equivalent density of amphibian embryos per species. Based on data from the previous year in similar ponds ( $n = 8$ ), we determined that mean ( $\pm 1$  SE) egg densities of 0.11 ( $\pm 0.04$ ) egg masses/m<sup>2</sup> were representative of *A. maculatum*, densities of 0.05 ( $\pm 0.02$ ) egg masses/m<sup>2</sup> were representative of *A. jeffersonianum*, and densities of 0.03 ( $\pm 0.01$ ) egg masses/m<sup>2</sup> were representative of *R. sylvatica*. We then determined the area for each pond by assuming that it had the shape of an ellipse. Multiplying the area of the pond by the average density of egg masses/m<sup>2</sup> for that species determined how many egg masses we would stock per that species.

### Net Ecosystem Production

We used the continuous diel oxygen method (Cole and others 2000) to quantify NEP in these ponds. In brief, we deployed YSI-Endeco sondes Yellow Springs, Ohio (model 600 XLM) in the upper mixed layer of these ponds. Previous observations had shown that the minimum depth of mixing in these ponds was 5 cm (M. J. Rubbo unpublished). The sondes were deployed in the ponds at a depth of 5 cm for 24 h. Sondes were placed in the ponds bi-weekly beginning on 9 April 2002 and ending on 27 May 2002. Each day, two sondes would be placed into two ponds; the next day, the sondes would be moved to two other ponds. The order in

which sondes were placed into the ponds was determined randomly. This sequence was then held constant each week.

Dissolved oxygen (DO), temperature, and pH were recorded every 15 min over the entire 24-h period. The change in DO in each sampling interval is the result of NEP and diffusive exchange with the atmosphere ( $D$ ). Therefore,  $\Delta O_2 = NEP + D$  (Cole and others 2000). Diffusion is given by  $D = k(O_2 - O_{2\text{ sat}})$ , where  $O_2$  is the measured concentration and  $O_{2\text{ sat}}$  represents the concentration at which oxygen levels in the water are in equilibrium with the atmosphere. The coefficient  $k$  represents the gas exchange for  $O_2$  at a given temperature and is modeled in terms of wind speed (MacIntyre and others 1995).

We measured the maximum wind speed 1 m above the surface of the pond weekly. We used a handheld anemometer (Skymate; Speedtech Instruments Great Falls, Vir) to measure the maximum wind speed during a 1-min interval in which the meter was held in the direction of the greatest wind speed. Because  $k_{\text{night}}$  and  $k_{\text{day}}$  typically differ in shallow, low-wind systems due to diel changes in wind speed and convection currents, we fit the ratio of  $k_{\text{night}}$  to  $k_{\text{day}}$  to the observed data by adding the additional constraint that GPP had to be a non negative number. We used a value of  $k_{\text{night}}$  of 0.9 and  $k_{\text{day}}$  of 0.26. These values were chosen because their average approximated our calculated value of  $k$  (that is, 0.5). We then used the equations given by Cole and others (2000) to determine NEP, GPP, and  $R$  for each 15-min sampling interval. These data were then averaged for the entire 24-h period to determine the daily values for NEP, GPP, and  $R$ . See Cole and others (2000) for additional details on these calculations and their assumptions.

### Aqueous Analyses

Dissolved organic carbon content of the surface water was determined by filtering samples through Whatman GF/F filters and then acidifying 20 ml of the filtrate with 0.2 ml of 2 N H<sub>2</sub>SO<sub>4</sub> to a pH of approximately 2. Samples were later analyzed for DOC content (as non-purgeable organic carbon) using a Shimadzu total organic carbon (TOC 5050) analyzer. Phytoplankton biomass was estimated by quantifying the chlorophyll *a* (chl *a*) content of the surface water using standard fluorometric methods (Wetzel and Likens 2000).

### Statistical Analyses

We grouped our response variables into two categories prior to statistical analysis. Ecosystem re-

sponses were given by NEP, R, and GPP. We then used repeated-measures analysis of variance (rANOVA), after Bonferroni adjustment, to determine if treatment influenced NEP, R, and GPP. Statistical significance was given by  $\alpha = 0.017$  for these tests. Pond attributes were given by chl a, DOC, pH, DO, and temperature. The chl a data were natural log-transformed to conform to the assumptions of parametric statistics. We also used rANOVA, after Bonferroni adjustment, to test these responses. Statistical significance was set at  $\alpha = 0.01$  for these tests.

## RESULTS

### Ecosystem Responses

Due to premature drying, we lost one of the removal ponds, leaving three replicates for that treatment. Net ecosystem production was significantly affected by experimental treatment ( $F_{(1, 5)} = 45.07$ ,  $P = 0.001$ ). It was significantly less negative in the removal treatment when compared to the control treatment (Figure 1A). Net ecosystem production did not differ among sampling dates ( $F_{(3, 15)} = 1.09$ ,  $P = 0.382$ ), and there was no interaction between treatment and the sampling date ( $F_{(3, 15)} = 0.70$ ,  $P = 0.568$ ). Treatment also had a significant effect on R ( $F_{(1, 5)} = 14.79$ ,  $P = 0.012$ ). Respiration was significantly lower in the removal than in the control treatment (Figure 1B). It also did not differ among sampling dates ( $F_{(3, 15)} = 0.969$ ,  $P = 0.433$ ), and there was no interaction between treatment and the sample date ( $F_{(3, 15)} = 0.887$ ,  $P = 0.470$ ). Gross primary production did not differ between treatments (Figure 1C:  $F_{(1, 5)} = 3.62$ ,  $P = 0.115$ ). It did not differ among sampling dates ( $F_{(3, 15)} = 0.81$ ,  $P = 0.508$ ), and there was no interaction between treatment and sampling date ( $F_{(3, 15)} = 0.973$ ,  $P = 0.432$ ).

### Pond Attributes

Dissolved organic carbon showed no response to treatment ( $F_{(1, 5)} = 0.35$ ,  $P = 0.581$ ). However, DOC levels differed among sampling dates ( $F_{(3, 15)} = 9.07$ ,  $P = 0.001$ ), but they showed no consistent trend (Table 1). The interaction between treatment and sampling date was not significant after Bonferroni adjustment ( $F_{(3, 15)} = 4.37$ ,  $P = 0.032$ ). Chl a did not differ between treatments ( $F_{(1, 5)} = 0.14$ ,  $P = 0.720$ ) as sampling date ( $F_{(3, 15)} = 0.92$ ,  $P = 0.456$ ), and there was no interaction between treatment and sampling date ( $F_{(3, 15)} = 0.21$ ,  $P = 0.887$ ). Levels of DO differed between treatments ( $F_{(1, 5)} = 35.33$ ,  $P = 0.002$ ), with DO showing higher values in the removal treatment (Table 1). There was no effect of

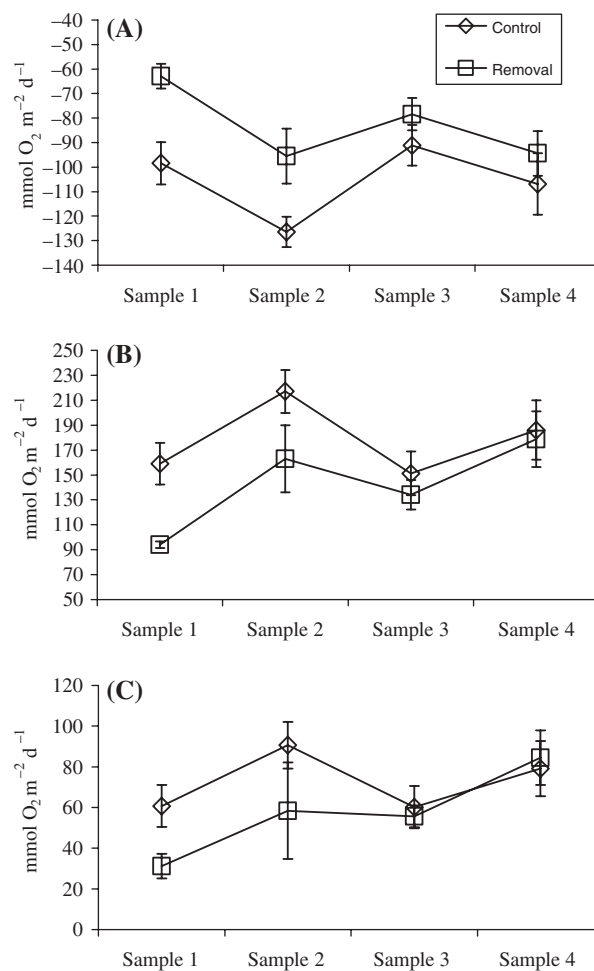


Figure 1. **A** Net ecosystem production, **B** respiration, and **C** gross primary production (mean  $\pm$  SE) in temporary forest ponds under control ( $n = 4$ ) and leaf-litter removal ( $n = 3$ ) treatments.

date ( $F_{(3, 15)} = 0.88$ ,  $P = 0.473$ ) or the interaction term ( $F_{(3, 15)} = 2.28$ ,  $P = 0.121$ ) for DO. For pH, there was no difference between treatments ( $F_{(1, 5)} = 4.64$ ,  $P = 0.084$ ), among sampling dates ( $F_{(3, 15)} = 2.72$ ,  $P = 0.081$ ), or for the interaction between the two ( $F_{(3, 15)} = 3.88$ ,  $P = 0.031$ ). Temperature also showed no response to treatment ( $F_{(1, 5)} = 0.22$ ,  $P = 0.659$ ), date ( $F_{(3, 15)} = 0.57$ ,  $P = 0.645$ ), or the interaction of terms ( $F_{(3, 15)} = 0.17$ ,  $P = 0.916$ ). The mean values for these data are given in Table 1.

## DISCUSSION

These data demonstrate that temporary woodland ponds are unproductive ecosystems. Net ecosystem production was consistently negative in all ponds (Figure 1A), indicating that R exceeded GPP. Therefore, organic carbon must be supplied

**Table 1.** Mean ( $\pm$ SE) Values of Dissolved Organic Carbon (DOC), Chlorophyll a, (Chl a), Dissolved Oxygen (DO), pH, and Temperature for Control ( $n = 4$ ) and Removal ( $n = 3$ ) Treatments in Temporary Forest Ponds

Factor	Treatment	Sample 1	Sample 2	Sample 3	Sample 4
DOC (ppm)	Control	22.37 (0.93)	24.31 (1.06)	21.16 (1.21)	11.27 (1.75)
	Removal	18.39 (1.11)	24.04 (2.52)	24.98 (3.45)	17.08 (3.99)
Chl a ( $\mu$ g/L)	Control	2.05 (0.77)	0.80 (0.16)	3.89 (2.14)	1.99 (0.94)
	Removal	2.31 (0.28)	1.62 (0.73)	3.54 (1.19)	1.95 (1.19)
DO (mg/L)	Control	4.54 (0.41)	2.99 (0.24)	3.91 (0.40)	3.64 (0.59)
	Removal	7.07 (0.10)	4.61 (0.57)	4.80 (0.30)	4.02 (0.21)
pH	Control	4.44 (0.05)	4.53 (0.12)	4.35 (0.10)	4.39 (0.14)
	Removal	4.55 (0.04)	4.43 (0.09)	4.91 (0.12)	4.70 (0.18)
Temp ( $^{\circ}$ C)	Control	11.61 (1.41)	11.58 (0.48)	15.45 (0.50)	12.59 (2.20)
	Removal	11.38 (0.92)	12.23 (0.52)	15.50 (0.62)	14.07 (2.12)

from external sources to maintain ecosystem and secondary production. This is most likely via inputs of leaf litter from overstory vegetation. The exclusion of leaf litter to these ponds decreased R (Figure 1B) suggesting that R occurred at the expense of leaf litter in the control ponds. Net ecosystem production was also less negative in removal than in control ponds. This effect was driven by a decrease in R in removal ponds; litter exclusion had no effect on GPP. However, the observed response of NEP to litter exclusion was temporary in nature; NEP differed between treatments only during the first two sampling periods (Figure 1A). We hypothesize that inputs of labile DOC via throughfall subsequent to spring leaf out or from thawing soils may have offset the loss of carbon in the removal ponds and stimulated NEP.

These data also support the general idea that many aquatic ecosystems are often net heterotrophic (del Giorgio and Peters 1994; Cole 1999). It appears that the minimal levels of primary production observed in this ecosystem are due to low light levels, resulting from the overstory canopy and the high DOC content of the water. These data also provide additional support for the idea that terrestrial subsidies of particulate carbon are important to the food webs of lotic systems. Terrestrial inputs of organic carbon have been shown to be important to headwater streams (Wallace and others 1997, 1999), but few studies have directly manipulated the inputs of particulate carbon to ecosystems such as lakes or ponds.

Previous research has shown that the exclusion of leaf litter from headwater streams can reduce DOC levels (Meyer and others 1998). Therefore, we initially hypothesized that removing leaf litter would cause NEP to become less negative via a decrease in DOC. This hypothesis was based on the assumption that, because DOC is generally correlated with microbial production (Cole 1999;

Jansson and others 2000), lower levels of DOC may decrease the degree of heterotrophy by decreasing rates of microbial production. Moreover, diminished DOC levels may enhance primary production (Carpenter and others 2001). However, in our experiment DOC did not respond to experimental treatment. We hypothesize that DOC did not differ between treatments due to elevated microbial production in the control treatment. That is, the excess DOC generated from the greater amount of litter may have been respired before it could be quantified. Support for this hypothesis is derived from an examination of the relationship between DOC and R in the ponds. For example, DOC decreased by approximately 10 mg/L in control ponds between the last two sampling periods (Table 1). Quantitatively, using the maximum pond depth observed during this sampling period (that is, 0.92 m), the loss of this DOC by oxidation implies an oxygen consumption of about 55 mmole/m<sup>2</sup>/d which is only about 30% of net oxygen consumption in these ponds during this period (that is, R > 150 mmole/m<sup>2</sup>/d; Figure 1B). Thus, it appears that the DOC was oxidized. An alternative explanation is that DOC levels may not have differed between treatments due to the leaching of organic compounds from litter prior to or immediately after abscission. Throughfall can represent a significant flux of soluble compounds to underlying areas (Meyer and others 1998; Cleveland and others 2004), and most of the soluble organic compounds in litter can leach in as little as 3 days (McDowell and Fisher 1976). Therefore, the labile DOC in the litter may have leached from the leaves, either during throughfall or immediately after abscission, and remained in the soil until it was resuspended when the ponds filled. Additional work is required to determine why the removal of litter did not affect DOC levels in the ponds.

Despite the lack of a DOC effect, eliminating the inputs of allochthonous particulate carbon did influence the metabolism of the ponds (Figure 1A). Although removing the litter had no effect on GPP, R decreased in removal ponds. This indicates that the difference in NEP between treatments was driven solely by a change in R. We hypothesize that microbes in intimate contact with litter may be responsible for the patterns observed. That is, the removal ponds may have offered less accessible organic matter for microbes or less available area for the colonization of litter. Microbes are typically associated with particulate detritus in benthic habitats (Meyer 1994; Hall and Meyer 1998); thus, the reduced quality or amount of litter in the removal ponds may have led to lower rates of microbial production. This hypothesis is consistent with the findings of elevated DO, decreased R, and decreased net heterotrophy in removal ponds.

Particle-associated microbes have been shown to be a significant trophic link between microbes and higher consumers (Meyer 1994; Hall and Meyer 1998; Hall and others 2000). In this system, microbes may represent a significant food resource to higher consumers via the grazing of leaf-litter biofilms. Tadpoles are abundant in this system, and have been shown to use the biofilms of dead organic matter as a food source (Skelly and Golon 2003). Moreover, elevated litter inputs have been shown to enhance the performance (that is, growth, survival) of tadpoles in experimental mesocosms (M. J. Rubbo and J. M. Kiesecker, unpublished). Therefore, inputs of allochthonous carbon may play an important role in the trophic dynamics of temporary ponds.

Terrestrial support of aquatic food webs appears to be a ubiquitous phenomenon (Wallace and others 1999; Pace and others 2004). This phenomenon appears to be mediated by a microbial–detrital trophic pathway (Pace and others 2004). The importance of microbial transfers of energy to higher trophic levels has been debated (Ducklow and others 1986), but recent evidence appears to support the assumption that, in unproductive ecosystems, microbes can serve as a significant trophic link. Temporary woodland ponds offer an ideal system in which to study the relationships among allochthonous inputs of detritus, microbial production, and food web dynamics, due to their low levels of endogenous production and high levels of respiration. Moreover, these ponds are amenable to ecosystem-level experimentation due to their small size and spatial clustering in the landscape. In addition to the quantity of allochth-

onous inputs of carbon, this food web also appears to be susceptible to variations in the types of detrital inputs (Rubbo and Kiesecker 2004). Because these ponds are breeding sites for amphibians, knowing how terrestrial inputs of organic matter influence food web dynamics will also enhance to our understanding of the factors that limit populations of amphibians.

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