

## Litter controls plant community composition in a northern fen

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The accumulation of litter or thatch can affect plant community composition by affecting the temperature, nutrient availability, and light availability of the soil environment, thereby forming a potentially important linkage between recent productivity and current ecosystem processes. To investigate the importance of litter on a fen peatland plant community, we conducted a litter addition and removal experiment in a fen in northern Minnesota, USA, between 1998 and 2001. The addition of litter had little effect on fen plant community composition or microenvironmental variables, despite a two-fold increase in litter mass compared to control plots. However, the removal of litter dramatically increased cover of *Rhynchospora fusca* and *R. alba*, and reduced cover of *Carex exilis*. Litter removal also increased availability of light and soil temperature and increased the phosphorus content of aboveground plant biomass. Our results indicate that litter is an important control of plant community composition in this northern fen.

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The accumulation of senescent plant material (litter) has long been recognized as a constraint on plant community structure. Litter acts as an important linkage between recent productivity and current community and ecosystem processes (reviewed by Facelli and Pickett 1991a). Specifically, the accumulation of litter can have direct and indirect effects on plant species composition, net primary production (NPP), nutrient cycling, fire regimes, herbivory, hydrology, and energy budgets (Facelli and Pickett 1991a, Xiong and Nilsson 1999).

Accumulations of litter may affect community and ecosystem processes through modifications of one or more microenvironmental conditions. For example, because light typically declines exponentially as it passes through the litter layer, the accumulation of litter reduces the availability of shortwave radiation at the soil surface (Facelli and Pickett 1991a, 1991b). An

extensive litter layer may also alter soil temperature regimes by intercepting incoming solar radiation and outgoing longwave radiation, thus reducing soil temperature variability over time (Facelli and Pickett 1991b). Insulation provided by litter may also protect plants against lethal frost events (McKinney 1929, Watt 1970, Facelli and Pickett 1991a). Litter can also affect ecosystem carbon and nutrient dynamics, either through changes in temperature that affect rates of mineralization, or, over longer time scales, through changes in the composition of the plant community that affect the quality of subsequent litter inputs (Facelli and Pickett 1991a, Chapin et al. 1995).

The role of litter in plant communities has been studied in a number of ecosystems, including old-fields (Carson and Peterson 1990, Facelli and Pickett 1991b, 1991c, Facelli and Facelli 1993, Facelli 1994, Foster and

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Gross 1997, 1998), prairies (Hulbert 1969, Knapp and Seastedt 1986), semi-arid shrublands (Boeken and Orenstein 2001), riparian corridors (Xiong and Nilsson 1997, Nilsson et al. 1999, Xiong et al. 2001), and tundra (Chapin et al. 1979). Litter effects on community structure and ecosystem processes have also been studied in wetlands (Rowell et al. 1985, van der Valk 1986, Brown and Bedford 1997, Atkinson and Cairns 2001, Grace 2001, Xiong et al. 2003), but these effects have rarely been investigated in peatlands (but see Berendse et al. 2001).

Peatlands, which represent more than half of the global wetland area, are wetlands that have accumulated >40 cm of surface organic matter (Bridgham et al. 2001). Globally, peatlands contain 1/3 of the terrestrial soil carbon and are important ecosystems in the context of the global carbon cycle and hence global climate change (Bridgham et al. 1995, Gorham 1995). Fens are a minerotrophic subclass of peatlands where hydrology and nutrient inputs result in a plant community dominated by graminoids, and interspersed with stunted shrubs and *Sphagnum* mosses (Bridgham et al. 1996). Despite relatively low aboveground net primary production (ANPP) in these systems (Weltzin et al. 2000, Chapin et al. 2004), litter can accumulate because of low temperatures and anaerobic conditions that slow decomposition (Bridgham and Lamberti 2005). Large interannual variations in ANPP are common in northern fens (Thormann and Bayley 1997a, b, Weltzin et al. 2000, Chapin et al. 2004) and may represent oscillations resulting from a time-delayed inhibitory effect of plant litter on plant productivity as has been suggested in fens (Weltzin et al. 2000) and other ecosystems (Tilman and Wedin 1991).

We established experimental plots in a fen in northern Minnesota to examine the effects of litter addition and removal on plant community (aboveground production, belowground biomass, species richness and diversity, and species cover) and microenvironmental (light, temperature, and nutrient) response variables over four growing seasons. We predicted that the quantity of litter would be inversely correlated with production, species richness and diversity, and would alter individual species abundances, because of concomitant reductions in light and temperature at the soil surface and lower rates of nutrient mineralization and availability.

## Methods

### Study site

Research was conducted at a fen in Alborn township in northeastern Minnesota (47°00'42" N, 92°34'30"W). Mean annual temperature in this region is 3.2°C and mean annual precipitation is 497 mm. This poor to intermediate fen contains about 4.4 m of herbaceous

peat overlying about 2 m of unconsolidated aquatic detrital peat, and has a basal age of  $9730 \pm 70$  years. The surface 0–25 cm of peat has a pH of 4.9, and averages 38% carbon, 22% ash, and 29% rubbed fiber content on a dry-mass basis (Bridgham et al. 1998).

The fen has microtopographic variation typical of other fens in the regions, with low and wetter areas (flarks) separated by higher and somewhat drier linear mounds 10–20 cm tall (strings). Flarks are dominated by the graminoid *Carex exilis* Dewey. Other graminoids include *C. limosa* L., *C. livida* (Wahl.) Wild., *C. lasiocarpa* Ehrh., *Rhynchospora alba* (L.) Vahl and *R. fusca* (L.) Ait. f. Pitcher plants (*Sarracenia purpurea* L.) are also present. Strings are dominated by graminoids as well as ericaceous shrubs (*Andromeda glaucophylla* Link and *Vaccinium macrocarpon* Ait.) and bryophytes including *Sphagnum papillosum* Lindb. and *S. angustifolium* (Russow) C. Jens.

Water tables in the fen during the growing season are usually close to or above the peat surface, and ranged from –5 cm to +10 cm during the course of this study. In the three years prior to this study (i.e. 1995–1997), water tables in four shallow wells sampled during the growing season averaged +0.8 ( $\pm 1.3$  cm; sd), +5.6 ( $\pm 1.0$  cm), and –0.1 ( $\pm 1.2$  cm), respectively (Chapin 1998).

### Experimental design

Between 1998 and 2001, we conducted a field experiment designed to assess the response of the fen plant community and ecosystem to differences in accumulation and removal of litter biomass. Before the start of the 1998 field season (defined for each year as the period between May–October), we established 15  $1 \times 1$  m<sup>2</sup> plots within the flarks at Alborn fen. Plots were 2 m to 10 m apart, and deliberately placed to avoid inclusion of strings. Wooden boardwalks at the site were constructed to minimize disturbance to plant communities and surface water flow regimes during sampling.

Plots were assigned at random to one of three litter manipulation treatments (n = 5): litter added (A), litter removed (R), and litter unmanipulated (=control, C). Prior to the field season in each year (i.e. 1998–2001), we removed all the litter from R plots by hand. In 1998, litter removed from each R plot was applied to a randomly designated A plot. In 1999, litter removed from R plots was air-dried, subsampled for determination of moisture content, and then applied to randomly designated A plots at a rate of  $98 \pm 11$  g m<sup>-2</sup> (mean  $\pm$  1 se, oven-dry mass). Because of treatment-induced changes in plant community composition, in 2000 and 2001 litter removed from R plots was discarded, and litter for A plots was collected from flarks near the experiment, air-dried and subsampled as before. Litter

was then applied to each A plot in equal amounts, at a rate of  $100 \text{ g m}^{-2}$  (oven-dry mass).

### Plant cover and biomass

We visually estimated foliar cover, to the nearest 5%, for all plant species within each plot at the estimated time of peak standing biomass (i.e. mid August) each year between 1998 and 2001. In 2001, we also visually estimated the percent coverage by litter within each plot. In each year, we estimated the depth of the litter layer above the peat surface at eight random locations within each plot.

We used a non-destructive double-sampling technique (Cook and Stubbendieck 1986) to estimate ANPP in 1998–2000. Standing live biomass at the estimated time of peak standing biomass was used as a proxy for ANPP because all aboveground leaf tissue senesced each winter. When double-sampling, we visually estimated ANPP within 26–42  $0.0625\text{-m}^2$  plots outside of, but within 5 m of, the experimental plots. Foliar tissue within the estimation plots was then clipped, oven-dried to constant mass, and weighed. For each year, we used least-squares regression analysis to establish power relationships between estimated and actual biomass in the estimation plots ( $R^2$  values for the regressions were 0.89, 0.65, and 0.89 in 1998–2000, respectively). We used these relationships to estimate biomass within each of the experimental plots based on non-destructive estimates within five  $0.0625\text{-m}^2$  subplots (averaged for subsequent analysis). In 2001, at experiment termination in the late growing season, we clipped all standing biomass at 2 cm above the peat surface within an  $80 \times 80 \text{ cm}^2$  quadrat centered within each plot to minimize edge effects, and separated the accumulated litter mass from the green biomass produced that season. As the litter removal treatment removed all litter at the start of each growing season, the litter collected at the end of the experiment from the litter removal treatment plots was only from the previous year of production. Litter in the control and litter addition treatment plots had accumulated over multiple growing seasons. Litter and green biomass were oven-dried at  $60^\circ\text{C}$  to constant mass.

Belowground root biomass was determined at experiment termination in 2001 by extracting 2 intact, randomly located, 6 cm diameter  $\times$  30 cm deep cores from each plot. Cores were weighed, split longitudinally into 2 units of equal mass, and one unit from each core was selected at random for root separation. Selected units were wet-sieved over a 40-mesh screen prior to hand-separation of live roots over 1 cm long. Root biomass was oven-dried at  $60^\circ\text{C}$  to constant mass and weighed to the nearest mg.

### Nutrient availability and concentration

Nutrient availability was estimated using ion-exchange resin bags placed 15 cm below the peat surface at three random locations within each plot. At each location, paired bags included the bicarbonate ( $\text{HCO}_3^-$ ) form of anion-exchange resin to estimate  $\text{PO}_4^-$  availability (Sen Tran et al. 1992), and the hydrogen-hydroxyl (H-OH) mixed-bed form of resin to determine  $\text{NH}_4^+$  and  $\text{NO}_3^-$  availability (Binkley and Hart 1989). Resin bags were placed into the plots in June 2000 and were removed in October 2001. Resins were oven-dried, then extracted with 2 M KCl and the extract was analyzed for  $\text{PO}_4^-$ ,  $\text{NO}_3^-$  and  $\text{NH}_4^+$  by spectrophotometric methods with a Lachat Quikchem 8000 autoanalyzer (Hach Corporation, Loveland, Colorado, USA).

Nutrient concentration of plant tissue was determined for bulk foliar green and litter biomass, and root biomass. Tissues were ground to a fine powder and phosphorus (P) content was determined by digesting with concentrated  $\text{H}_2\text{SO}_4$  and 30%  $\text{H}_2\text{O}_2$  (Allen 1989) followed by spectrophotometric analysis on a Lachat Quikchem 8000 analyzer. Carbon (C) and nitrogen (N) content were determined using a CHN analyzer (LECO 2000, St. Joseph, Michigan, USA).

### Canopy light interception and soil temperature

Interception of photosynthetically active photons (PPFD, 400–700 nm,  $\text{mol m}^{-2} \text{ s}^{-1}$ ) by the combined canopy and litter was determined at mid-day during the 1998–2001 growing seasons (1998–2 dates; 1999–4 dates; 2000–2 dates; 2001–1 date). On each date, we measured PPFD at 2 cm above the surface of the peat at three random locations within each plot using a line-integrating ceptometer (AccuPAR, Decagon Devices, Inc., Pullman, Washington, USA). PPFD above the plant canopy was measured concurrently using a LI-COR quantum sensor (LI-COR Inc., Lincoln, Nebraska, USA) equilibrated to the ceptometer. Estimates of interception of PPFD (%) by the canopy, including litter, were averaged for each plot.

Soil temperature ( $^\circ\text{C}$ ) was determined at mid-day several times during the 1998 (2 dates) and 1999 (4 dates) growing seasons. On each date, temperatures were measured at 5 cm below the peat surface at three locations within each plot using T-type thermocouples and a hand-held temperature probe (YSI Inc., Yellow Springs, Ohio, USA).

### Statistical analysis

We analyzed ANPP for each of the years 1998 through 2001, belowground biomass for 2001, litter depth for 1998–2001, litter cover and mass for 2001, soil nutrient

availability and plant nutrient concentration for 2001, and canopy light interception and soil temperature at each sampling date for (fixed) effects of treatment using a one-way ANOVA (GLM; SAS Institute 1989). We analyzed plant species cover for main and interactive (fixed) effects of year and treatment using repeated measures multivariate analyses of variance (MANOVA; Pillai's trace in SAS procedure GLM; SAS Institute 1989) for 7 species that had cover >3% averaged over 1998–2001. We used species presence and cover data for all species present in 2001 to determine species richness (S), Shannon diversity index ( $H'$ ) and evenness ( $J'$ ) on a plot-wise basis (Shannon and Weaver 1962), and analyzed S and  $H'$  for effects of treatment with a one-way ANOVA model. We used Pearson correlation analysis to determine relationships between mean annual ANPP for the control treatment only, and mean annual ANPP for all treatments, versus mean growing season (May–October) and mean annual air temperature and precipitation from the nearest national weather station (Hibbing FAA Airport, Minnesota;  $n=4$ ).

Prior to statistical analysis, the distributions of all data within each treatment were tested for normality with the Shapiro–Wilk W-statistic (Shapiro and Wilk 1965). Data not normally distributed ( $P<0.05$ ) were arcsine-square root or log-transformed prior to analysis. We used Fisher's protected LSD (Fisher 1960) a posteriori mean separation tests to compare levels within treatment ( $\alpha<0.05$ ). We used detrended correspondence analysis (DCA) to analyze and display vegetation patterns based on species cover data for 1998–2001 using the PC-ORD software (McCune and Medford 1997, McCune and Grace 2002). We removed species present in less than 5% of the plots from each dataset before ordination (Gauch 1982); this left 14 species for ordination (listed in Fig. 1b).

## Results

### Production, diversity, and species composition

In 1998, ANPP was greater in R plots than in A or C plots, which did not differ significantly (Table 1).

However, between 1999 and 2001, ANPP did not differ among treatments ( $P>0.05$ ). At experiment termination in 2001, root mass did not differ between treatments (Table 1). There was substantial interannual variation in ANPP during the course of the experiment; between 1998 and 2001, ANPP increased in all treatments by a factor of about 3. ANPP for the control treatment, and for all treatments combined, was not correlated with growing season or annual air temperature and precipitation ( $P>0.16$ ; data not shown).

In contrast with the lack of response in productivity, plant community composition responded strongly to the litter manipulation treatments. In the first year of the experiment (1998), all plots had negative scores on axis I and were generally clustered together, which indicates homogeneity of species composition in all treatment plots (Fig. 1a). However, between 1999 and 2001, plots where litter had been removed (R) had positive axis I scores, whereas plots where litter was unmanipulated (control, C), or added (A), had negative axis I scores. Thus, the composition and abundance of species in A and C plots changed little throughout the experiment, whereas the composition and abundance of species in R plots changed greatly after the first year of the experiment.

Observed shifts in the composition of the fen plant community throughout the experiment were driven by the response of a few key species to removal of litter, with *Rhynchospora fusca* driving axis I scores (Fig. 1b). In 1998, foliar cover of *R. fusca* was low in all treatments; in subsequent years, cover of *R. fusca* in R plots increased to over 50%, whereas it remained low in A and C plots (Fig. 2a). In contrast, by experiment termination, the foliar cover of *C. exilis* in R plots declined to 30%, whereas its cover in A and C plots increased to 60% (Fig. 2b). Cover of *R. alba* remained low in A and C plots, but increased from about 1% to over 7% in R plots (Fig. 2c). Cover of a co-dominant graminoid, *C. lasiocarpa*, did not differ among treatments throughout the experiment ( $P=0.55$ ,  $9\pm 3\%$ , mean  $\pm$  se). Foliar cover values for all other graminoids, forbs, and shrubs were uniformly low (i.e. <3% each) and were unaffected by the litter treatments. Species richness ( $8.2\pm 0.3$ , mean  $\pm$  se),

Table 1. Mean ( $\pm 1$  se) aboveground net primary production (ANPP) in 1998–2001, and root biomass (to 30 cm depth) in 2001, within replicate plots ( $n=5$ ) in a Minnesota fen where litter was either added, left unmanipulated (=control), or removed at the start of each growing season. P-values are for the ANOVA for ANPP or root mass in each year; within columns, means with the same lower-case letter did not differ (Fisher's protected LSD;  $P>0.05$ ).

Litter treatment	ANPP ( $\text{g m}^{-2} \text{y}^{-1}$ )				Root mass ( $\text{g m}^{-2}$ )
	1998	1999	2000	2001	2001
P-value	0.0004	0.56	0.20	0.05	0.06
Added	$76\pm 8$ a	$140\pm 14$ a	$185\pm 16$ a	$344\pm 25$ a	$282\pm 63$ a
Control	$87\pm 2$ a	$147\pm 3$ a	$213\pm 19$ a	$459\pm 34$ a	$470\pm 79$ a
Removed	$116\pm 4$ b	$157\pm 12$ a	$231\pm 15$ a	$325\pm 49$ a	$249\pm 34$ a

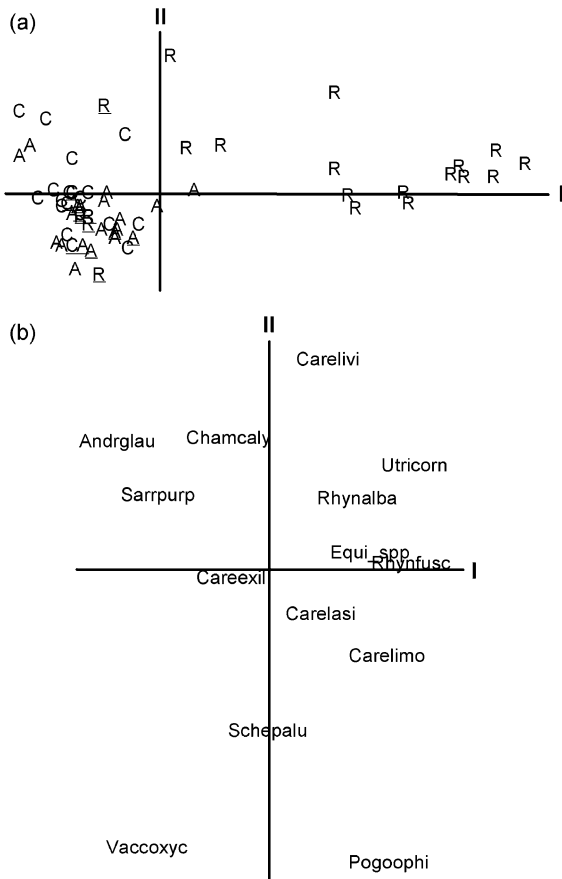


Fig. 1. Ordination of sample (a) and species (b) scores for the fen plant community based on species cover in 1998–2001. In (a), codes correspond to litter manipulation treatments: A = litter added, C = control, and R = litter removed at the start of each growing season, and underlined letters represent data from 1998. In (b), species codes are comprised of the first four letters of the genus and species, except for *Equisetum* spp., for the following taxa: *Andromeda glaucophylla*, *Chamaedaphne calyculata*, *Carex exilis*, *C. lasiocarpa*, *C. limosa*, *C. livida*, *Pogonia ophioglossoides*, *Rhynchospora alba*, *R. fusca*, *Sarracenia purpurea*, *Scheuchzeria palustris*, *Utricularia cornuta* and *Vaccinium oxycoccos*.

Shannon–Wiener diversity of cover ( $1.06 \pm 0.07$ ), and evenness of cover ( $0.50 \pm 0.03$ ) in 2001 did not differ among litter treatments ( $P > 0.23$ ).

### Litter depth, mass and cover

The depth of the litter layer was greater in A and C plots than in R plots, and depth of litter did not differ between C and A plots except in 2000 (Table 2). At experimental termination in 2001, the mass of litter in A plots was about 2 times that in C plots, and 10 times that in R plots (Table 2). There was a practically continuous cover by litter in A and C plots in 2001, but litter was sparse in R plots (Table 2).

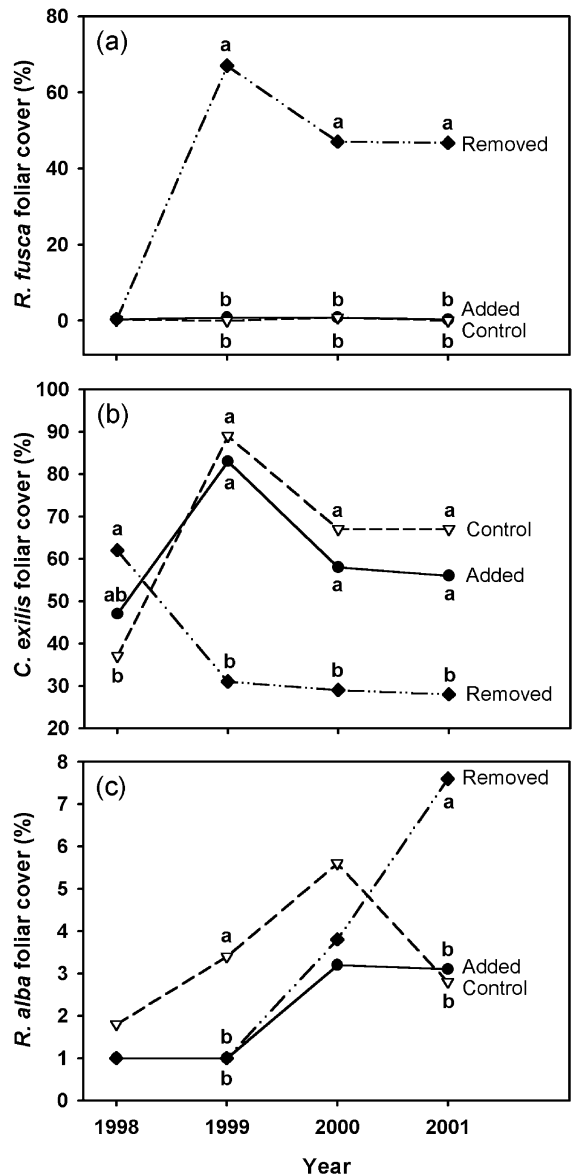


Fig. 2. Foliar cover for (a) *R. fusca*, (b) *C. exilis*, and (c) *R. alba* between 1998 and 2001 in plots where litter was either added, left unmanipulated (=control), or removed at the start of each growing season. For each species, the year  $\times$  treatment effect was  $< 0.06$ ; for each species on each date, means with the same lower-case letter did not differ ( $P > 0.05$ ).

### Canopy light interception and soil temperature

Interception of PPFD was greater in both A and C plots than in R plots on all 9 sampling dates between 1998 and 2001 (Table 3). However, with the exception of one date (22 June 1999), interception of PPFD did not differ between A and C plots. Soil temperatures were greater in R plots than in A or C plots, which did not differ, on both sampling dates in 1998 and on one of four sampling

Table 2. Mean ( $\pm 1$  se) litter depth (1998–2001), litter mass (2001), and litter cover (2001), within replicate plots ( $n=5$ ) in a Minnesota fen where litter was either added, left unmanipulated (=control), or removed at the start of each growing season. P-values are for the ANOVA for litter depth, mass, or cover in each year; within columns, means with the same lower-case letter did not differ (Fisher's protected LSD;  $P>0.05$ ).

Litter treatment	Litter depth (cm)				Litter mass ( $\text{g m}^{-2}$ )	Litter cover (%)
	1998	1999	2000	2001	2001	2001
P-value	<0.0001	<0.0001	<0.0001	0.002	<0.0001	<0.0001
Added	17 $\pm$ 2 a	11 $\pm$ 1 a	14 $\pm$ 1 a	17 $\pm$ 2 a	610 $\pm$ 40 a	99 $\pm$ 1 a
Control	17 $\pm$ 2 a	10 $\pm$ 1 a	18 $\pm$ 1 b	20 $\pm$ 2 a	335 $\pm$ 52 b	96 $\pm$ 2 a
Removed	2 $\pm$ 1 b	1 $\pm$ 1 b	9 $\pm$ 1 c	11 $\pm$ 1 b	59 $\pm$ 7 c	13 $\pm$ 2 b

dates in 1999. On the remaining three sampling dates in 1999, soil temperatures did not differ among the litter treatments (Table 3).

### Nutrient dynamics in tissue and soil solution

Nutrient concentrations in plant tissues differed among treatments, depending on the specific component investigated (i.e. live shoot tissue, litter or roots). Concentration of phosphorus in bulk green shoot tissue was greater in R plots than in A or C plots, which did not differ (Table 4). Nitrogen content of green shoot tissue and roots did not differ among treatments, but litter from A plots had higher concentrations of nitrogen than litter from either C or R plots, which did not differ. This difference in nitrogen concentration of litter affected the C:N of litter, which was greater in R plots than in A plots. Integrated availability of nitrate, ammonium, and phosphorus, as measured by ion-exchange resins in the soil solution, did not differ among treatments (Table 4).

### Discussion

Our results demonstrate that litter is a critical internal control of plant community composition and

microenvironmental variables in this fen. In particular, removal of litter caused dramatic shifts in plant community composition and affected the availability of light at the soil surface, the temperature of soil, and the concentration of nutrients in bulk shoot tissues. These findings are consistent with numerous other studies that demonstrate the control of litter over the structure and function of plant communities and their ecosystems (Carson and Peterson 1990, Facelli and Pickett 1991a, Facelli 1994, Foster and Gross 1998, Xiong and Nilsson 1999).

In contrast, additions of litter had minor effects on community production or composition, interception of light, soil temperatures, or concentrations of nutrient in plant and litter tissues. These results are inconsistent with studies in other ecosystems wherein addition of litter affected production, composition, and microenvironments (reviewed by Facelli and Pickett 1991a, Xiong and Nilsson 1999). Although our litter addition treatment effectively doubled the mass of litter relative to the control plots, these additions of litter did not affect depth or coverage of the litter layer which may be more important than litter mass in controlling community composition in this fen.

In all treatments, ANPP in this fen exhibited considerable interannual variation. The reason this variation was not clear; ANPP was uncorrelated with mean or growing season air temperatures or

Table 3. Mean ( $\pm 1$  se) interception of photosynthetically active photons (PPFD) in 1998–2001, and soil temperature in 1998–1999 ( $n=5$ ) in a Minnesota fen where litter was either added, left unmanipulated (=control), or removed at the start of each growing season in 1998–2001. For each response variable on each sampling date, means with the same lower-case letter did not differ (Fisher's protected LSD;  $P>0.05$ ).

Date	Interception of PPFD (%)			Temperature ( $^{\circ}\text{C}$ ) at 5-cm depth		
	Added	Control	Removed	Added	Control	Removed
23 July 1998	99 $\pm$ 0 a	97 $\pm$ 1 a	56 $\pm$ 5 b	15.4 $\pm$ 0.2 a	15.8 $\pm$ 0.2 a	18.7 $\pm$ 0.2 b
31 August 1998	99 $\pm$ 0 a	96 $\pm$ 1 a	64 $\pm$ 4 b	14.1 $\pm$ 0.4 a	14.6 $\pm$ 0.3 a	18.6 $\pm$ 0.6 b
22 June 1999	95 $\pm$ 2 a	88 $\pm$ 2 b	57 $\pm$ 4 c	–	–	–
25 July 1999	88 $\pm$ 2 a	82 $\pm$ 2 a	50 $\pm$ 5 b	20.7 $\pm$ 0.4 a	19.7 $\pm$ 0.3 a	21.0 $\pm$ 0.5 a
26 August 1999	94 $\pm$ 2 a	92 $\pm$ 1 a	67 $\pm$ 3 b	19.9 $\pm$ 0.2 a	19.4 $\pm$ 0.4 a	20.6 $\pm$ 0.7 a
11 October 1999	–	–	–	7.6 $\pm$ 0.2 a	7.8 $\pm$ 0.1 a	8.9 $\pm$ 0.1 b
28 October 1999	98 $\pm$ 0 a	98 $\pm$ 1 a	80 $\pm$ 3 b	4.3 $\pm$ 0.1 a	3.8 $\pm$ 0.1 a	4.0 $\pm$ 0.2 a
23 May 2000	88 $\pm$ 1 a	91 $\pm$ 2 a	55 $\pm$ 1 b	–	–	–
8 June 2000	88 $\pm$ 2 a	88 $\pm$ 1 a	69 $\pm$ 3 b	–	–	–
26 July 2001	87 $\pm$ 3 a	89 $\pm$ 2 a	69 $\pm$ 2 b	–	–	–

Table 4. Mean ( $\pm 1$  se) nitrogen (%), carbon (%), C:N ratio, and phosphorus (%) for green shoot tissue, roots, and litter collected at experiment termination in October 2001, and  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$ , and  $\text{PO}_4\text{-P}$  ( $\mu\text{g g}^{-1}$  resin) from mixed-bed or anion resin bags placed at 7–10 cm depth below the soil surface between June 2000 and October 2001, within replicate plots ( $n = 5$ ) in a Minnesota fen. Plots were assigned three treatments, wherein litter was either added, left unmanipulated (=control), or removed at the start of each growing season. P-values are for the ANOVA for each variable; within row, means with the same lower-case letter did not differ (Fisher's protected LSD;  $P > 0.05$ ).

System component	P-value	Litter treatment		
		Added	Control	Removed
Green shoot tissue				
N	0.14	0.88 $\pm$ 0.07 a	0.81 $\pm$ 0.04 a	0.97 $\pm$ 0.05 a
C	0.08	43.98 $\pm$ 0.12 a	44.21 $\pm$ 0.11 a	44.35 $\pm$ 0.08 a
C:N ratio	0.20	51.62 $\pm$ 4.48 a	55.45 $\pm$ 3.05 a	46.20 $\pm$ 2.29 a
P	0.04	0.038 $\pm$ 0.003 a	0.035 $\pm$ 0.001 a	0.048 $\pm$ 0.004 b
Roots				
N	0.63	0.51 $\pm$ 0.02 a	0.48 $\pm$ 0.02 a	0.51 $\pm$ 0.03 a
C	0.89	46.87 $\pm$ 0.31 a	46.68 $\pm$ 0.36 a	46.91 $\pm$ 0.38 a
C:N ratio	0.68	92.91 $\pm$ 4.56 a	97.37 $\pm$ 3.88 a	92.66 $\pm$ 4.37 a
P	0.09	0.015 $\pm$ 0.001 a	0.014 $\pm$ 0.0004 a	0.016 $\pm$ 0.001 a
Litter				
N	0.02	1.07 $\pm$ 0.07 a	0.93 $\pm$ 0.03 b	0.84 $\pm$ 0.04 b
C	0.89	43.55 $\pm$ 0.15 a	43.71 $\pm$ 0.15 a	43.62 $\pm$ 0.33 a
C:N ratio	0.03	41.55 $\pm$ 3.01 a	47.28 $\pm$ 1.63 ab	52.51 $\pm$ 2.65 b
P	0.19	0.034 $\pm$ 0.003 a	0.029 $\pm$ 0.002 a	0.028 $\pm$ 0.002 a
Nutrient availability				
$\text{NO}_3\text{-N}$	0.30	5.04 $\pm$ 0.67 a	10.65 $\pm$ 4.23 a	6.74 $\pm$ 0.74 a
$\text{NH}_4\text{-N}$	0.68	80.19 $\pm$ 14.28 a	71.64 $\pm$ 5.26 a	67.64 $\pm$ 9.01 a
$\text{PO}_4\text{-P}$	0.29	2.91 $\pm$ 0.37 a	2.24 $\pm$ 0.15 a	2.41 $\pm$ 0.33 a

precipitation. However, large interannual variations in production are common at this site (Weltzin et al. 2000, Chapin et al. 2004) and at other fens (Thormann and Bayley 1997a, 1997b), and appear to be the norm rather than the exception for northern fens. Moreover, our estimates of production are well within the range of production for this fen (Weltzin et al. 2000, Chapin et al. 2004), and for other fens at similar latitudes worldwide (Reader 1978, Szumigalski and Bayley 1996, Thormann and Bayley 1997a, 1997b, Mitsch and Gosselink 2000).

### Microenvironmental controls over fen community composition

Litter likely altered the plant community in this fen through modifications of one or more microenvironmental conditions. There are numerous biotic and abiotic variables that could lead to such changes in species performance and subsequent shifts in community composition; however, these variables are not mutually exclusive, and may interact with one another (Facelli and Pickett 1991b, Bonan 2002, Noormets et al. 2004). Thus, while it would be misleading to suggest that one particular variable is driving community responses to litter manipulation, we evaluate the potential mechanisms that may have contributed to observed shifts in community structure in our experiment, especially in response to litter removal.

Changes in litter depth, cover, and mass caused by removal of litter increased the availability of light at the soil surface by about 30%. Similar changes in radiation regimes caused by the experimental manipulation of litter have been observed in a variety of other ecosystems (Weaver and Rowland 1952, Knapp and Seastedt 1986, Facelli and Pickett 1991b), and have contributed to differential effects on seed germination, seedling establishment, and plant growth (Goldberg and Werner 1983, Facelli and Pickett 1991b, Foster and Gross 1998, Xiong and Nilsson 1999). Availability of light is known to be an important variable in structuring peatland plant communities (Vitt and Slack 1975, Vitt et al. 1990, Anderson et al. 1996) and may be a limiting factor for many of the species present in our experimental system (Wheeler et al. 1983, Santelmann 1991, Anderson et al. 1996). For example, abundance of both *R. fusca* and *R. alba* increased after the removal of shrub neighbors increased availability of light along lakeshore margins (Keddy 1989, Rossell et al. 1995). These results suggest that increased light availability may be an important mechanism leading to shifts in community structure in response to litter removal in our experiment.

Effects of litter on soil temperature regimes in other systems include changes in the timing and duration of the growing season, changes in minimum and maximum soil temperatures, physical disruption of soil by frost heaving, and frost damage to meristems and leaf tissue, with implications for seed germination, plant growth, and total production (Watt 1970, Knapp and

Seastedt 1986, Facelli and Pickett 1991a). In the current study, removal of litter tended to increase soil temperatures, depending on season and year. However, all temperatures were estimated at discrete time points during the growing season, and thus may have been inadequate to capture potential treatment effects on diel or seasonal temperature patterns. Further, the lack of consistent responses of soil temperature may have been caused by the hydrology of the site; water tables were typically above the soil surface, although water-table depth varied because of variations in precipitation and the downstream activities of beavers (Chapin 1998).

Removal of litter increased the phosphorus content of bulk green shoot tissue material by 37% compared to the control treatment (Table 4). The observed increase of *R. fusca* cover (and the concomitant decrease in cover of *C. exilis*) may explain this increase in phosphorus content as previous work has indicated that *R. fusca* green shoot material has >30% more phosphorus than *C. exilis* in this fen (Chapin 1998).

However, manipulations of litter had little effect on the integrated availability of nutrients as measured by resin bags within each of the plots. The lack of an effect of litter manipulations on nutrient availability is somewhat surprising, because (1) changes in temperature are often attributed to changes in rates of mineralization and availability of nutrients (Knapp and Seastedt 1986, Pastor et al. 1987, Chapin et al. 1995) and (2) the incorporation of phosphorus-rich *R. fusca* litter into peat could act as a positive feedback on nutrient cycling in this ecosystem. The annual physical redistribution of litter required by our experimental design may have obscured the potential feedbacks caused by in situ production of *R. fusca* litter. Over longer time scales, linkages between the structure of the plant community and phosphorus cycling could have important implications in this phosphorus-limited fen ecosystem (Bedford et al. 1999, Chapin et al. 2004).

## Conclusion

Our results strongly support previous work demonstrating that litter may act as an important control of plant community composition. In the current study, the addition and removal of litter had very different effects on fen plant community composition and microenvironmental response variables, suggesting that there may be important thresholds in the response of plant communities to litter accumulation. In contrast with the paucity of effects of addition of litter in this ecosystem, the removal of litter led to dramatic shifts in the plant community in the fen. These observed shifts were likely mediated by modifications of one or more microenvironmental conditions; our results suggest

that physical effects of litter on light and/or temperature may be more important in controlling fen plant community composition than effects of litter on processes such as nutrient cycling over the timeframe of this experiment.

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