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Research Article

Airborne carbon deposition on a remote forested lake

Nicholas D. Preston[1]*, Stephen R. Carpenter[1], Jonathan J. Cole[2] and Michael L. Pace[3]

[1] Center for Limnology, University of Wisconsin, Madison, Wisconsin 53706, USA
[2] Cary Institute of Ecosystem Studies, P.O. Box AB, Millbrook, New York 12545, USA
[3] Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22904, USA

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Abstract. Airborne inputs of terrestrial particulate organic carbon (TPOC) were measured during summer stratification for an oligotrophic north temperate lake located in a forested watershed. These inputs were episodic and associated with wind and rain events. The rate of deposition decreased exponentially with distance from shore. Yet, about 55 % of the total airborne TPOC input occurred more than 12 m from shore on this 25.8 ha lake. Of total deposition, 39 % was less than 153 μm in diameter – a size fraction not commonly measured in prior studies. Average airborne deposition was 5 mg C m^{-2} d^{-1}, which is consistent with measurements from other lakes and equivalent to about 1.1 % of daily net primary production in our study lake. C:N ratios of TPOC were between 6:1 and 22:1 (molar), much lower than the values for terrestrial leaves which were between 39:1 and 48:1 (molar). These low C:N ratios suggest that TPOC may be a useful substrate for aquatic consumers and may supplement in-lake primary production as a food source, especially after wind and rain events when airborne TPOC inputs are high.

Key words. Allochthony; organic carbon; airborne deposition; subsidies; empneuston.

Introduction

In 1927, Birge and Juday observed that Lakelet Mary appeared to be receiving much of its carbon from an outside source (Birge and Juday, 1927). This observation was among the first that recognized the coupling of dynamic lake processes with the biogeochemical cycles of the surrounding landscape (Leopold, 1941; Goldman, 1961; Likens and Bormann, 1974; Hasler, 1975). For example, elemental budgets derived from small watershed manipulations in the Hubbard Brook Valley conclusively demonstrated that aquatic processes were intimately coupled to the biogeochemical cycles of their watersheds, airsheds, and beyond (Bormann and Likens, 1967). Furthermore, these manipulations exposed imbalances and uncertainties in then-current models of aquatic ecosystems.

One imbalance receiving recent attention is the excess of respiration over primary production that occurs in many lakes (del Giorgio and Peters, 1993; Cole et al., 2000). In these net heterotrophic ecosystems, inputs of allochthonous carbon – produced outside the lake – are necessary to balance the carbon budget (Carpenter et al., 2005). These findings have renewed interest in the importance of terrestrial organic carbon as an external subsidy of aquatic food webs (Cole et al., 2007). Specifically, the contribution of airborne organic matter to the carbon budget of lakes has attracted attention from food web modelers, biogeochemists, and microbial ecologists.

Dissolved organic carbon is a major source of terrestrial carbon to aquatic ecosystems (Hessen and

* Corresponding author phone: +1-608-698-6425; fax: +1-608-265-2340; e-mail: npreston@wisc.edu
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Tranvik, 1998; Bade et al., 2007). Yet, recent analyses of whole-lake stable isotope manipulations suggest that terrestrial particulate organic carbon (TPOC) also provides a key connection between allochthonous carbon sources and food webs (Cole et al., 2006). There are numerous pathways for terrestrial particulate inputs to lakes, including surface run-off, shoreline erosion, atmospheric deposition, shoreline vegetation, and fluvial inputs as well as other anthropogenic and zoological sources. Indeed, many of these sources have been shown to be important to river productivity (Vannote et al., 1980; Naimen and Décamps, 1997; Nakano and Murakami, 2001). Historically, few studies have addressed these inputs to lakes and even fewer have isolated the contribution of deposition from vegetation and the atmosphere (discussed below).

Studies on the pathways of particulate inputs have focused on the autumn, the period of peak litterfall in northern forests (referred to as empneuston by Szczepanski, 1965; Mathews and Kowalczewski, 1969; Gasith and Hasler, 1976; Hanlon, 1981; France and Peters, 1995; Sebetich and Horner-Neufeld, 2000). However, summer deposition, coinciding with the period of peak metabolism, has been largely overlooked as a carbon source. Furthermore, few studies address the deposition of airborne particles in size ranges that are available for ingestion by aquatic invertebrates, despite indications that aquatic invertebrates receive up to 40% of their biomass from allochthonous sources (Meili et al., 1996; Grey et al., 2001; Karlsson et al., 2003; Pace et al., 2007). In this study we focus exclusively on airborne TPOC deposition during summer to determine if it could explain allochthony in aquatic invertebrates.

We studied airborne particulate deposition to a 25.8 ha rain-fed clear-water lake with high landscape position and minor groundwater input. Surface inflows of terrestrial matter were negligible due to the porous sandy soils in the region (Cardille et al., 2007). In the absence of fluvial inputs, airborne deposition appears to be one of the unique pathways for the input of particulate terrestrial matter. Herein, we quantify and characterize airborne inputs to assess the significance of this pathway to the lake carbon budget. Further, we identify key features driving this flux and evaluate this flux in the context of a whole-lake $\delta^{13}C$ isotope addition designed to measure the allochthonous carbon support of consumers.

Methods

Site description

Crampton Lake is a remote oligotrophic lake (25.8 ha), located at the University of Notre Dame Environmental Research Center (UNDERC) near Land O' Lakes, Wisconsin (89°32'W, 46°13'N). The shoreline is entirely forested with conifers and small pockets of deciduous trees on the north and northeast shores. The lake is primarily rain-fed with no visible inlet; however, some water enters the lake as groundwater seepage. During this study, Crampton Lake was the subject of a whole-lake $\delta^{13}C$ isotope addition described in Pace et al. (2007).

Airborne deposition measurements

Deposition was measured biweekly for 56 days from 13 June to 7 August 2005. We deployed plastic collectors (area 0.05 m^2, height 12 cm), containing 1L of filtered water (reverse-osmosis), and floated in inner tubes. The wetted surface was 10 cm below the upper rim of the collector and 2 cm above the surface of the lake. A wet surface was chosen to simulate deposition on the lake surface (Lewis, 1983). Collectors with low sides were chosen to avoid wind turbulence that might enhance particulate deposition (Cole et al., 1990).

The collectors were deployed in 5-member transects at distances of 2, 6, 12, 25, and 50 m from shore, perpendicular from the midpoints of the N, S, E, and W shores. This design resulted in four spatially replicated transects of distance from shore. Additionally, paired (replicate) collectors were anchored in the middle of the lake (Fig. 1). Short, 72 h, deployments were intended to minimize the influence of leaching and microbial activity. The initial and final water volumes of the containers were recorded to monitor for possible flooding by lake water. At the two sites with rock bars (i.e. shallow areas of the lake), floating collectors were paired with replicate collectors set on stakes (20 cm above the lake surface), as an additional test for contamination from wave action (see BAR and W in Fig. 1).

Size fractionation of deposition

We separated the terrestrially derived particulate organic carbon (TPOC) into three size fractions within 24 h of collection. The samples were serially filtered through 153 μm and 35 μm Nitex nets. The particulates retained on each net, and the filtrate of the 35 μm pre-filter, were then passed through separate pre-combusted Whatman glass-fiber filters (GF/F; nominal pore size 0.7 μm). The filtration scheme yielded two major size fractions: large particulates (LPOC) captured by the 153 μm net and a small

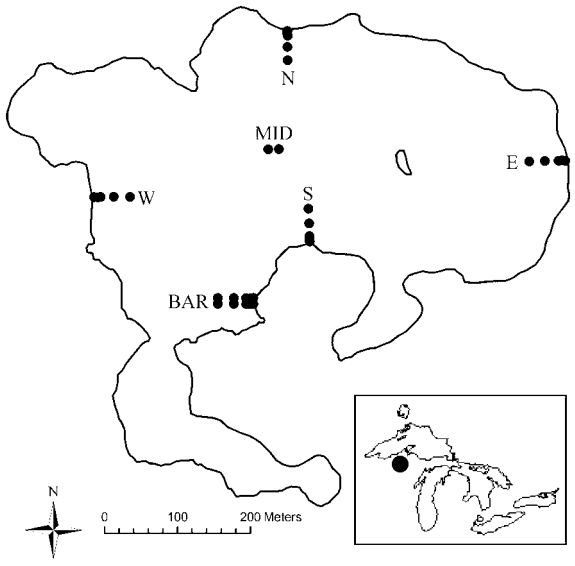

Figure 1. Map of Crampton Lake, Wisconsin, showing the locations of the TPOC collector transects, deployed at the mid-point of each shoreline by cardinal orientation (N, E, S, W), mid-lake (MID), and rock bar (BAR). The inset shows the position of Crampton Lake in relation to the Laurentian Great Lakes, North America.

particulate (SPOC) filtrate collected on the 35 μm net and GF/F filters. We further subdivided the SPOC into coarse (35 to 153 μm) and fine (0.7 to 35 μm) size fractions.

All filters were dried for 72 h at 40 °C and stored in desiccators. Total organic carbon (TOC) and total organic nitrogen (TON) for size fractions <153 μm were measured by combustion in a Carlo-Erba elemental auto-analyzer (NC2500). Additionally, a subset of filters was analyzed for $\delta^{13}C$ on a Finnigan MAT 251 Isotope Ratio Mass Spectrometer at the University of California Davis Stable Isotope Laboratory. TOC for LPOC (>153 μm) was determined as 50 % of ash-free dry mass (5 h at 450 °C). Inputs of insects to lakes are a minor contribution to the overall carbon budget (Cole et al., 2006) and were removed from all samples.

Wind speed and direction were measured at 5-minute intervals with a Young anemometer (Campbell Scientific) deployed at a height of 1 m on a floating raft placed on the lake 100 m from shore. Precipitation was measured with a Tru-Check rain gauge located near Crampton Lake.

Statistical analyses

Atmospheric deposition was log-transformed and fit to a multiple regression model using the linear modeling function in R (R-Cran Foundation for Statistical Computing, http://www.r-project.org/). Model selection, from amongst the candidate models, was made on the basis of Akaike's Information Criterion (Akaike, 1974). Two models were developed, one with SPOC as the response variate and another with LPOC as the response variate, and both were fitted to maximum daily wind speed and precipitation. The model outputs daily deposition estimates at 2 m intervals from shore to the center of the lake. These values were weighted by the total surface area of the lake within each 2 m interval to generate an estimate of daily lake-wide deposition.

Net primary production

Gross primary production (GPP) of the surface mixed layer was calculated from continuous measurements of dissolved oxygen concentration taken at 5 min intervals from YSI-Endeco sondes deployed at four depths in the lake (Coloso et al., 2008). Net Primary Production (NPP) was estimated to be 75 % of GPP (Cole et al., 2000).

Results

Total deposition

The mean deposition of TPOC, across all collectors and size fractions, was 14.4 ± 0.96 mg C m^{-2} d^{-1} (n = 319). Deposition was non-zero in every collector we deployed. Spatially paired replicates were not significantly different ($p = 0.95$, $n = 34$, t-test) and there was no significant difference between the masses of TPOC deposited in replicate staked-tall collectors versus floating-short collectors, even during heavy rain events ($p = 0.76$, $n = 54$, t-test). Similarly, the $\delta^{13}C$ values of the TPOC were not significantly different between paired staked versus floating collectors ($p = 0.83$, $n = 8$, t-test).

TPOC deposition decreased exponentially toward a non-zero asymptote between 12 and 25 m from shore (Fig. 2). The size distribution of the deposition also varied as a function of distance from shore (see black versus white bars in Fig. 2). While the gradient of deposition from shore was continuous to an offshore asymptote, in our analysis we distinguished between a narrow nearshore zone (0–12 m from shore) and a wider offshore zone (>12 m from shore). This distinction was made on the basis of the discrete locations of our deposition collectors. TPOC deposition in the collectors at 2, 6, and 12 m from shore was consistently greater than deposition in those collectors at 25, 50, and 100 m from shore; deposition amongst these offshore collectors was not significantly different. We employed this nearshore boundary to account for the spatial heterogeneity and render the descriptive statistics more meaningful. The nearshore had high SPOC deposition rates that ranged from 1 to 52 mg C m^{-2} d^{-1} and LPOC

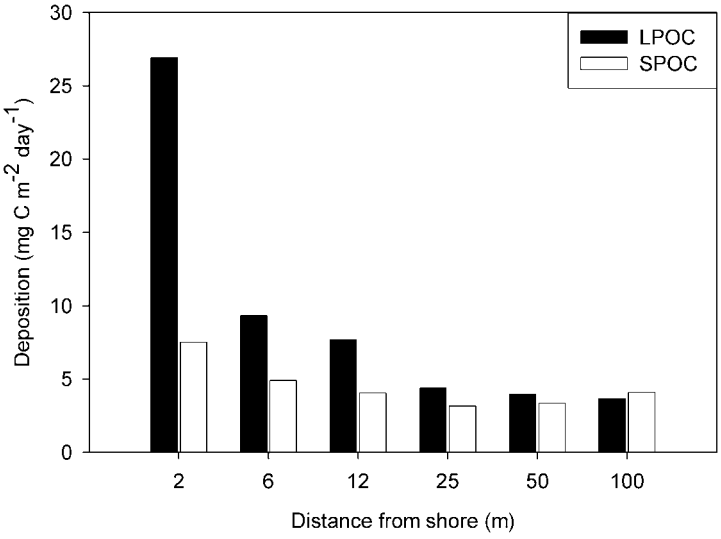

Figure 2. Deposition of airborne organic carbon as it declines with distance from shore. Mean LPOC deposition (black) and SPOC deposition (white) for all collectors deployed on Crampton Lake from 13 June to 07 August 2005 (n = 319).

from 1.5 to 105 mg C m^{-2} d^{-1}. Towards the offshore zone, the deposition rate reached an asymptotic value with no significant differences in deposition among offshore collectors greater than 12 m from shore ($p > 0.9$). Offshore SPOC varied from 0.8 to 12.8 mg C m^{-2} d^{-1} and offshore LPOC varied from 0.5 to 19.9 mg C m^{-2} d^{-1}.

On Crampton Lake, 45 % of TPOC was deposited nearshore while 55 % was deposited offshore. LPOC contributed 59 % of total nearshore deposition but only 12 % of total offshore deposition. Across the lake surface, the proportional size distribution was 39 % SPOC and 61 % LPOC.

Drivers of deposition. Deposition was enhanced during the three major storm events of the summer (Fig. 3). Our study period encompassed 16 % of annual precipitation in 2005 (USWS – Lakeland Airport). In the absence of strong wind or rain, the nearshore collectors received mean deposition of 3.1 mg C m^{-2} d^{-1} (SPOC) and 8.2 mg C m^{-2} d^{-1} (LPOC), while the mean deposition in offshore collectors was 2.1 mg C m^{-2} d^{-1} (SPOC) and 3.2 mg C m^{-2} d^{-1} (LPOC). During heavy rain events (41 to 106 mm), mean deposition increased approximately fivefold. Nearshore deposition increased to 17 mg C m^{-2} d^{-1} (SPOC) and 33 mg C m^{-2} d^{-1} (LPOC) and offshore deposition to 11 mg C m^{-2} d^{-1} (SPOC) and 7 mg C m^{-2} d^{-1} (LPOC). The decay curve for deposition from shore was steepest during storm events, while asymptotic offshore deposition was consistently high across the lake; the lake-wide increase was most pronounced for SPOC (Fig. 4). Beyond 41 mm of precipitation, the increase in deposition due to rain appeared to saturate; storm deposition was influenced more by wind than by the increase in the quantity of precipitation. Deposition was greatest when both wind and precipitation were high.

Stoichiometry. Coarse SPOC had molar C:N ratios of 22.4:1 (±11.3 SD, n=69) while fine SPOC had ratios of 6:1 (±0.9 SD, n=71). LPOC material consisted mostly of recognizable vegetation (e.g., leaves and buds), hence it was deemed to have values similar to that of the surrounding vegetation (39:1 to 48:1 in Pastor et al., 1984). The carbon isotope ($\delta^{13}C$) values of SPOC varied by size fraction: -25.2 ± 0.3 per mil (0.7–35 μm, n = 26) and -26.1 ± 0.24 per mil (35–153 μm, n = 24). The $\delta^{13}C$ of LPOC had a similar value to shoreline vegetation (-28 per mil), which has been reported elsewhere (France, 1997; Carpenter et al., 2005; Bade et al., 2006). There was a significant difference between the $\delta^{13}C$ value of dry SPOC deposition at -26.8 per mil and the $\delta^{13}C$ value of wet SPOC deposition at -24.8 per mil ($p<0.001$, d.f. = 34, t-test).

Deposition model. We compared alternative regression models for predicting particulate deposition for Crampton Lake from environmental conditions. The best models for SPOC and LPOC – determined as having lowest AIC amongst the candidate models – combined maximum wind (m/s), total precipitation per deployment (mm), and distance from shore (m). A plot of predictions versus observations indicates that the two models adequately fit the data [LPOC (R^2 = 0.43, Fig. 5a) and SPOC ($R^2 = 0.77$, Fig. 5b)]. Overall, these models explained much of the total variance in

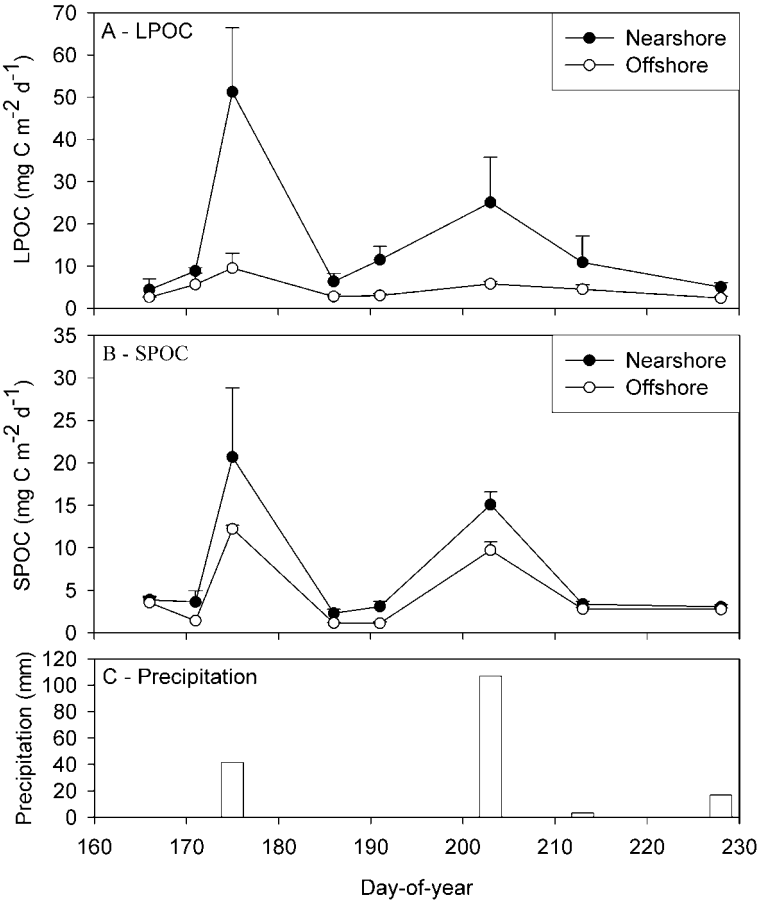

Figure 3. Summer time-series of airborne organic carbon deposition on Crampton Lake. A) LPOC deposition, and B) SPOC deposition. The solid dots show nearshore deposition (within 12 m of shore) and the hollow dots show offshore deposition (beyond 12 m from shore). C) Total precipitation during each 3 day collector deployment. All error bars are 1 SE.

deposition, although LPOC deposition was more variable. TPOC deposition from the 6 days that experienced more than 5 mm of precipitation, accounts for 20% of total deposition from our 56 day summer sampling period.

Our most comprehensive lake-wide seasonal estimate for TPOC deposition was generated from the means of the model outputs (Fig. 6); these values are half to a third of those based uniquely on the collector means or spatially-weighted means. The model estimates are 2.08 ± 0.21 mg C m^{-2} d^{-1} (SPOC, $n = 65$) and 3.09 ± 0.19 mg C m^{-2} d^{-1} (LPOC, $n = 65$), which yields a mean TPOC deposition estimate of 5.16 ± 0.4 mg C m^{-2} d^{-1} ($n = 65$).

Primary production. During the 56-day TPOC collection period, mean NPP in Crampton Lake was 485 ± 48.5 mg C m^{-2} d^{-1}. Our TPOC estimate (5.16 mg C m^{-2} d^{-1}) represents 1.1% of NPP. During the most intense storm event of the summer (day 178), TPOC deposition amounted to 17.4% of daily NPP. However, NPP was comparatively low on this day (137.3 mg C m^{-2} d^{-1}), as is likely during storms due to cloud cover and reduced light penetration.

Discussion

In this study, we quantified the deposition of TPOC on an oligotrophic lake. Previous studies have focused on LPOC inputs (i.e. leaves) during the fall – the period of highest terrestrial deposition on lakes. We build upon these studies by describing weather-related temporal variability and within-lake spatial patterns of summer inputs of SPOC and LPOC. While our observation period was short and confined to summer, our deposition estimates are comparable to other autumn-based studies (Table 1). Furthermore, allochthonous subsidies during the summer period may have a disproportionate impact on aquatic food webs due to elevated lake metabolism and competition for resources. Our collections coincided with a whole-lake $\delta^{13}C$ isotope addition (Pace et al., 2007), which provides an ecosystem context for the TPOC

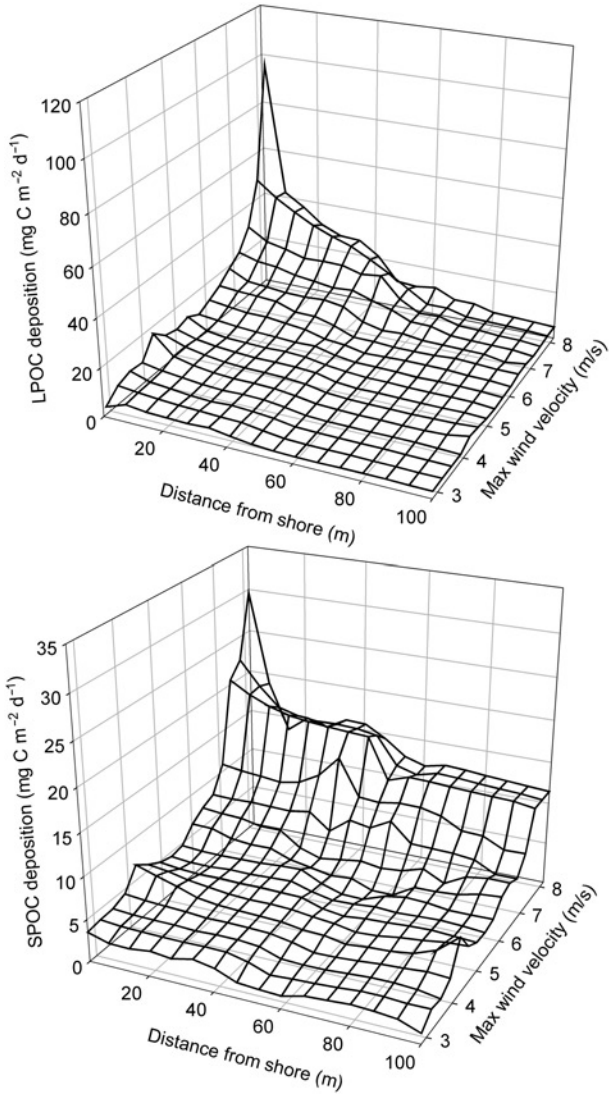

Figure 4. The influence of distance from shore (x-axis) and maximum wind speed (z-axis) on: A) LPOC and B) SPOC deposition (y-axis). High winds were invariably associated with rain events. The 3-dimensional surface was interpolated from field data (n = 319) by inverse-distance smoothing (Sigma Plot 8.0). Note the 3-fold difference in scale between the y-axes.

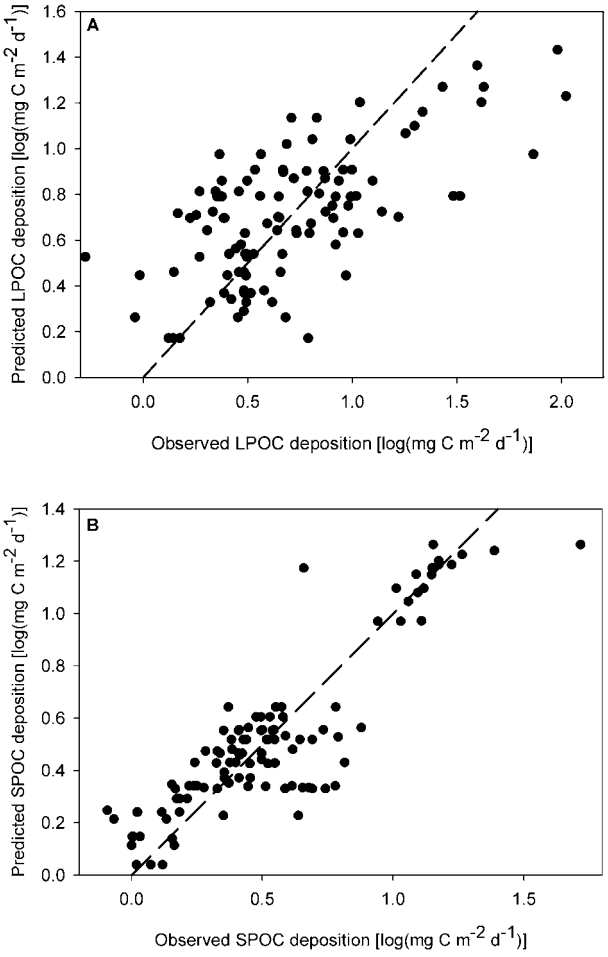

Figure 5. Predictions from a linear model of daily deposition and the deposition observed on Crampton Lake in 2005: A) LPOC and B) SPOC. The predictions were generated from daily precipitation (b_1), maximum wind (b_2), and distance from shore (b_3). The model equations are $LPOC = 0.43 + 0.0034\,b_1 + 0.11\,b_2 - 0.018\,b_3 + 0.00014\,(b_3)^2 + \varepsilon$ with $R^2 = 0.43$ and $SPOC = 0.0082 + 0.0068\,b_1 + 0.12\,b_2 - 0.010\,b_3 + 0.000077\,(b_3)^2 + \varepsilon$ with $R^2 = 0.77$. Deposition is in $\log_{10}$ units and the dashed line represents 1:1.

estimates, in that many other carbon fluxes (e.g. primary production) as well as allochthonous resource use were measured (see below).

Study evaluation

We used collectors with a wet surface and a low height-to-width ratio to mimic lake surface properties (Lewis, 1983; Cole et al., 1990). The similarities in deposition mass and $\delta^{13}C$ signature between collectors on stakes versus floating replicates suggest minimal contamination by lake water. Some early nearshore samples were excluded due to contamination with lake water from wave action. Subsequently, all nearshore collectors (2 m from shore) were set on stakes to limit contamination. We cannot exclude the possibility that the sides of our collectors may have blocked or accelerated deposition by disrupting airflow. Crampton Lake did not have a significant population of waterfowl, which may present a serious challenge for a similar study in some lakes. Additionally, there was no evidence of contamination by other abiotic or biotic phenomena, other than the possibility that the collectors provided a perch for flying or emergent insects. Although we removed insects from our samples, remnants or byproducts of decomposition may have influenced our estimates (see Anderson and Downing, 2006). Regardless, the measured fluxes compared favorably with other measures (see below).

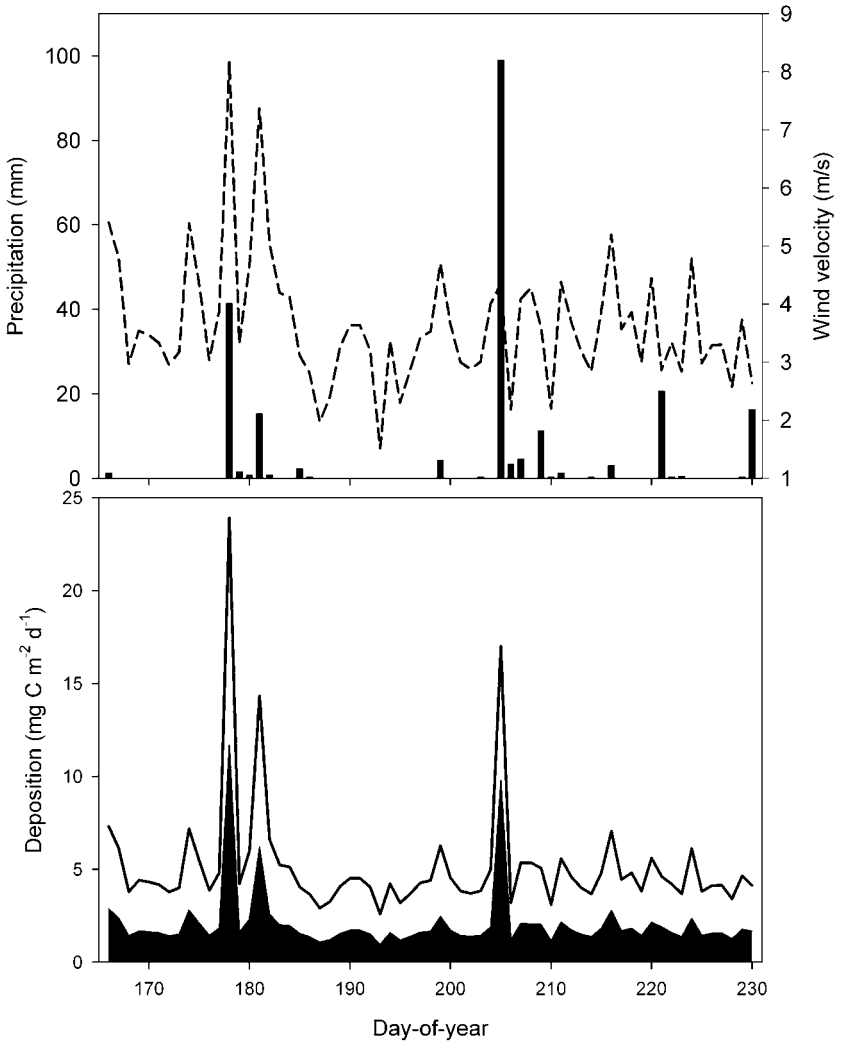

Figure 6. A) Daily precipitation (bars – left axis) and daily maximum wind speed (dashed line – right axis), B) A model-based estimate of daily particulate deposition on Crampton Lake: SPOC (shaded area) and total TPOC (white area). The daily deposition model estimates were generated from a linear model including maximum wind speed, distance from shore, and precipitation. Deposition was highest during storm events with both strong wind and heavy rain.

Nearshore deposition (<12 m)

As wind speed increased, a broad size-range of particles were deposited nearshore. The deposition of large identifiable tissues from shoreline vegetation (LPOC) was limited to this zone. However, the nearshore zone also received a considerable input of SPOC, likely a combination of carbon from both the atmosphere and shoreline vegetation. Leaf canopies accumulate atmospheric deposition, particularly at forest edges (Weathers et al., 2001), which then becomes deposited on the lake via throughfall and wind. Additional edge effects, such as wind eddies from offshore winds interacting with shoreline vegetation, may further enhance nearshore deposition. These nearshore inputs have been the focus of previous studies (Gasith and Hasler, 1976; Jones and Momot, 1981; Hanlon, 1981), leading to speculation that allochthonous subsidies are constrained to the nearshore. However, in our study, this material contributed only about half of total lake-wide deposition.

Offshore deposition (>12 m)

Dry deposition did not vary significantly among offshore collectors with distance from shore. This spatial consistency represents a constant non-zero flux of dry deposition to the lake. As precipitation increased, we observed a significant increase in deposition across the entire lake surface. Wet deposition contains particles which contribute to rain formation and are scavenged from the atmosphere, including aerosols, particulate organic debris, and fine particulates (Pomeroy and Brun, 2001). The relative contributions of wet versus dry deposition to the

carbon balance of Crampton Lake varied with storm events.

Episodic inputs

Deposition variability was best explained by wind and rain. By chance, our sampling schedule coincided with the major rain events of summer 2005; indeed, three storm events accounted for 60 % of the total deposition that we collected (n = 314). Estimates based uniquely on these samples would overestimate actual rates due to the disproportionate sampling of storm events. Hence, we generated our best estimate of TPOC deposition with a multiple linear regression model into which we input daily maximum wind and precipitation. On the basis of the model output, six days of precipitation contributed 20 % of total summer deposition. This model presents both an approach for weighting deposition to the entire lake surface, and a tool for estimating deposition in previous years or on lakes of similar size with similar shoreline vegetation. The model estimates were lower than our estimates that did not account for temporal and spatial variability.

Characterization of airborne deposition

The ratio of carbon-to-nitrogen (C:N) is recognized as an indicator of lability, or the availability of organic matter for metabolism. Typical molar C:N ratios for leaf litter from tree species found on the Crampton Lake shoreline range from 39:1 to 48:1 (Pastor et al., 1984). If TPOC deposition originated exclusively from shoreline vegetation, we would expect the C:N ratios to reflect similar recalcitrance and be of limited availability to aquatic consumers. However, the SPOC we collected in this study – which contributed 39 % of total deposition – had low C:N ratios. Coarse SPOC (35–153 μm) had lower C:N ratios (22.4 ± 11.3, n = 69) and fine SPOC (0.7–35 μm) had even lower C:N ratios (6 ± 0.9, n = 71) than terrestrial leaves. The ratios for fine SPOC were similar to the Redfield ratio for algae (6.7:1 mol in Redfield, 1934) and below those of algae from Crampton Lake using a separation technique (10.4:1, n = 19) (see Pace et al., 2007).

The similarity between SPOC and algal C:N ratios suggests that SPOC is labile and could represent an alternate food source for aquatic grazers, such as zooplankton. SPOC inputs consisted of both identifiable fragments of shoreline vegetation and more complex aggregates, perhaps formed in the atmosphere. These atmospheric influences, specifically nitrogen deposition (Andraski and Bundy, 1990), may have contributed to the low C:N ratios. Overall, low C:N ratios for airborne TPOC probably reveal an alternate, and little studied, pathway for the flow of labile allochthonous material to aquatic primary consumers.

Atmospheric influences

It is difficult to distinguish between contributions from long-distance atmospheric deposition and those from nearby vegetation. For instance, detritus blown from vegetation during intense wind events is a significant source of fine atmospheric organic litter. One case in point is that epicuticular waxes from leaf surfaces can become airborne when leaves rub against each other in the wind (Mason, 1970; Nolte et al., 2002). Stable isotope end-members may be useful for distinguishing between these sources. Atmospheric carbon has more positive nominal $\delta^{13}C$ value than is typically reported for material from terrestrial photosynthesis. The enriched $\delta^{13}C$ values for fine SPOC (-25 per mil) may indicate an atmospheric origin while coarser SPOC (-26 per mil) and LPOC (-28 per mil) have values more representative of nearby vegetation. Similarly, the more positive $\delta^{13}C$ values for deposition collected during rain events suggest transport via atmospheric pathways.

Atmospheric deposition includes particles from both anthropogenic and biogenic sources. These include primary compounds that are emitted directly into the atmosphere via combustion, chemical, geologic, or biogenic processes as well as secondary compounds that are formed from the oxidation of organic gases in the atmosphere. Particles transported long-distances by the atmosphere rarely exceed 100 μm in diameter, and most are less than 35 μm (Seinfeld and Pandis, 1998). The particulate deposition we collected was bimodal with a peak mass between 0.7–35 μm, and another >153 μm. Interestingly, there was little deposition between 35 μm and 153 μm. Similar patterns of modality in atmospheric dry deposition are described in Seinfeld and Pandis (1998). Our study site is in a remote region with correspondingly low levels of atmospheric particulates. Atmospheric particulate deposition is likely to be more important on lakes closer to population centers.

TPOC fluxes from prior studies

There is considerable variability among prior estimates of TPOC deposition rates on lakes. Current estimates vary from 1.1 mg C m^{-2} d^{-1} (Szczepanski, 1965) to 781 mg C m^{-2} d^{-1} (Gosz et al., 1972; Jordan and Likens, 1975). Our best empirical estimate for Crampton Lake is 10 mg C m^{-2} d^{-1} and our modeled estimate is 5 mg C m^{-2} d^{-1}. Variability among studies is likely related to the following factors: delineation of the deposition surface, collector design, methods for determining organic carbon, seasonal averaging, and collection frequency.

Table 1. Summary of comparable studies of TPOC deposition on lakes. Psenner (1984), Cole et al. (1990), and our study include estimates of summer deposition while the others are autumnal. TPOC (final column) is shown in terms of g C per m of shoreline per day to facilitate comparison with prior studies. Note, there is considerable variability in the collector types and the length of deployments amongst studies.

Authors	Year	Lake name	Lake area (ha)	SPOC (mg C m^{-2} d^{-1})	LPOC (mg C m^{-2} d^{-1})	TPOC (g C m d^{-1})
Cole et al.	1990	Mirror	15	18.50	25	0.97
France and Peters	1995	Various	-		6.85	
Gasith and Hasler	1976	Wingra	130			3.51
Hanlon	1981	Llyn Frongoch	7.2		2.51	1.13
Preston et al.	This study	Crampton	25.8	2.10	3.20	0.37
Psenner	1984	Piburger See	13.4	4.80	5.6	0.59
Rau	1976	Findley	128		4.66	1.13
Szczepanski	1965	Mikolajki	459		1.10	5.43
Wissmar et al.	1977	Findley	128		1.37	

Prior studies differed in deposition surface delineation primarily between nearshore collections (1–5 m in Gasith and Hasler, 1976; 0.6 m in Jones and Momot, 1981; 1–10 m in Hanlon, 1981) and lake-wide transects (Psenner, 1984; Cole et al., 1990; France and Peters, 1995). In all studies, nearshore deposition was elevated, and many showed a similar exponential decay with distance from shore (Szczepanski, 1965; Rau, 1976; Francis et al., 2007). Thus extending the nearshore rate to the entire lake surface would overestimate lake-wide deposition. Studies that integrated across the lake surface generated estimates comparable to ours (4.7 mg C m^{-2} d^{-1} in Rau, 1976; 43.6 mg C m^{-2} d^{-1} in Cole et al., 1990).

Offshore deposition has been reported as low and trivial. However, 74 % of Crampton Lake lies beyond 12 m from shore. Given the magnitude of the offshore area, the cumulative effect of low deposition across the water surface amounts to 55 % of total airborne TPOC inputs to Crampton Lake. Hence, these offshore inputs are a significant component of particulate carbon fluxes to lakes.

Collector design influences the size range and quantity of material collected. We used non-porous deposition collectors that retained all size fractions. Amongst the examples of the collectors used elsewhere are the following: muslin cloth (Gosz et al., 1972), mesh bags (Hanlon, 1981), and wire mesh (Gasith and Hasler, 1976). The widespread use of coarse mesh collectors misses the SPOC fraction, which in this study contributed 39 % of total deposition – nearly doubling our estimates. Those studies that collected SPOC present similar deposition estimates as ours (e.g. Psenner, 1984; Cole et al., 1990).

In our study, 60 % of the material we collected was deposited during the 70 h that spanned three major storm events. Interestingly, the increase in deposition due to rain appeared to saturate, such that differences between storms were related to wind speed. This suggests that the atmosphere is not a limitless source of particles and may washout during storm events (Anderson and Downing, 2006). Omitting storm events during sampling reduces the overall estimate for summer deposition, which may account for some disagreement among studies. For example, in Crampton Lake in 2005, a sampling campaign that excluded the storm events would result in spatially weighted, non-model based, estimates of 1.5 mg C m^{-2} d^{-1} (SPOC) and 3 mg C m^{-2} d^{-1} (LPOC), in contrast to our estimates of 4 mg C m^{-2} d^{-1} (SPOC) and 6 mg C m^{-2} d^{-1} (LPOC) – a difference of nearly 50 %. Our estimates, which are derived exclusively from summer deposition, are comparable to rates in most of the other annual and autumnal deposition studies mentioned previously (Table 1). While it is difficult to compare studies due to the differences identified above, our estimates converge due in part to the inclusion of both SPOC and offshore deposition.

Ecological significance

The time and location of the study coincided with a 56 day whole-lake $\delta^{13}C$ isotope manipulation. Consequently, it is possible to compare our estimates of TPOC inputs to those predicted by the $\delta^{13}C$-driven model. Total modeled TPOC deposition on Crampton Lake was 5 mg C m^{-2} d^{-1}. This represents a modest input of approximately 1–3% of daily NPP to the oligotrophic system. Accordingly, summer airborne deposition alone is unlikely to explain the 12 % of the pelagic POC pool that is of terrestrial origin (Pace et al., 2007).

Some studies have found that litterfall is an insignificant pathway of POC flux to lakes (Szczepanski, 1965; Hanlon, 1981), while others describe it as an important source of carbon and nutrients for animal production (Wissmar et al., 1977; Richey and Wissmar, 1979; Wetzel, 2001). Our results from summer deposition suggest that, while TPOC is more labile than previously believed, and a large portion of the deposition is in a size range (<153 μm) that would be theoretically available to aquatic grazers, the total amount of deposition is small relative to NPP in

Crampton Lake. Accordingly, summer deposition on Crampton Lake (25.8 ha) is not the dominant pathway for terrestrial particles to aquatic grazers. There must be alternative explanations for the finding that 12 % of POC and 8 % of zooplankton carbon in Crampton Lake is of terrestrial origin (Pace et al., 2007). Such explanations include the long residence time of particulates, DOC flocculation, resuspension, turbulent mixing, hydrologic inputs, and particle generation from bacterial and invertebrate processing of autumn litterfall. Amongst these, DOC flocculation is receiving renewed interest as a potential source of TPOC (Hayakawa et al., 2003; von Wachenfeldt et al., in press).

While deposition is low relative to NPP, the similarities between our deposition estimates and those from autumnal studies suggest that the magnitude of these inputs may yet be important (Table 1). This would be especially true if a higher proportion of TPOC inputs are metabolized in summer than in autumn due to favorable temperatures and increased biological activity. Or similarly, if summer deposition is of higher quality, given that a lesser proportion of the materials are derived from senescence as suggested by the C:N ratios. Additionally, when comparing our inputs to NPP, it should be noted that NPP is highest during the summer, while TPOC is deposited year-round, such that summer inputs of labile TPOC may be more significant in terms of annual productivity. These seasonal asynchronies between forest and lake productivity (Nakano and Murakami, 2001) are an important consideration in the interpretation of the overall significance of TPOC as a source of energy for aquatic ecosystems.

A continuous year-round input of labile allochthonous material may indicate an important role for the atmosphere and shoreline vegetation in regulating the carbon budget of low-productivity aquatic ecosystems, especially if TPOC provides critical sustenance for zooplankton or other invertebrates during times of low productivity. Saunders (1969) describes a buffering effect, whereby organisms in low productivity lakes rely on detritus during the terminal phases of major phytoplankton pulses or during periods of phytoplankton collapse. Atmospheric deposition is highest during summer (Seinfeld and Pandis, 1998), which may coincide with the period of food scarcity during the mid-summer decline in algae due to intense zooplankton grazing. This could explain how Crampton Lake zooplankton came to be 8 % allochthonous even though deposition is low relative to NPP. It may even suggest, although seemingly unlikely, that zooplankton selectively feed on the relatively nutritious SPOC. Evidence that zooplankton graze on TPOC would represent a direct mechanism for linking terrestrial inputs to aquatic secondary production via predation on aquatic primary consumers.

Few studies have conducted chemical analysis of those components of airborne deposition that may be of biological significance (Hicks et al., 2000; Sheesley et al., 2005). As a result, the ecological significance of atmospheric particles for lake organisms remains unknown. Similarly, the value of atmospheric TPOC as a food resource to remote lakes also remains unknown; however, Sheesley et al. (2005) reported that trace metals, and possibly secondary organic carbon, in atmospheric deposition are toxic to zooplankton, at least in some systems.

Evidence of a direct subsidy to aquatic consumers from atmospheric particles would argue for greater exploration of the interconnectivity of lakes and the atmosphere, especially given that particulate composition and concentration in the atmosphere have been greatly influenced by anthropogenic activity. While this study shows that the quantity of summer TPOC deposition in relation to autochthonous production is low, direct ingestion of airborne particulate deposition by aquatic consumers could signify a relatively unknown pathway for both nutrients and contaminants.

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