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Coupling of boreal forests and lakes: Effects of conifer pollen on littoral communities

Mark D. Graham and Rolf D. Vinebrooke
Freshwater Biodiversity Laboratory, Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

Michael Turner
Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada

Abstract

Conifer pollen deposition is a visually striking spring event in boreal lakes, representing a potentially major allochthonous input of limiting nutrients. We conducted a lake survey and mesocosm experiment at the Experimental Lakes Area in northwestern Ontario to test the hypothesis that jack pine (*Pinus banksiana*) pollen inputs subsidize littoral nutrient levels and stimulate algal growth and zooplankton abundance. A series of floating litterfall collectors were deployed along transects that span a 0.27-km^2 headwater lake (Lake 373) and monitored after ice-out to quantify pollen deposition over a 45-d period. Lake 373 (L373) received 11–56 μmol P m^{-2} d^{-1} from pollen, or an annual total of about 10 kg of P. These data were used to determine pollen amendment levels (ambient, 3×, 10×) for an experiment involving 18, 1-m^3 littoral mesocosms distributed over three lakes (L239, L373, and L442). Pollen amendments significantly increased total phytoplankton and herbivorous zooplankton biomass, resulting in greater abundance of inedible filamentous green algae and large diatoms. Pollen also exerted a positive lake-specific effect. Periphyton biomass also increased in response to pollen additions, especially filamentous green algae and diatoms in L239 and L442. Conifer pollen subsidizes nutrient levels and promotes production in small boreal lakes.

Terrestrial environments are hypothesized to strongly affect most lakes because they are relatively small ecosystems (<1 km^2 surface area, <10 m mean depth; Wetzel 1990). However, despite being considered an important future direction of limnology, land–water linkages within lakes remain poorly understood (Schindler and Scheuerell 2002). In particular, allochthonous inputs (e.g., pollen, insects, leaves, soil, and wood) from relatively productive terrestrial environments are expected to heavily subsidize small oligotrophic boreal lakes (Wehr et al. 1998; Doskey and Talbot 2000; Pace et al. 2004).

For example, large amounts of wind-dispersed, nutrient-rich conifer pollen are deposited annually onto small northern lakes during late May to early June (Lee et al. 1996; Doskey and Talbot 2000). Yet, pollen is not considered as a major allochthonous input because most studies that have examined the importance of litterfall to lakes were performed either after the period of maximal pollen deposition (e.g., Cole et al. 1990) or in lakes that have small catchment area : volume ratios (e.g., Lake Tahoe; Richerson et al. 1970). In contrast, Lee and Booth (2003) suggested that the rapid decomposition and enzymatic release of nutrients from conifer pollen grains contribute substantial amounts of nutrients to whole boreal catchments.

The productive capacity of small oligotrophic boreal lakes is expectedly enhanced by inputs of conifer pollen because ~60% of its total phosphorus is released in a soluble reactive form (Doskey and Ugoagwu 1989). In addition, pollen can also be an important source of organic carbon to small unproductive lakes (Doskey and Talbot 2000). Although pollen grains contribute substantial amounts of sedimentary organic carbon to lakes because of the recalcitrant nature of their exines (Doskey and Ugoagwu 1989; Doskey and Talbot 2000), they might also supply dissolved organic carbon (DOC) to lakes because of their labile organic content and external polysaccharide layer. Therefore, pollen-derived phosphorus and organic carbon might subsidize boreal lakes that are net heterotrophic systems, relying heavily on allochthonous carbon inputs (del Giorgio et al. 1999).

The main goals of our study were to quantify conifer pollen deposition in boreal lakes and to determine its effect on littoral communities as it accumulates along sheltered shorelines. Unlike previous survey studies (Doskey and Ugoagwu 1989; Doskey and Talbot 2000), we experimentally tested for the response of extant biological communities to pollen. Survey data from a headwater lake were used to quantify pollen deposition and establish pollen amendment levels for a mesocosm experiment. We hypothesized that P-rich pollen inputs enhance benthic and planktonic algal abundance, thereby increasing the potential production of herbivorous zooplankton and, in particular, P-limited cladocerans (Brett et al. 2000).

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Fig. 1. A block of duplicated pollen-amended (ambient, intermediate, high) mesocosms deployed in the southern littoral area of L239 on day 1 in June 2001. Pollen amendments can be seen floating above 0.5-m submerged periphyton tiles in each 1,000-liter mesocosm. Pollen slicks are most evident in the two high-amendment mesocosms (lower right) and in the surrounding lake. Photo credit: R. Vinebrooke.

Methods

The study was conducted in three unmanipulated lakes located in the Experimental Lakes Area (ELA) of northwestern Ontario (49°30′–49°45′N, 93°30′–94°00′W). These oligotrophic lakes are situated on granitic Precambrian bedrock, which is overlain by glacial moraine deposits, and thin podzolic sandy soils. Vegetation consists primarily of jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* (Miller)), white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.). In each lake, average ice-free epilimnetic total dissolved phosphorus (TDP) and nitrogen (TDN) concentrations ranged from 2 to 3 and 200 to 300 μg L^{-1}, respectively. Lake 239 (L239), L373, and L442 had average DOC values of 7, 3.8, and 6.7 mg L^{-1}, respectively. Detailed bathymetric and catchment data are provided by Brunskill and Schindler (1971).

Litterfall and pollen deposition—A sampling protocol for aerial litterfall (Cole et al. 1990) was used to quantify pollen deposition in L373 during May and June 2001. Before the onset of conifer pollen deposition, 18 floating collectors plus three sealed controls were deployed along transects that traversed the lake. Each collector consisted of a 10-liter conical container that had a collection aperture of 0.050 m^2. All collectors were constructed of opaque white polyethylene and were acid-washed and filled with 2 liters of deionized water before deployment. A NaCl solution was added to each collector to achieve a conductivity of 100 μmhos, which was used to correct for volumetric gains or losses caused by rainfall or evaporation, respectively. The collectors were inserted into anchored 1-m^2 floating frames of high-density foam board and sampled biweekly. Contents of each trap were passed through a 500-μm mesh to concentrate any insect and plant parts, which were stored frozen in Ziploc bags. Then, a precise volume (0.25–1.00 liter) of the sieved water was filtered through a combusted, prerinsed Whatman™ GF/C filter to collect pollen and other particulates. Inspection of the concentrated seston with a stereoscope (×50 magnification) revealed that it consisted primarily of conifer pollen, dominated by *P. banksiana*, which was then combusted and measured as ash-free dry weight. Filtrate was collected in acid-washed 250-mL polypropylene bottles from Nalgene™ and kept frozen for nutrient analysis. Collectors were cleaned by hand and rinsed with deionized water before being redeployed after each sampling event.

Pollen experiment—The experimental design consisted of three pollen treatment levels (ambient deposition, intermediate [3×], high [10×]) that were randomly duplicated within each of three unperturbed lakes (blocks) for a total of 18 mesocosms (Fig. 1). A complete pollen exclusion treatment level was not established because it would have required the use of a sealed canopy over each mesocosm, resulting in potentially confounding effects involving altered light and thermal regimes. The blocking effect involved six black polyethylene (1,000-liter capacity, 2-m diameter) mesocosms being deployed in L373, L442, and L239. Each block of mesocosms was suspended in a floating acrylonitrile butadiene styrene (ABS) frame located 2 m from the shoreline along a 1-m depth contour. Mesocosms were filled with lake water with a 5-hp water pump. At the start of the 2-week experiment, which was begun 1 June, 40 preconditioned unglazed ceramic tiles were placed in the center of each mesocosm at a depth of 0.5 m. Tiles (50 cm^2) were preconditioned for a 30-d period within the littoral zone at a depth of 0.5 m in each study lake.

Data from day 14 of the litterfall survey were used to determine pollen treatment levels for the experiment. Specifically, pollen deposition rates during May revealed that each control mesocosm contained approximately 3 g of pollen; hence, we added 10 and 30 g of pollen to the intermediate and high amendment levels, respectively. Pollen amendments were intended to simulate differences in wind-driven accumulation of pollen slicks among exposed and sheltered shorelines of boreal lakes.

Pollen was collected from ripe anthers harvested from the lower canopies of the most abundant tree species in ELA, namely *P. banksiana*, with garden shears over a 3-d period in late May 2001. We determined that no other tree species could provide sufficient amounts of pollen for our experiment because of their relative low abundance or lack of pollen production during early summer. Anthers were dried at 55°C for 24 h to a constant weight before pollen grains were concentrated with the use of a double-bucket collector. The collector consisted of a sealed cover and 500-μm mesh floor onto which the anthers were placed and then shaken so that pollen fell into the bottom bucket. Pollen was then weighed and stored frozen in Ziploc bags until amendments were performed. Amendments were dispensed and mixed beneath the water surface of each mesocosm to prevent loss of pollen grains to wind. Pollen additions were performed twice (day 0 and 7) during the

experiment to simulate the gradual accumulation rates in lakes during early summer.

Response variables included total dissolved phosphorus (TDP), DOC, and the total abundance and taxonomic composition of phytoplankton, zooplankton, and periphyton communities. A single 2-liter Van Dorn sample was collected from the center of each mesocosm for the purposes of nutrient and phytoplankton analyses. One liter of water was filtered through Whatman GF/C filters. Filtered water samples and filters were kept frozen until nutrient and chlorophyll analyses were performed. A 250-mL sample of unfiltered water was preserved with Lugol's solution for taxonomic enumerations. Phytoplankton were then settled in Utermöhl chambers and counted with a Leica DM-IRB inverted microscope at ×400 and ×1,000 magnification. Chloroplast integrity was used to determine cell viability. A minimum of 300 viable cells was counted in each sample. Biovolumes were calculated by measuring cell dimensions with Openlab version 2.2.0 and approximating cell shape with geometric solids of known volume. Biovolumes were converted to biomass by assuming a specific gravity of 1. Taxa were identified according to Prescott (1982). Five Van Dorn samples were then taken from each mesocosm, and the pooled sample was passed through a 64-μm sieve to concentrate zooplankton, which were preserved in a 2% sugared formaldehyde solution. Entire zooplankton samples were later taxonomically enumerated with a Leica MZ7.5 stereomicroscope. DOC analysis was performed with a TOC system and 5000A Analyzer (Shimadzu). TDP was analyzed by the acid molybdate technique after high-temperature digestion with persulfate (APHA 1998). Periphyton was harvested with a hard-bristle toothbrush and distilled water rinses from five tiles selected randomly from each mesocosm and pooled into a single sample. Each pooled sample was analyzed for chlorophyll content according to a standard colorimetric method (Wetzel and Likens 2000). Also, a 100-mL subsample was preserved in Lugol's solution for taxonomic analysis. Periphyton biomass and taxonomic composition were quantified at ×400. A minimum of 300 viable cells was enumerated per sample. Our use of a factorial design with replicated randomized blocking enabled us to test for the lake-dependent effect of pollen (i.e., treatment-blocking interaction) on each community with a two-factor analysis of variance (Quinn and Keough 2002).

Results and discussion

Pollen deposition—Conifer pollen from *P. banksiana* was the largest component of litterfall collected in all aerial traps deployed in L373. This result was expected because peak boreal pollen production is disproportionately represented by jack pine and varies over a 2- to 3-week period between May and June depending on local climatic conditions (Lee et al. 1996). In comparison, conifer needles, insects (ants, adult chironomidae, caterpillars, exuviae), spiders, and bird feathers accounted for a minor fraction (<5%) of the total litterfall biomass and occurred only in traps that were located within 10 m of the shoreline.

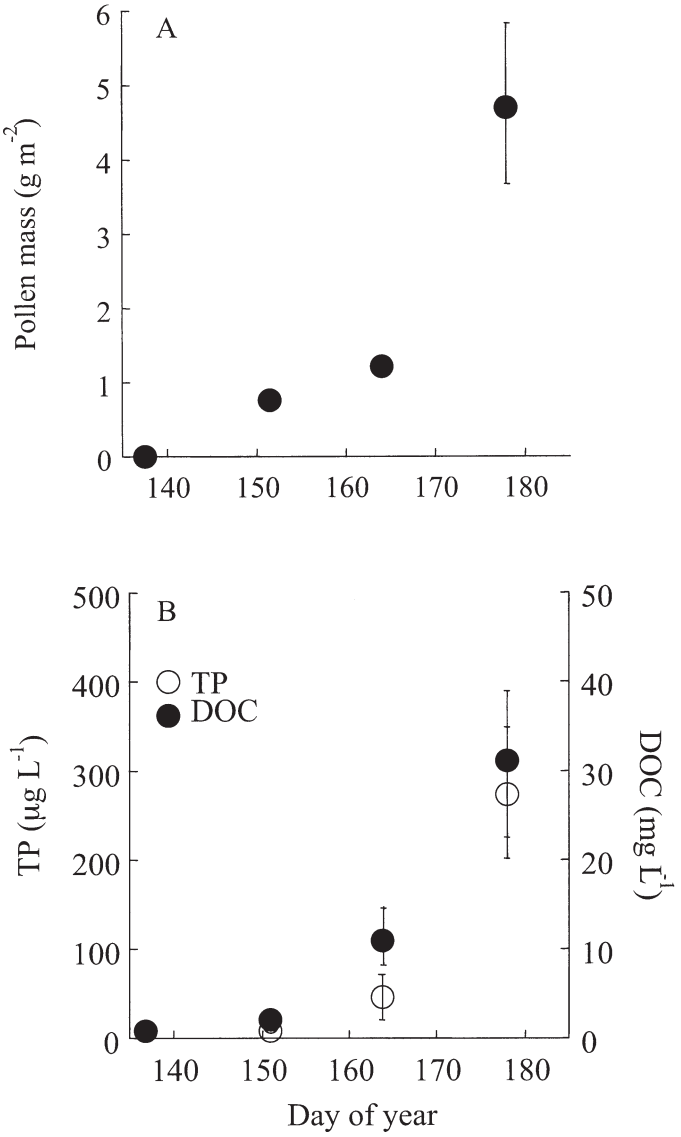

Fig. 2. (A) The total amount of pollen and (B) pollen-derived total dissolved phosphorus (TDP) and dissolved organic carbon (DOC) collected in deposition collectors deployed in L373 in June 2001 (n = 16, ±SE).

However, we believe that this larger allochthonous matter would have been of greater significance if our study spanned a longer timescale (i.e., annual inputs).

Average conifer pollen deposition rates ranged from 0.07 to 0.35 g m^{-2} d^{-1} in L373 during May and June 2001 (Fig. 2A). Hence, an estimated 7 kg km^{-2} of conifer pollen was deposited onto the lake, which was greater than earlier reports of deposition rates (1.6–2.5 kg km^{-2}) over boreal forests (Lee et al. 1996), likely because pollen was not intercepted by tree canopy. Chemical analysis of the conifer pollen revealed that it contained 0.5% phosphorus by weight, suggesting a potential subsidy to the lake of 11–56 μmol P m^{-2} d^{-1}, or 10 kg of P total. These estimates are similar to atmospheric P deposition rates (i.e., range between 3 and 70 μmol P m^{-2} d^{-1}) for lakes examined by other investigators during the summer period (*see* Cole et

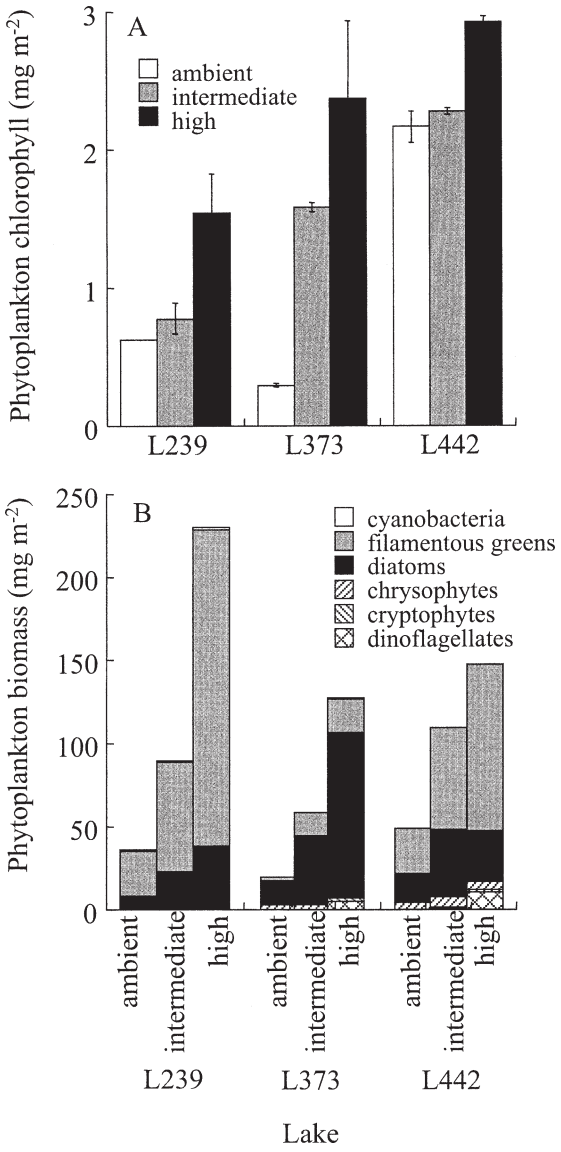

Fig. 3. Mean (±SE) (A) total chlorophyll and (B) biovolume-based taxonomic composition of phytoplankton in littoral mesocosms under ambient (control) and pollen-amended (intermediate 3×, high 10×) conditions in three study lakes.

al. 1990). Unlike an earlier report of litterfall rates consisting primarily of heavier material, such as plant and insect parts (Cole et al. 1990), conifer pollen deposition was not a significant negative function of trap distance from the shoreline, likely because lighter *Pinus* pollen grains are more evenly dispersed by wind because of their air bladders (Bassett et al. 1978). As a result, we expect that conifer pollen deposition rates were similar across the other ELA reference lakes during our study.

Conifer pollen deposition resulted in substantial increases in TDP and DOC in open collectors relative to closed controls (Fig. 2B). Specifically, TDP increased from undetectable levels (day 0) to 300 μg L^{-1} (day 45), whereas DOC concentration rose by 30 mg L^{-1}. These results support previous reports (Doskey and Ugoagwu 1989, 1992; Lee et al. 1996) that approximately 60% of the total P content of conifer pollen is water soluble. However, macronutrients in pine pollen can be solubilized in water within 24 h (Lee et al. 1996). Therefore, our findings likely underestimate the amount of soluble P released by pollen because of nutrient uptake by biofilms that developed inside the open collectors.

Pollen effects on littoral communities—Pollen amendments formed floating mats until day 3 in all mesocosms (Fig. 1). Thereafter, pollen grains became waterlogged and began to sink. Pollen remained suspended in the mesocosms for several days, but eventually adhered to submerged surfaces in each mesocosm.

Pollen exerted significant positive effects on phytoplankton chlorophyll (Fig. 3A; pollen effect, $F_{2,9} = 40.35$, $p < 0.001$) and total biomass (Fig. 3B; $F_{2,9} = 22.34$, $p < 0.001$). Furthermore, the effect size of pollen on phytoplankton chlorophyll varied significantly among lakes (Fig. 3A; pollen-blocking interaction, $F_{4,9} = 8.76$, $p = 0.004$), having its greatest effect in the most chemically dilute lake, namely L373 (Fig. 3A). Positive effects of pollen on phytoplankton abundance were primarily attributable to increases in diatoms (*Achnanthidium, Asterionella, Synedra, Tabellaria*) in L373 and filamentous green algae (*Bulbochaete, Oedogonium, Mougeotia*) in L239 and L442 (Fig. 3B). Many of these genera are also benthic, indicating that the observed effect of pollen on phytoplankton was linked to stimulation of the periphyton (*see below*).

The lack of a cyanobacterial response to nutrient fertilization in littoral mesocosms in boreal lakes is not unprecedented. Levine and Schindler (1999) also reported that fertilization at low N : P ratios did not stimulate heterocystous cyanobacteria, which constituted of <1% of the total phytoplankton biomass. Certain environmental conditions (e.g., cold average temperature <22°C) might preclude a cyanobacterial response to pollen during our experiment (Graham and Vinebrooke unpubl. data). Also, pollen-derived DOC could have organically bound P, reducing its bioavailability.

Although bacterial responses to pollen input were not quantified, bacterioplankton abundance also likely increased along with phytoplankton given their strong positive correlation along lake productivity gradients (Cole and Pace 1994). Therefore, pollen inputs could also possibly benefit phagotrophic protists, such as chrysophytes (Bird and Kalff 1986). However, we did not detect increased abundance of mixotrophic phytoplankton in pollen-amended mesocosms, perhaps because wind-driven mixing of the water column was insufficient to facilitate the growth of many pelagic species.

Pollen also significantly enhanced the abundance of littoral zooplankton (Fig. 4; pollen effect, $F_{2,9} = 8.565$, $p = 0.008$) in all lakes. Zooplankton biomass in pollen-amended mesocosms consisted primarily of increased abundances of Holopedidae and Polyphemidae in L239, Diaptomidae in L373, and Bosminidae and Diaptomidae in L442. Positive effects of pollen on zooplankton were likely indirect via its nutritive effect on edible phytoplankton and other smaller food items (e.g., protozoans, bacteria) rather than direct via consumption. Although we do not have

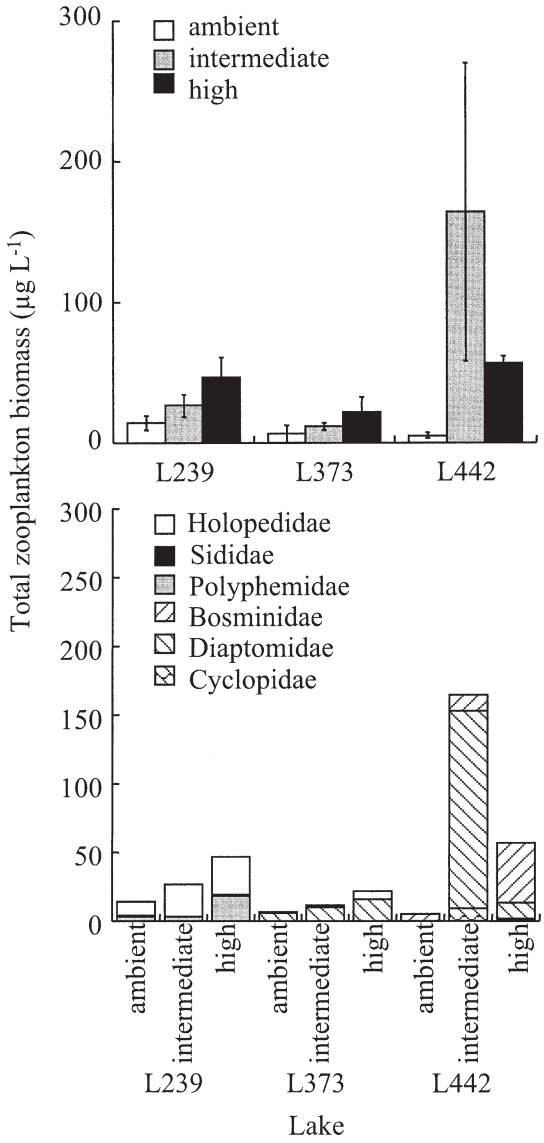

Fig. 4. Mean total biomass and taxonomic composition of zooplankton in mesocosms placed under ambient (control) and pollen-amended (intermediate 3×, high 10×) conditions in three lakes.

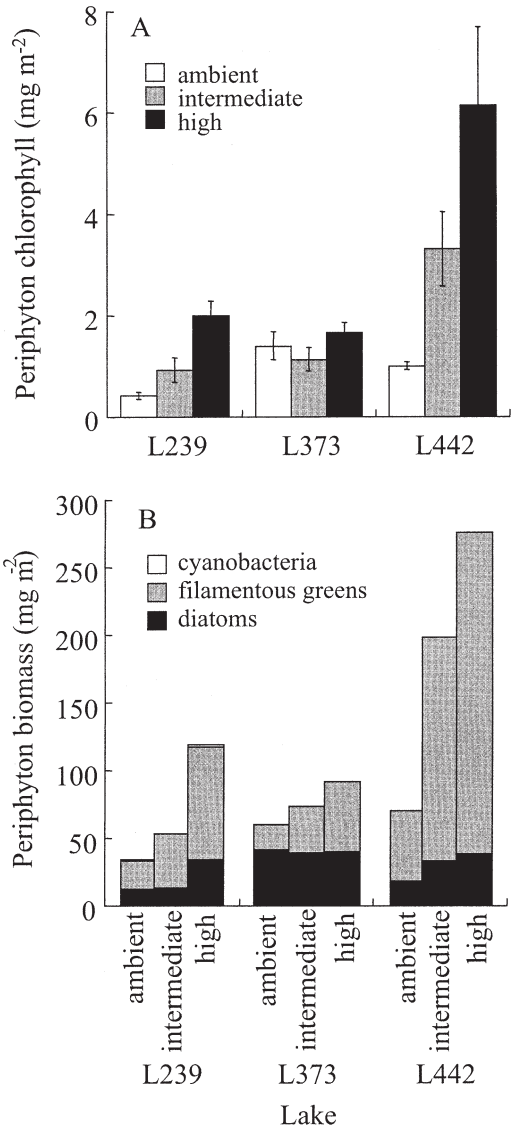

Fig. 5. Mean (± SE) (A) total chlorophyll and (B) biovolume-based taxonomic composition of periphyton in littoral mesocosms under ambient (control) and pollen-amended (intermediate 3×, high 10×) conditions in three lakes.

direct evidence of pollen consumption (via microscopic gut analyses), we suspect that pollen grains are relatively inedible, owing to their large size (60 μm diameter; *see* Bassett et al. 1978). The observed high abundance of herbivorous zooplankton and scarcity of edible (<35 μm) cryptophytes and dinoflagellates in the pollen-amended mesocosms support the expected effects of donor control of aquatic food webs by allochthonous inputs, which increases top-down forces by subsidizing higher trophic levels (Polis and Hurd 1996).

Pollen amendments significantly enhanced periphytic chlorophyll (Fig. 5A; $F_{2,9} = 21.11$, $p < 0.001$) and total biomass (Fig. 5B; $F_{2,9} = 26.68$, $p < 0.001$). The positive effect of pollen on periphytic chlorophyll differed among lakes (Fig. 5A; pollen-blocking interaction, $F_{4,9} = 5.41$, $p = 0.017$): amendments stimulated periphyton in L239 and L442 but not in L373. Positive effects of pollen on periphytic biomass were mainly attributable to responses by filamentous green algae, such as *Bulbochaete*, *Mougeotia*, and *Oedogonium* (Fig. 5B). Increased diatom (*Achanthidium, Cymbella, Tabellaria*) biomass also contributed to increased periphytic biomass in pollen-amended mesocosms in L239 and L442. Periphytic cyanobacteria occurred only in relatively low abundances in the high-pollen mesocosms. The prevalence of filamentous green algae and diatoms in the pollen-amended mesocosms was expected, given that these algae are major components of periphyton in shallow littoral areas of the ELA (Donahue et al. 2003).

Planktonic and benthic communities showed strong responses to pollen amendments, indicating expectedly tight riparian linkages to littoral habitats (Schindler and

Scheuerell 2002; Vadeboncoeur et al. 2002). We cannot generalize our findings beyond boreal systems because litterfall effects on lakes are likely dependent on context. Lakes situated within more productive temperate deciduous forests are likely more affected by inputs of leaves and insects (e.g., Cole et al. 1990), whereas our findings suggest that pollen is an important link between conifer-dominated terrestrial and aquatic boreal habitats. In addition, inputs of coarse woody debris would further link riparian and littoral habitats in both cases (Christensen et al. 1996). Paleolimnological evidence of relationships among proxies of primary production (e.g., fossilized algal pigments) to pollen deposition rates could corroborate our hypothesized effects of allochthonous inputs on small boreal lakes. Importantly, pollen inputs might enhance the productive capacity of oligotrophic small lakes for harvestable sport fish by stimulating littoral zooplankton, an important food resource for forage fish. Finally, conifer pollen production is influenced by climate (Lee et al. 1996), suggesting that predicted climate change scenarios could affect the productivity of small boreal lakes by altering the magnitude and timing of this annual major allochthonous input.

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