CO_2 and H_2O exchange from understory species in an Alaskan boreal forest

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Introduction

Black spruce is the most widespread boreal forest type in North America. This type of forest is relatively open, due to the narrow canopy and low density of trees. A substantial proportion of solar energy therefore reaches the forest floor, resulting in a significant role for the understory vegetation in CO_2 and energy exchange. The ground cover is often dominated by mosses, feathermosses such as *Hylocomium splendens* and *Pleurozium schreberi* in the shady areas and peatmosses (*Sphagnum* spp.) in more exposed and wetter sites. The vascular-plant component consists mainly of low shrubs, and lichens are locally abundant.

Mosses may have strong effects on the ecosystem. They insulate the soil, intercept atmospheric nutrients, and decompose very slowly, thereby reducing soil temperatures and rates of nutrient supply (Oechel and Van Cleve, 1986). Despite these potentially strong effects of mosses, very little is known about the role of the understory vegetation. Recent eddy covariance measurements have resulted in CO_2 and energy exchange data for boreal forests (Chapin et al., 2000), but these whole-ecosystem measurements do not differentiate among the effects of species or functional groups within the ecosystem.

We conducted chamber flux measurements in an Alaskan black spruce forest in order to compare CO_2 and water vapour exchange among patches of understory vegetation dominated by feathermoss (*Hylocomium*), peatmoss (*Sphagnum*), vascular plants (mainly low shrubs), or lichens. In addition, we used lysimeters to study the role of mosses in boreal forest evapotranspiration. Details of these studies can be found in Heijmans et al. (2004a, 2004b).

Methods

Research site

Both chamber flux measurements and lysimeter experiment were conducted in a black spruce forest in Fairbanks, central Alaska (64°52'N, 147°51'W, 155-180 m elevation). This mature boreal forest is situated on a north-facing slope underlain by permafrost and exhibits a gradient from dense forest on the midslope to open forest on the lower slope to bog towards the valley bottom. Black spruce (*Picea mariana*) is the dominant tree species over this entire gradient. The regional climate is strongly continental with a mean January temperature of –22.8 °C and a mean July temperature of 16.7 °C. Mean annual temperature is –3.3 °C and average annual precipitation is 263 mm.

Chamber flux measurements

CO_2 and water vapour flux measurements were made in four understory vegetation types in each of six sites within the open black spruce forest. The sites were selected for the occurrence of pure mats of *Hylocomium* and *Sphagnum* moss vegetation near each other. We established 22 plots by installing transparent plastic collars in patches of vegetation dominated by either *Hylocomium splendens*, *Sphagnum capillifolium*, vascular plants (mainly *Ledum groenlandicum*, *Vaccinium vitis-idaea* and *Vaccinium uliginosum*; these are low shrub species), or lichens (only at 4 of the 6 sites). Measurements were made six times, spread out over the 2002 growing season. Measurements were made between 9:30 and 15:00 Alaska daylight time, and represent a midday flux. CO_2 and water vapour fluxes were measured inside a transparent chamber (15 cm diameter, 36 cm height) placed on top of the collar. The chamber was connected to a LI-6262 CO_2/H_2O analyser in a closed circuit. CO_2 and water vapour fluxes were calculated from the linear change in CO_2 and water vapour concentration during the first minute of measurement.

Lysimeter experiment

We filled 48 plastic containers of 16 cm diameter and 15 cm deep with intact moss/soil columns of *Hylocomium splendens* or *Sphagnum capillifolium*. These lysimeters were inserted in 12 sites, 4 in each of the 3 habitats: dense forest, open forest and bog. Within each site, the containers were placed in patches of open moss vegetation or in patches of denser and taller vascular plant vegetation. The experimental design was thus 2 moss species by 2 surrounding vegetation types in 3 habitats, replicated 4 times. The lysimeters were weighed weekly during the entire growing season.

Results

Chamber flux measurements

There were large differences in CO_2 exchange among the understory vegetation types (Fig. 1A). The *Sphagnum* and vascular-plant plots showed net CO_2 uptake, whereas the lichen plots lost CO_2 to the atmosphere. The CO_2 fluxes in the *Hylocomium* plots were near zero. Note that the fluxes in this study represent instantaneous midday fluxes, which cannot be extrapolated to daily or seasonal carbon gain or loss. The differences among vegetation types were much smaller for water vapour exchange (Fig. 1B). This is probably because evapotranspiration is more constrained by climatic variables such as solar radiation and wind.

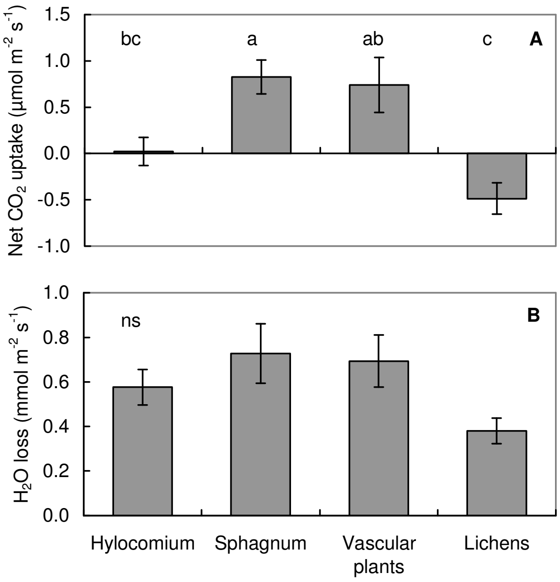

Fig. 1. Differences among understory vegetation types for (A) net CO_2 uptake, and (B) evapotranspiration. Data are mean values ± SE (*n* = 20-30 measurements, 5 dates x 4-6 plots). Different letters indicate significant differences (Tukey test). ns means no significant differences among vegetation types.

The seasonal pattern of variation in CO_2 exchange was also different among the understory vegetation types. The *Sphagnum* and vascular-plant plots showed net CO_2 uptake during the entire season, although the fluxes on a cloudy day in mid-July were near zero (Fig. 2). The highest uptake rates were on partly cloudy or sunny days in the middle of the growing season. Net CO_2 uptake in these vegetation types was strongly related to PAR (Fig. 3A). In contrast, the *Hylocomium* and lichen plots lost CO_2 during the middle of the growing season, but could increase the net CO_2 uptake at the end of the season when the soil had cooled down (Fig. 2). In these vegetation types, net CO_2 uptake was not related to PAR, but to soil temperature, with net CO_2 loss on days with high soil temperature (Fig. 3B).

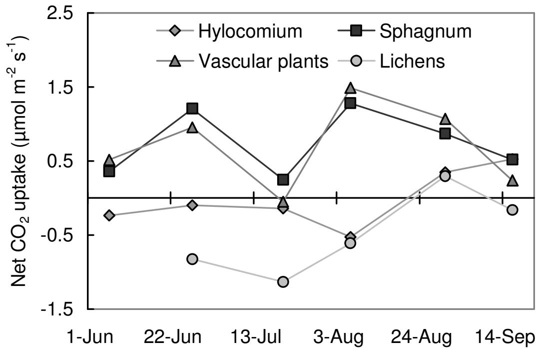

Fig. 2. Seasonal pattern of net CO_2 uptake for four understory vegetation types. Data are mean values (*n* = 4-6 plots).

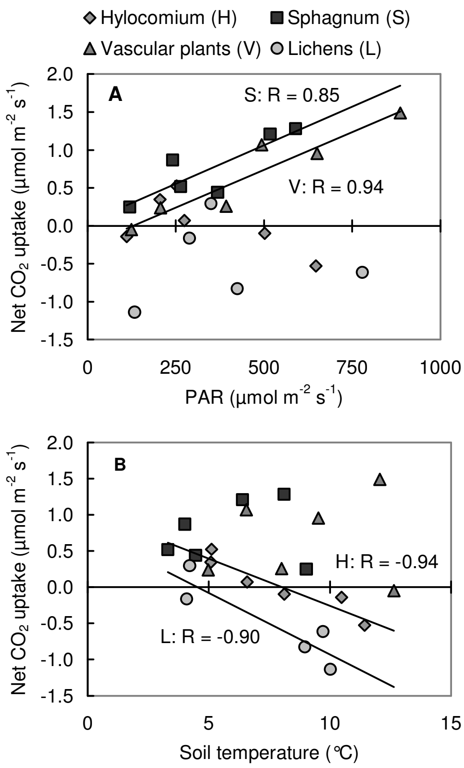

Fig. 3. Seasonal variation in net CO_2 uptake in relation to (A) PAR, and (B) soil temperature. Data are mean values (*n* = 4-6 plots) for each vegetation type and date. Pearson correlation coefficients (R) are indicated for vegetation types where they are significant.

Contrasting patterns were also observed for the relation between CO_2 and water vapour exchange. In the vascular-plant plots, and to a lesser degree in the *Sphagnum* plots, net CO_2 uptake was positively correlated to water loss. However, in the *Hylocomium* vegetation type this correlation was negative, thus on days with high evaporation rates net CO_2 uptake was lowest. This occurred because on the sunny days the top cm of moss dries out, which reduces photosynthesis more than evapotranspiration. This high sensitivity to evaporative stress (Busby et al., 1978) might contribute to the low CO_2 uptake of black spruce forest on days of high PAR (Jarvis et al., 1997)

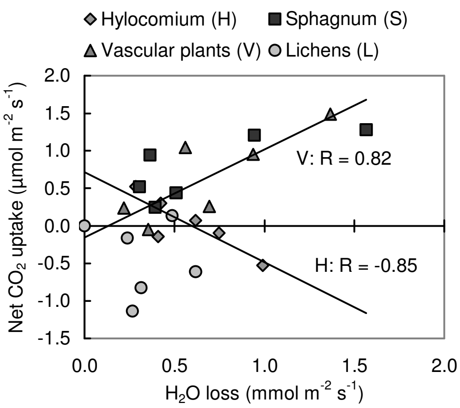

Fig. 4. Relation between CO_2 and water vapour exchange. Data are mean values (n = 4-6 plots) for each vegetation type and date. Pearson correlation coefficients (R) are indicated for vegetation types where they are significant.

Lysimeter experiment

Moss evaporation rates between 1 June and 8 September averaged 0.3, 0.9 and 1.5 mm day^{-1} in the dense forest (*Hylocomium*), open forest (*Hylocomium* and *Sphagnum*) and bog (*Sphagnum*) respectively. Unfortunately, we cannot compare our moss evaporation rates directly with simultaneously measured total forest evapotranspiration rates. However, earlier work on water vapor fluxes in boreal coniferous forests shows that the total forest evapotranspiration rates are relatively consistent, showing growing season evapotranspiration rates around 2 mm day^{-1} (Kelliher et al., 1997). Assuming a total forest evapotranspiration rate of 2 mm day^{-1}, this study shows that moss evaporation contributes considerably (15-45%) to boreal black spruce forest evapotranspiration. Moss evaporation rates depended strongly on the openness of the forest and to a lesser degree on moss species (Figure 5). Moss evaporation in the dense forest was only one quarter of that in the open forest.

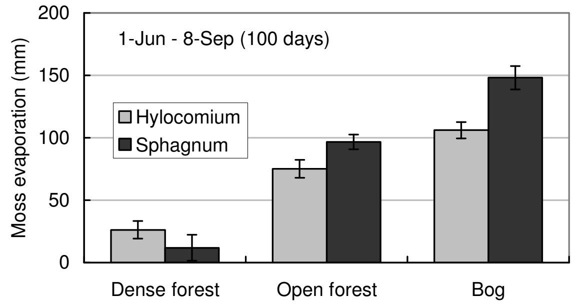

Fig. 5. Moss evaporation as affected by habitat and moss species for the entire period of measurement (100 days). Data are mean values ± SE (n = 4 containers).

The difference between the moss species was relatively small over the entire period of measurement, but the species effect depended on the weather conditions. In rainy weeks there was no species difference at all, but in dry weeks evaporation from the *Sphagnum* containers was much larger than in the *Hylocomium* containers, particularly in the bog (Figure 6). The dry week in Figure 6 was sunnier than the preceding rainy week. As a result, *Sphagnum* evaporation increased, while *Hylocomium* evaporation did not.

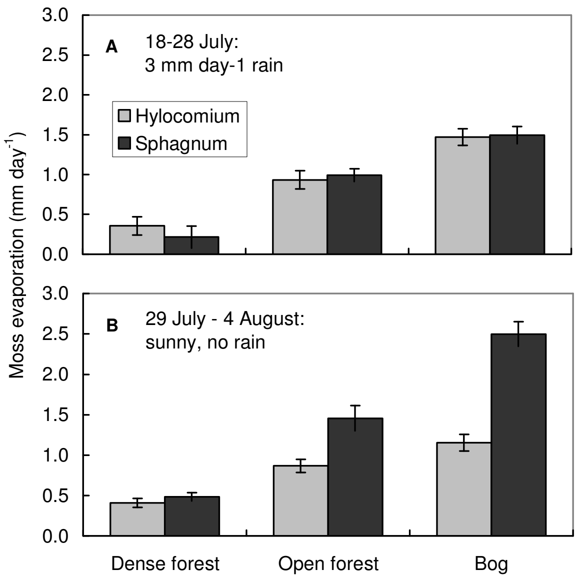

Fig. 6 Moss evaporation as affected by habitat and moss species for (A) a rainy and (B) a sunny dry week. Data are mean values ± SE (n = 4 containers).

An additional moisture experiment (see Heijmans et al., 2004b) made clear that the lower evaporation rates for *Hylocomium* containers in dry periods in the habitat experiment were the result of drying out of the *Hylocomium*. *Sphagnum* is famous for its large water holding capacity. In addition, *Sphagnum* is capable of supplying the top parts (capitulum) with water from below by capillary rise. The period of measurement (summer 2002) was much wetter than normal, resulting in relatively small differences between *Hylocomium* and *Sphagnum* evaporation over the entire growing season.

Conclusions

We found large differences between understory vegetation types with respect to midday net CO_2 exchange, including different controls on the seasonal pattern. This suggests that species composition of the understory should be taken into account when discussing understory contributions.

Assuming a total forest evapotranspiration rate of 2 mm day^{-1}, this study shows that moss evaporation can contribute considerably (15 to 45%) to boreal black spruce forest evapotranspiration. The moss contribution depends strongly on the openness of the forest. Given the large moss evaporation rates in this study, understory contributions cannot be ignored when interpreting eddy covariance data for whole forests.

There were remarkable differences between the two moss species studied, both with respect to CO_2 exchange and evapotranspiration. Midday net CO_2 uptake rates and its seasonal pattern of variation in vegetation dominated by *Sphagnum* were similar to rates measured in vegetation dominated by vascular plants, but differed from CO_2 exchange in *Hylocomium*, even though light conditions and quantities of biomass and soil organic matter were similar between the two types of moss plots. The two moss species differed in moisture content. It seems that net CO_2 uptake in *Hylocomium* is very sensitive to evaporative stress, whereas CO_2 uptake and evapotranspiration in *Sphagnum* was never limited by moisture in this forest. The seasonal pattern of CO_2 exchange in *Hylocomium* was inversely related to evapotranspiration, contradicting the general coupling between forest evapotranspiration and photosynthesis.

In dry periods, *Hylocomium* evaporation was reduced relative to *Sphagnum* evaporation, particularly in the more exposed sites. Due to limited water holding and transporting capacities, this species dries out quickly, whereas *Sphagnum* can continue evaporating at a high rate. When both moss types are important contributors to the understory vegetation, they should not be lumped together as one component of the boreal forest ecosystem.

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