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Research paper

Will changes in root-zone temperature in boreal spring affect recovery of photosynthesis in *Picea mariana* and *Populus tremuloides* in a future climate?

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Future climate will alter the soil cover of mosses and snow depths in the boreal forests of eastern Canada. In field manipulation experiments, we assessed the effects of varying moss and snow depths on the physiology of black spruce (*Picea mariana* (Mill.) B.S.P.) and trembling aspen (*Populus tremuloides* Michx.) in the boreal black spruce forest of western Québec. For 1 year, naturally regenerated 10-year-old spruce and aspen were grown with one of the following treatments: additional N fertilization, addition of sphagnum moss cover, removal of mosses, delayed soil thawing through snow and hay addition, or accelerated soil thawing through springtime snow removal. Treatments that involved the addition of insulating moss or snow in the spring caused lower soil temperature, while removing moss and snow in the spring caused elevated soil temperature and thus had a warming effect. Soil warming treatments were associated with greater temperature variability. Additional soil cover, whether moss or snow, increased the rate of photosynthetic recovery in the spring. Moss and snow removal, on the other hand, had the opposite effect and lowered photosynthetic activity, especially in spruce. Maximal electron transport rate (ETR_{max}) was, for spruce, 39.5% lower after moss removal than with moss addition, and 16.3% lower with accelerated thawing than with delayed thawing. Impaired photosynthetic recovery in the absence of insulating moss or snow covers was associated with lower foliar N concentrations. Both species were affected in that way, but trembling aspen generally reacted less strongly to all treatments. Our results indicate that a clear negative response of black spruce to changes in root-zone temperature should be anticipated in a future climate. Reduced moss cover and snow depth could adversely affect the photosynthetic capacities of black spruce, while having only minor effects on trembling aspen.

Keywords: chlorophyll fluorescence, climate warming, electron transport rate, moss cover, photosynthesis, *Picea mariana*, *Populus tremuloides*, quantum yield of PSII, soil temperature, snow cover, stable isotopes.

Introduction

The Intergovernmental Panel on Climate Change fourth assessment report predicts that climate warming in the boreal zone is likely to exceed the global mean warming in other world

areas (Christensen et al. 2007). Changes averaged over 21 climatic models project an increase in winter temperature of 5–7 °C for western Québec, Canada (Christensen et al. 2007). This warming could be accompanied by 10–25% more

Table 1. Abbreviations.

A	CO ₂ assimilation rate
C	carbon
c _a	ambient CO ₂ concentration
c _i	leaf intercellular CO ₂ concentration
c _i /c _a	ratio between leaf intercellular and ambient CO ₂ concentrations
ETR	rate of electron transport (μmol m ⁻² s ⁻¹)
ETR _{max}	maximal rate of electron transport (μmol m ⁻² s ⁻¹)
F _m	maximum fluorescence yield of a dark-adapted leaf
F _o	minimum fluorescence yield of a dark-adapted leaf
F _v	variable fluorescence yield of a dark-adapted leaf (F _v = F _m - F _o)
F _v /F _m	potential quantum yield of PSII
g _s	stomatal conductance
IPCC	Intergovernmental Panel on Climate Change
N	nitrogen
PPFD	photosynthetic photon flux density (μmol m ⁻²)
PPFD _{sat}	saturating photosynthetic photon flux density (μmol m ⁻²)
PSI and PSII	photosystems I and II
ΔF/F _m	effective quantum yield of PSII
δ ¹³ C	measure of the ratio of stable isotopes ¹³ C: ¹² C (‰)
δ ¹⁸ O	measure of the ratio of stable isotopes ¹⁸ O: ¹⁶ O (‰)

precipitation relative to actual conditions (Christensen et al. 2007). Recent climate simulations suggest that this increase in precipitation will not be sufficient to compensate for the increased evapotranspiration caused by higher temperatures, limiting moisture availability (Girardin and Mudelsee 2008). These drier conditions, coupled with an increase in forest fire activity (Bergeron et al. 2010), could limit moss accumulation on the forest floor (Fenton et al. 2005). Conversely, if the level of precipitation was to exceed that of evapotranspiration, moss colonization could be favoured. Another direct consequence of climate warming could include delayed beginning of the snow season in autumn, and accelerated soil thawing in spring, which would shorten the snow season and increase soil frost occurrence and severity in autumn and spring (Campbell et al. 2005).

Mosses and snow are important insulators of soils in the boreal zone. Mosses intercept incoming solar radiation and use it for photosynthesis. In contrast, uncovered soil directly absorbs solar energy, which results in increased soil temperature (Miller et al. 1980). Given their lower thermal conductivity compared with soil, mosses create a physical barrier, further preventing soil warming (Hinzman et al. 1991). The colder soil conditions associated with the presence of a moss cover on the forest floor affect soil nutrient dynamics by slowing down organic matter decomposition and therefore reducing nutrient availability (Fenton et al. 2005, Simard et al. 2007). Snow, having a low thermal conductivity, prevents soil freezing in winter, and large temperature variations in autumn and spring. Given their direct dependence on climatic conditions, the

covers of mosses and snow are susceptible to rapid change with climatic warming (Campbell et al. 2005, Gornall et al. 2007). Hence, their potential to influence tree growth requires better understanding.

In the boreal zone, forest productivity is largely constrained by low air and soil temperatures. In autumn, photosynthesis in conifers and deciduous trees is down-regulated after the first daytime frosts (Ensminger et al. 2009) and essentially shut down in winter (Kozłowski and Pallardy 1996). In spring, photosynthesis is resumed in response to increasing air temperature (Bergh and Linder 1999, Tanja et al. 2003, Mäkelä et al. 2004) and its recovery is largely controlled by intermittent frosts (Ensminger et al. 2008). The photosynthetic capacity of trees during the winter–spring transition will to a large extent determine the annual carbon gain of forests, and thus productivity. In spring, soil temperature plays a major role in the recovery of photosynthesis, which is restricted by soil frost and low root-zone temperature (DeLucia and Smith 1987, Bergh and Linder 1999, Ensminger et al. 2008). Soil frost prevents water uptake by roots by increasing the viscosity of water and decreasing the permeability of roots (Kramer 1983). In addition, cold soil inhibits the metabolism and growth of roots, which in turn reduces root water flow (Kozłowski et al. 1991). In conifers, water deficit in needles may occur during spring when high air temperature increases the evaporative demand of leaves and frozen soil prevents water uptake (Berg and Chapin 1994). Influences of the timing of air and soil warming on the recovery of photosynthesis and thus forest productivity are still poorly understood, and potential interactions of changes in winter precipitation and earlier warming in spring on photosynthetic production are not well known.

Several studies have investigated the response of boreal tree species to varying soil temperature (Bergh and Linder 1999, Domisch et al. 2001, 2002, Strand et al. 2002, Repo et al. 2004, 2005, 2007, Ensminger et al. 2008). These experiments were carried out either in controlled environments of growth chambers or under natural conditions in Fenno-Scandinavian forests. These studies indicate that cold soil temperatures inhibit the spring recovery of photosynthesis or phenological events such as budburst. Yet, few experiments have investigated the effects of soil temperature on Canadian boreal tree species (but see Peng and Dang 2003, Dang and Cheng 2004) in Québec's forests, which differ climatically from Fenno-Scandinavia by greater temperature extremes between summer and winter, a thicker snow cover in winter, or the presence of a thick moss cover on the forest floor (Simard et al. 2007). In these ecosystems, root-zone temperature is likely to be controlled to a greater extent by mosses and snow, and therefore changes in soil cover insulation might have a greater impact on the physiological processes of trees. We thus controlled soil temperature in the

field through moss and snow manipulation and monitored the physiological response of two of the most ecologically and economically important tree species of the Canadian boreal forest, black spruce (*Picea mariana* (Mill.) B.S.P.) and trembling aspen (*Populus tremuloides* Michx.). Black spruce proliferates on cold, poorly drained soils (Burns and Honkala 1990a) and has a photosynthetic rate tolerant to cold soil temperatures (Dang and Cheng 2004). In contrast, trembling aspen performs better on warmer, well-drained soils (Burns and Honkala 1990b), being more sensitive to cold soil temperatures (Dang and Cheng 2004). We hypothesized that warmer soil temperatures caused by moss removal or snow removal in the spring would particularly favour the spring recovery of trembling aspen, while colder soil temperatures caused by moss addition or snow addition in the spring would impair the recovery of both species.

Methods

Experimental site

This experiment was carried out in Québec's western boreal forest (79°2'W, 49°44'N), within the black spruce–feather moss (*Pleurozium schreberi* (Bird) Mitt.) bioclimatic zone (Doucet and Côté 2009). The experiment was set up in a 10-year-old black-spruce-dominated stand that was naturally regenerated after a forest fire in 1997. The soil type in the study area was a clay classified as gleysol (Soil Classification Working Group 1998). These clay soils are prone to paludification, which is common in this area, which is part of the clay belt of Québec and Ontario. The experimental site was covered with a continuous feather and sphagnum moss ground cover on a raw humus layer that is ~20 cm thick. The area has a mean annual temperature of 1.2 °C, with the highest (16.1 °C) and lowest (−18.8 °C) mean monthly temperatures in July and January, respectively. Mean annual precipitation is 910 mm, with 222 mm occurring as snow (Environment Canada 2008).

Biological materials and treatments

The 42 spruces and 42 aspens used for this study were selected in an area of ~20 ha according to their size (from 1.2 to 2.5 m of height) and general appearance (no disease or damage). Stand density was typical of a post-fire stand with sparse saplings and no canopy trees. The experiment was done as a blocked randomized experiment with seven blocks. Within each block, one sapling of each species was randomly assigned to one of six treatments (Table 2), control (C), nitrogen addition (F), moss addition (M+), moss removal (M−), delayed soil thawing (S+) and accelerated soil thawing (S−), so that the treatments were homogeneously distributed over the area. In the C treatment, the snow and moss covers were kept intact and no fertilizer was added. Treatment F was meant to test nitrogen (N) limitations on photosynthesis

Table 2. Stages of photosynthetic recovery for all treatments in spruce, their duration, mean air temperature (°C) and occurrence of night frosts.

Phase	Recovery stage	Duration	Mean air temperature (°C)	Night frosts
I	Initial recovery	May 7–17	7.5	May 9
II	Frost	May 18–30	5.5	May 20, 26, 27, 28, 29, 30
III	Frost recovery	May 31–June 17	14	June 4, 12
IV	Full recovery	June 18–August 13	16	None

under prevalent conditions, and consisted of the application of the equivalent of 140 kg ha^{−1} slow-release N fertilizer on a 2.0 m radius around the saplings. In the M+ treatment, the objective was to create lower soil temperatures in the summer, and a sphagnum moss layer ~15.0 cm thick was added in September 2007 to cover a 1.5 m radius area around the saplings. At the same time, all moss was manually removed on a 1.5 m radius around the saplings assigned to treatment M− to raise soil temperatures during the summer of 2008. In the S+ treatment, where the objective was to keep the soil at lower temperatures during spring, the snow was shovelled in February 2008, allowing the soil to freeze deeply. In April 2008, the ground was insulated with a layer of hay 15.0 cm thick and covered with an additional 60.0 cm of snow. The hay was kept in place until mid-July 2008. Treatment S− was meant to create higher soil temperatures in the spring and consisted of shovelling the snow in April 2008 to accelerate soil thawing.

Climatic data and soil temperature measurements

Climatic and soil temperature measurements were recorded from September 2007 to October 2008 (Figure 1). Soil temperature, at a depth of 10.0 cm, was recorded every 6 h with data loggers (iButton DS1990, Maxim Electronics, Dallas, TX, USA) buried in the vicinity of 63 saplings. Hourly air temperature and precipitation were measured with an onsite meteorological station. Other climatic measurements included relative air humidity as well as wind speed and direction (data not shown).

Bud development

From the beginning of bud development in May (for spruce) and June (for aspen), bud development of the leader shoot of a selected branch was visually monitored every second day for each sapling. For spruce, the buds were assigned to one of the six developmental stages described in Numainville and Despons (2004). Aspens were evaluated according to the International Phenological Gardens Illustrated Guide (IPGIG 1966).

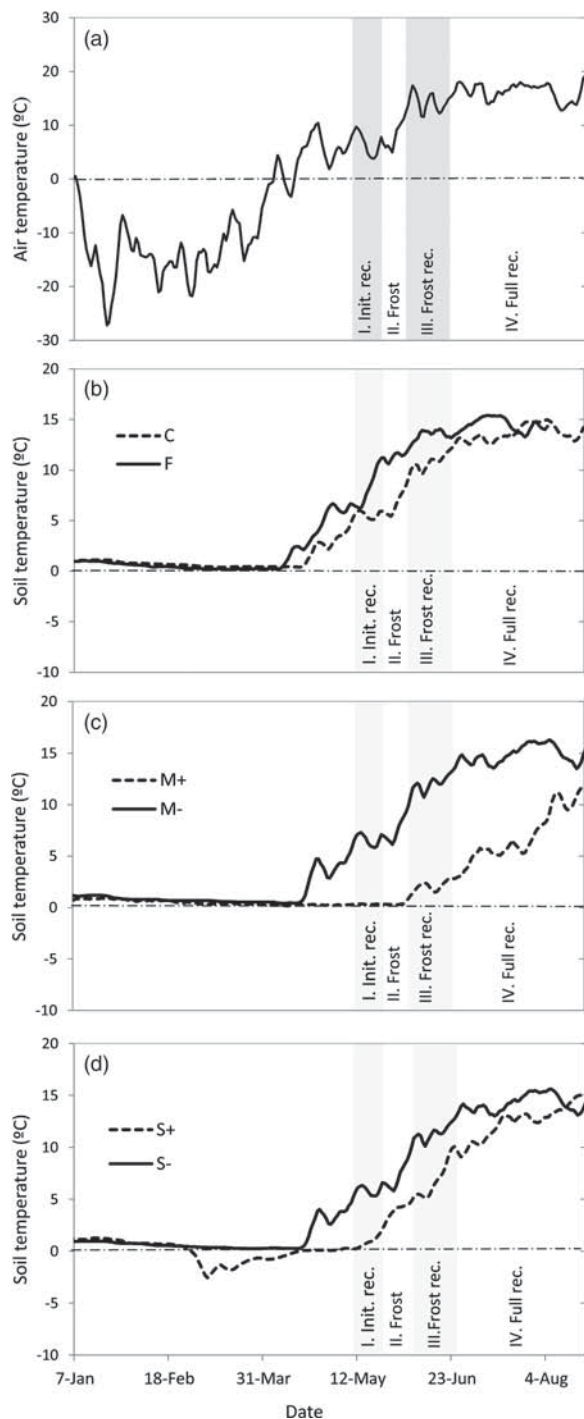


Figure 1. Effects of fertilization and thermal insulation on seasonal variations in (a) 5-day running average air temperature, (b) 5-day running average soil temperature in the control (C; dashed line) and fertilized treatment (F; solid line), (c) 5-day running average soil temperature in the treatment with additional moss (M+; dashed line) and in the treatment with moss removed (M-; solid line) and (d) 5-day running average soil temperature in the treatment with delayed thawing (S+; dashed line) and in the treatment with accelerated thawing (S-; solid line). Vertical sections indicate the four phases of photosynthetic development: I (initial recovery), II (frost), III (recovery after frost) and IV (full recovery).

Chlorophyll *a* fluorescence

For the determination of photosynthetic activity throughout the growing season, chlorophyll *a* fluorescence measurements were performed during spring and summer 2008. The spruce saplings were each measured on 20 occasions from early May until mid-August. Measurements on aspen saplings started mid-June following leaf development, were repeated eight times on each sapling, and lasted until mid-August. The pulse-amplitude-modulated fluorometer PAM-2100 (H. Walz GmbH, Effeltrich, Germany) was used for the measurements. In the case of black spruce, the measurements were performed on attached previous-year (2007) needles, always on the same shoot on a given sapling. For trembling aspen, the measurements were always taken on the same leaf. For both species, a saturating light pulse was first applied to a dark-adapted (20 min) leaf or to a group of needles for the determination of minimal and maximal fluorescence yield (F_0 and F_m , respectively). The potential quantum yield of PSII was calculated as the ratio of variable to maximum fluorescence yield (F_v/F_m ; Genty et al. 1989). The specimens were then exposed, for a period of 6 min, to 12 levels of increasing actinic light intensity (0 – $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$), and the effective quantum yield of PSII ($\Delta F/F_m$) at each level was recorded. $\Delta F/F_m$ was calculated as $(F'_m - F_t)/F'_m$, where F'_m is the maximal fluorescence in the light and F_t is the steady-state fluorescence yield at a given light intensity (Genty et al. 1989). To determine the maximal rate of electron transport (ETR_{max}) and the saturating photosynthetic photon flux density (PPFD_{sat}), the resulting $\Delta F/F_m$ versus PPFD curves were fitted using a single exponential function according to Rascher et al. (2000):

$$\text{ETR} = \text{ETR}_{\text{max}}(1 - e^{-b\text{PPFD}})$$

where b is an independent parameter and PPFD_{sat} is attained at $0.9 \text{ ETR}_{\text{max}}$. The model was fitted by non-linear regression using the NLIN procedure in SAS v. 9.2 (SAS Institute Inc., Cary, NC, USA).

Isotope analyses

The photosynthetic carbon isotope discrimination and consequent carbon isotope composition ($\delta^{13}\text{C}$) of organic matter mainly depend on the ratio between intercellular and ambient CO_2 concentrations (c_i/c_a ; Farquhar et al. 1982). Therefore, $\delta^{13}\text{C}$ reflects variations in CO_2 assimilation rate (A) and in stomatal conductance (g_s), as both influence c_i . To determine to what extent the variations in c_i are caused by the changes in A or in response to drought by variations in g_s , $\delta^{13}\text{C}$ measurements can be performed in combination with the analysis of oxygen isotope composition ($\delta^{18}\text{O}$). $\delta^{18}\text{O}$ is also dependent on g_s , but is not influenced by A . The combined $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analyses are, therefore, a suitable tool to disentangle the stomatal responses of plants and thus the effect of water

stress in a time-integrated manner (Scheidegger et al. 2000, Keitel et al. 2003).

For analyses of foliar carbon and oxygen isotope composition, as well as for foliar C and N concentrations, shoot samples were collected from all saplings on 15 May, 24 June and 13 August 2008. After the shoots were oven-dried at 65 °C for 48 h, spruce needles as well as aspen leaves and buds were detached from their twigs with a scalpel. The needle, leaf and bud material was ground and homogenized with a bead mill, and samples of 0.5–1.0 mg were transferred into tin capsules for ^{13}C analysis or into silver capsules for ^{18}O analysis (IVA Analysentechnik, Meerbusch, Germany). The samples were combusted in an elemental analyser (NA 2500; CE Instruments, Milan, Italy) for $\delta^{13}\text{C}$, total C and total N analysis, and in a high-temperature conversion/elemental analyser (TC/EA ThermoFisher GmbH, Bremen, Germany) for $\delta^{18}\text{O}$ analysis, both coupled to an isotope ratio mass spectrometer (Delta Plus or Delta Plus XP; ThermoFisher GmbH). The isotopic values are expressed in delta notation (in ‰ units) relative to the VPDB (Vienna Pee Dee Belemnite) for carbon and the VSMOW (Vienna Standard Mean Ocean Water) for oxygen.

Statistical analyses

Initial visual analysis revealed that the recovery of the photosynthetic activity in spruce was not a continuous process but that distinct phases of recovery could be identified.

Therefore, the data set was divided into four subsets, each representing a distinct phase of the winter–spring transition. Photosynthesis increased until the last week of May, when the initial recovery of photosynthetic activity was temporarily inhibited by a cold spell. During that cold spell, temperatures frequently dropped below freezing at night. As of the beginning of June, the photosynthetic activity gradually recovered from this frost period until it reached a plateau in the third week of June. Using daily averages of F_v/F_m , we arbitrarily distinguished four different phases of recovery from winter stress: I. initial recovery, II. frost, III. frost recovery and IV. full recovery (Figure 2; Table 2). The effects of the treatments on F_v/F_m , ETR_{max} and PPFD_{sat} during each phase were estimated using analysis of variance for repeated measures. The variable *block* was treated as a random variable. Within each phase and for each parameter, the unstructured, compound symmetry, first-order autoregressive and first-order antedependence covariance structures were tested for best fit based on the Akaike information criterion. The analysis was performed using the procedure MIXED in SAS v. 9.2 (SAS Institute Inc., Cary, NC, USA). Within each phase, means from different treatments were systematically compared against each other with Tukey's test, and differences were considered significant at $P \leq 0.05$. The recovery of photosynthetic activity in aspen was constant and fluorescence data were averaged over the entire measuring period.

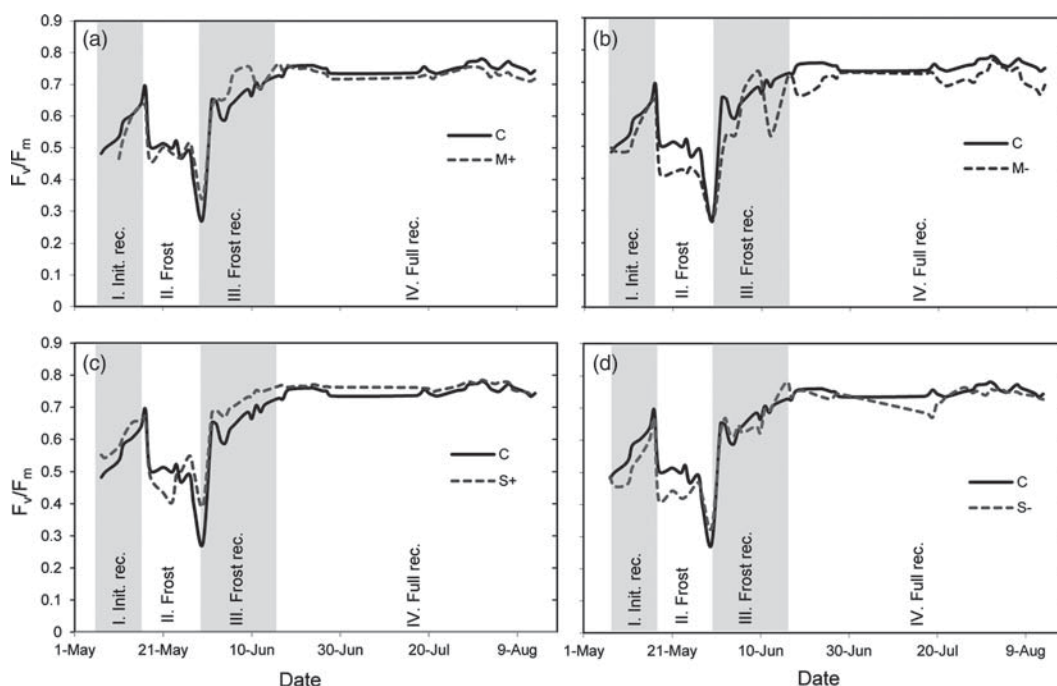


Figure 2. Effects of thermal insulation on seasonal variations in F_v/F_m in spruce from control and (a) treatment with additional moss, (b) treatment with moss removed, (c) treatment with delayed thawing and (d) treatment with accelerated thawing. Vertical sections indicate the four phases of photosynthetic development: I (initial recovery), II (frost), III (recovery after frost) and IV (full recovery).

Results

Air and soil temperature

Average daily air temperature on the study site was constantly lower than freezing point during winter, with recorded average temperatures of -13.3 , -16.0 and -12.0 °C in January, February and March, respectively. Above-freezing daily temperatures were recorded as of the beginning of April (Figure 1a).

Mean soil temperatures in the vicinity of control saplings and saplings assigned to treatment F were similar to each other and around freezing point during the entire winter season. After fertilizer application at the beginning of May, mean soil temperature in treatment F rapidly increased by ~ 1 °C and remained considerably higher than the control for the entire summer season (Figure 1b and Table 3).

Soil in treatments M+ and M– retained temperatures near the freezing point through the entire winter season (Figure 1c). Mean soil temperatures in treatment M– were slightly higher than the control as of the beginning of January 2008, and increased rapidly during snowmelt at the end of April (Figure 1c). Soil in treatment M+ stayed frozen 3 weeks longer than in treatment M–, and maintained lower temperatures until the end of the summer (Figure 1c and Table 4). From April to July, the amplitude of diurnal temperature variation was greater in treatment M– by ~ 1 °C compared with treatment M+ (data not shown).

Until snow removal at the end of February 2008, treatments S+ and S– had also maintained soil temperatures near the freezing point (Figure 1d). The bare soil in treatment S+ rapidly

cooled and temperature dropped by 5.0 °C within 1 week after the soil was uncovered. The soil in treatment S+ stayed frozen 3 weeks longer than in treatment S–, and remained colder until the end of the summer (Figure 1d and Table 3). From April to July, the amplitude of diurnal variation in soil temperature was higher in treatment S– than in treatment S+. Largest differences were observed in May, June and July, where the soil in treatment S– varied daily by 1.4 °C more than in treatment S+ (data not shown).

Bud development

Budbreak in spruce occurred on average between 14 May and 19 May, and was not significantly affected by fertilization, moss or snow treatments (data not shown). In aspen, however, budburst occurred 2 days earlier in saplings with accelerated thawing than in saplings with delayed thawing (Table 4).

Chlorophyll fluorescence

F_v/F_m

Fertilization had no effect on F_v/F_m in fertilized spruce or aspen saplings (Figure 3a). During all four phases of spruce photosynthetic recovery, saplings from treatment M– showed significantly lower F_v/F_m than control saplings (Figure 3a and Table S2 available as Supplementary Data at *Tree Physiology* Online). At full recovery, F_v/F_m in spruce was significantly lower by 0.04 in saplings from treatment M– than in control saplings. Moss treatments did not, however, affect F_v/F_m in aspen (Figure 3a and Table S3 available as Supplementary Data at *Tree Physiology* Online).

Table 3. Mean soil temperature \pm SD (°C) for each treatment during the four stages of photosynthetic recovery. Temperatures measured in the vicinity of spruce and aspen from control (C), fertilized (F), moss addition (M+), moss removal (M–), delayed thawing (S+) and accelerated thawing (S–) treatments.

Phase	Mean soil temperature \pm SD (°C)					
	C	F	M+	M–	S+	S–
I. Initial recovery	5.1 ± 1.3	5.7 ± 1.4	4.6 ± 2.3	6.3 ± 1.5	2.8 ± 1.8	5.5 ± 1.9
II. Frost	5.5 ± 0.9	6.2 ± 1.1	5.6 ± 1.3	6.4 ± 1.2	5.0 ± 0.9	5.9 ± 1.4
III. Frost recovery	9.7 ± 1.7	10.5 ± 2.2	9.8 ± 2.1	11.0 ± 1.9	9.0 ± 1.7	10.3 ± 2.0
IV. Full recovery	13.4 ± 1.5	14.0 ± 1.8	13.6 ± 1.8	14.7 ± 1.4	13.4 ± 1.7	14.0 ± 1.6

Table 4. Effects of thermal insulation of soil on the timing of budbreak phase transitions (bud stages 1–5) on a trembling aspen shoot from control (C), fertilized (F), moss addition (M+), moss removal (M–), delayed thawing (S+) and accelerated thawing (S–) treatments. Each value represents the mean of $n = 7$ measurements \pm SD. Within columns, significant differences between treatments are indicated by different letters ($P \leq 0.05$ with Tukey's test).

Treatment	Phase 1	Phase 2	Phase 3	Phase 4	Phase 5
C	June 03 \pm 3.6 ab	June 07 \pm 1.1 ab	June 09 \pm 2.8 ab	June 15 \pm 2.8 ab	June 19 \pm 2.1 b
F	June 02 \pm 4.8 b	June 05 \pm 3.0 b	June 09 \pm 2.2 b	June 14 \pm 3.3 b	June 18 \pm 3.0 b
M+	June 04 \pm 4.7 ab	June 07 \pm 2.4 ab	June 10 \pm 3.1 ab	June 16 \pm 3.6 ab	June 21 \pm 3.1 ab
M–	June 04 \pm 4.6 ab	June 07 \pm 2.2 ab	June 09 \pm 2.1 b	June 15 \pm 3.4 ab	June 20 \pm 3.9 ab
S+	June 06 \pm 1.4 a	June 08 \pm 1.3 a	June 11 \pm 3.0 a	June 17 \pm 0.7 a	June 22 \pm 1.6 a
S–	June 02 \pm 3.3 b	June 06 \pm 2.0 ab	June 08 \pm 1.6 b	June 14 \pm 2.7 b	June 19 \pm 2.5 b

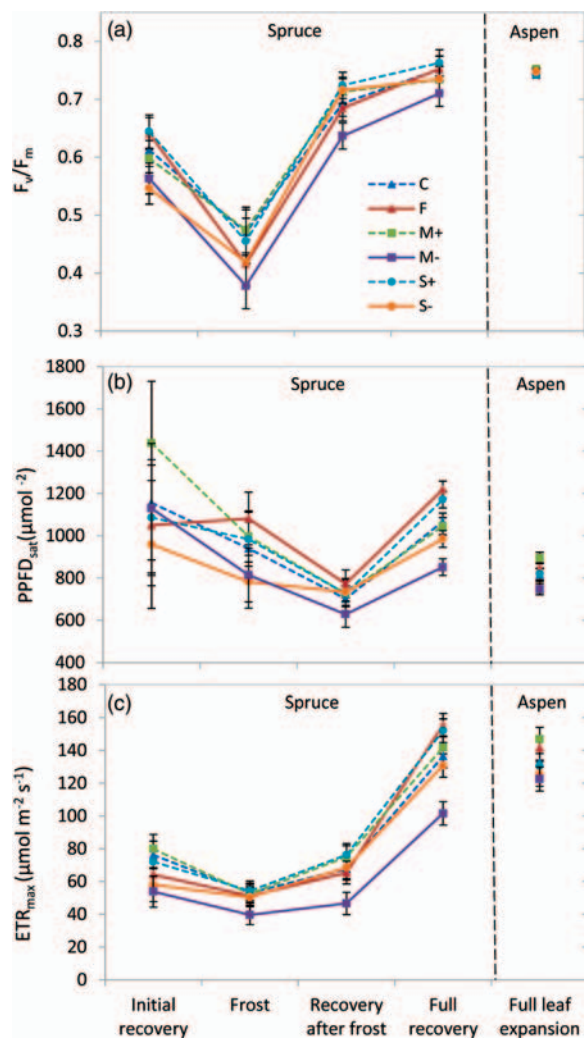


Figure 3. Effects of thermal insulation of soil on photosynthetic recovery of black spruce and trembling aspen. (a) Effective quantum yield (F_v/F_m), (b) saturating photosynthetic photon flux density ($PPFD_{sat}$; $\mu\text{mol m}^{-2}$) and (c) maximal rate of electron transport (ETR_{max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) in needles or leaves from control (C), fertilized (F), moss addition (M+), moss removal (M-), delayed thawing (S+) and accelerated thawing (S-) treatments. For spruce, data points represent the mean of $n = 14$ measurements \pm SD for initial recovery, $n = 26$ measurements \pm SD for the frost episode, $n = 38$ measurements \pm SD for recovery after frost and $n = 70$ measurements \pm SD for full recovery. For aspen, each data point represents the mean of $n = 56$ measurements \pm SD for the entire period when leaves were fully expanded.

During the initial recovery of spruce, saplings from treatment S- with accelerated thawing had significantly lower F_v/F_m than either control saplings or saplings from treatment S+ (Figure 3a and Table S2 available as Supplementary Data at *Tree Physiology* Online). The snow treatments had no effect on F_v/F_m in spruce during the frost episodes at the end of May and the successive recovery after frost (Figure 3a and Table S2 available as Supplementary Data at *Tree Physiology* Online). At full recovery, spruce from treatment S- was not different from the control but showed significantly lower

F_v/F_m than spruce from treatment S+ (Figure 3a and Table S2 available as Supplementary Data at *Tree Physiology* Online). During that period, F_v/F_m in spruce was lower by 0.028 in treatment S- than in spruce from treatment S+. In aspen, snow treatments did not affect F_v/F_m (Figure 3a and Table S3 available as Supplementary Data at *Tree Physiology* Online).

$PPFD_{sat}$

In spruce saplings, $PPFD_{sat}$ was not affected by fertilization during their initial recovery, the frost period or the recovery after frost, but was significantly higher than in control saplings at full recovery (Figure 3b and Table S2 available as Supplementary Data at *Tree Physiology* Online). $PPFD_{sat}$ in aspen saplings was not affected by fertilization (Figure 3b and Table S3 available as Supplementary Data at *Tree Physiology* Online).

In spruce, the moss treatments did not affect $PPFD_{sat}$ during the initial recovery, the frost episode and the successive recovery after frost (Figure 3b and Table S2 available as Supplementary Data at *Tree Physiology* Online). At full recovery, spruce saplings from treatment M- showed significantly lower $PPFD_{sat}$ values than either control saplings or saplings from treatment M+ (Figure 3b and Table S2 available as Supplementary Data at *Tree Physiology* Online). Treatment M+ in aspen also caused significantly higher $PPFD_{sat}$ values compared with control and treatment M- (Figure 3b and Table S3 available as Supplementary Data at *Tree Physiology* Online).

The snow treatments had no effect on $PPFD_{sat}$ in spruce during its initial recovery, the frost episode and the successive recovery after frost (Figure 3b and Table S2 available as Supplementary Data at *Tree Physiology* Online). However, at full recovery, spruce from treatment S- showed significantly lower $PPFD_{sat}$ than spruce from treatment S+ (Figure 3b and Table S2 available as Supplementary Data at *Tree Physiology* Online). In fertilized spruce saplings, $PPFD_{sat}$ was significantly higher than the control at full recovery. In aspen, no differentiation in $PPFD_{sat}$ was observed between control saplings and saplings from treatments S+ or S- (Figure 3b and Table S3 available as Supplementary Data at *Tree Physiology* Online).

ETR_{max}

Fertilization did not significantly affect ETR_{max} in spruce or aspen at any time during the season (Figure 3c and Tables S2 and S3 available as Supplementary Data at *Tree Physiology* Online). During the initial recovery of spruce, saplings from treatment M- showed significantly lower ETR_{max} than either control saplings or saplings from treatment M+ (Figure 3c and Table S2 available as Supplementary Data at *Tree Physiology* Online). The moss treatments did not affect ETR_{max} during frost (Figure 3c and Table S2 available as Supplementary Data at *Tree Physiology* Online). However,

during their recovery after frost, spruce saplings from treatment M– showed significantly lower ETR_{max} than control saplings or saplings from treatment M+ (Figure 3c and Table S2 available as Supplementary Data at *Tree Physiology* Online). At full recovery, spruce saplings from treatment M– showed significantly lower ETR_{max} than control saplings or saplings from treatment M+ (Figure 3c and Table S2 available as Supplementary Data at *Tree Physiology* Online). During that period, ETR_{max} was 25.6% lower in spruce from treatment M– than in control spruce.

The snow treatments had no effect on ETR_{max} in spruce during its initial recovery, the frost episode and the successive recovery after frost (Figure 3c and Table S2 available as Supplementary Data at *Tree Physiology* Online). At full recovery, no significant differences were observed between trees from either treatments S+ or S– and the control, but ETR_{max} was significantly lower in spruce from treatment S– than in spruce from treatment S+ (Figure 3c and Table S2 available as Supplementary Data at *Tree Physiology* Online). In trembling aspen, snow treatments had no effect on ETR_{max} (Figure 3c and Table S3 available as Supplementary Data at *Tree Physiology* Online).

Isotope analyses

Foliar $\delta^{13}C$

In both spruce and aspen, no statistically significant difference was observed, at any sampling time, between control trees and saplings from moss, snow or fertilization treatments (Figures 4a and 5a, Tables S4 and S5). It is, however, noteworthy that spruce saplings from treatment M– consistently showed more negative values compared with control and other treatments (Figure 4a and Table S4 available as Supplementary Data at *Tree Physiology* Online).

Foliar $\delta^{18}O$

Fertilization, moss or snow treatments did not affect $\delta^{18}O$ in spruce or aspen (Figures 4b and 5b, Tables S4 and S5).

Foliar $\delta^{15}N$

In spruce saplings, no differences were observed between treatments in spring. In early summer, however, saplings from treatments S+ and S– both showed significantly lower $\delta^{15}N$ values than control saplings. No differences were observed in late summer. In aspen saplings, the fertilization, moss and snow treatments had no effect on $\delta^{15}N$.

Foliar %N and C/N

In spruce, the effects of fertilization were visible in early and late summer, when significantly higher %N and lower C/N were recorded in F saplings (Figure 4d and e, Table S4 available as Supplementary Data at *Tree Physiology* Online). In aspen, significantly higher %N and lower C/N were observed in spring

and late summer (Figure 5d and e, Table S5 available as Supplementary Data at *Tree Physiology* Online).

During spring, %N was significantly lower and C/N higher in spruce saplings from treatment M– than in either control saplings or saplings from treatment M+ (Figure 4d and e, Table S4 available as Supplementary Data at *Tree Physiology* Online). In early summer, C/N in saplings from treatment M– was not significantly different from the control, but was significantly higher than in treatment M+ (Figure 4e, Table S4 available as Supplementary Data at *Tree Physiology* Online). Moss treatments did not affect %N and C/N in late summer (Figure 4d and e, Table S4 available as Supplementary Data at *Tree Physiology* Online). During spring and early summer, moss treatments had no effect on %N and C/N in aspen. In late summer, aspen saplings from treatment M+ showed significantly higher %N than control saplings and saplings from treatment M– (Figure 5d and e, Table S5 available as Supplementary Data at *Tree Physiology* Online).

In spring, spruce saplings from treatment S– showed significantly lower %N than control saplings (Figure 4d, Table S4 available as Supplementary Data at *Tree Physiology* Online). In early and late summer, snow treatments had no effect on leaf nutrition in spruce. In aspen, snow treatments did not affect foliar %N and C/N at any sampling time (Figure 5d and e, Table S5 available as Supplementary Data at *Tree Physiology* Online).

Discussion and conclusions

This study shows the importance of both moss and snow soil cover controlling the rate of spring recovery of photosynthesis in boreal forests. Removal of moss and snow delayed the spring recovery of photosynthesis in black spruce. The insulation capacity of snow and moss maintained stable soil conditions, and buffered against aboveground temperature fluctuations. The influence of soil insulation on the photosynthetic recovery of aspen was, however, minimal (Figure 3 and Table S3 available as Supplementary Data at *Tree Physiology* Online).

Effects of moss cover on the spring recovery of photosynthesis

Moss addition delayed soil thawing by more than 3 weeks in the spring, whereas moss removal caused warmer soil temperatures from snowmelt throughout the entire growing season. Delayed soil thawing did not affect the recovery of photosynthesis in spruce, but faster soil warming was associated with slower recoveries of both F_v/F_m and ETR_{max} (Figure 3a and c, Table S2 available as Supplementary Data at *Tree Physiology* Online). These results contrast with previous studies that documented delayed recovery of photosynthesis in cold soil (Bergh and Linder 1999, Strand et al. 2002).

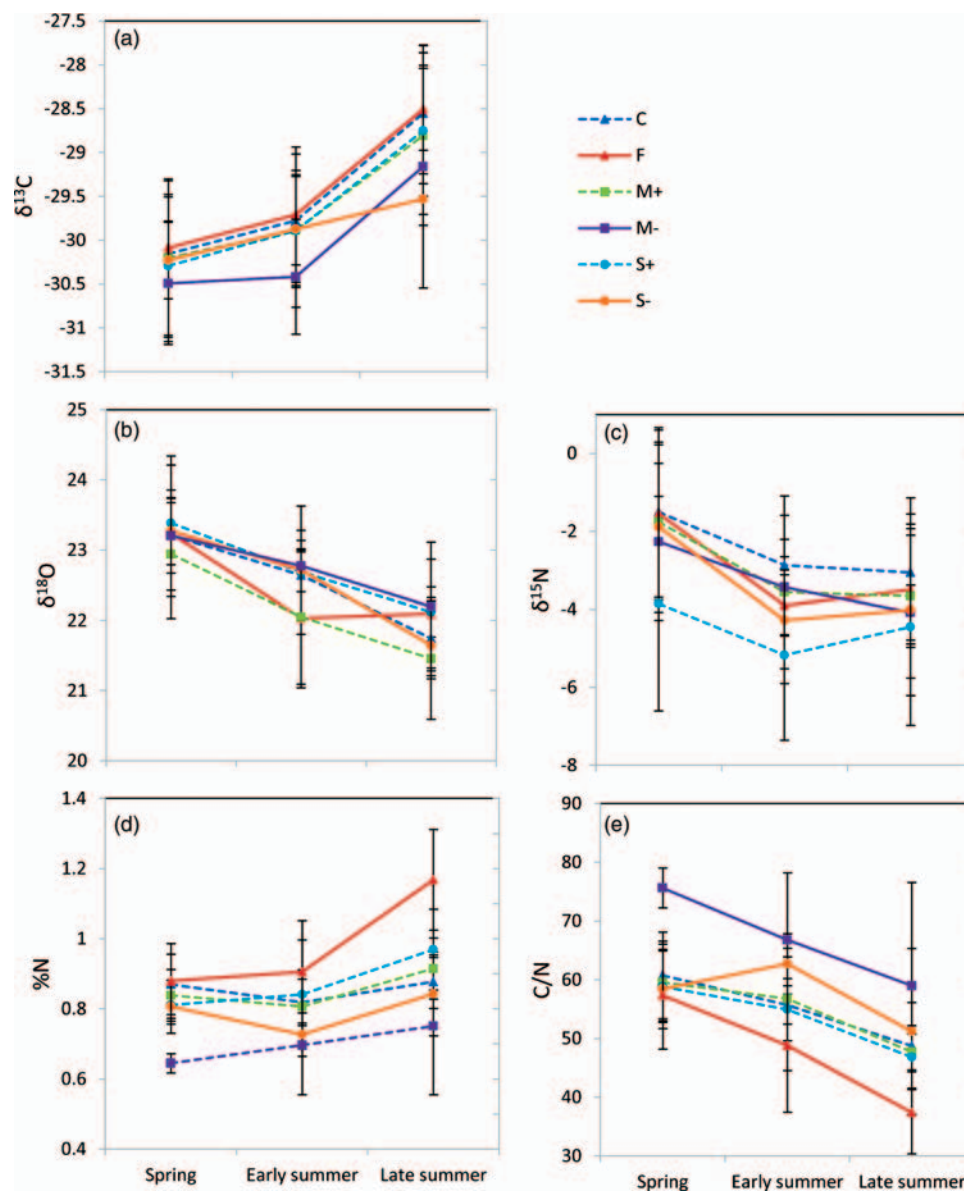


Figure 4. Effects of thermal insulation of soil on (a) $\delta^{13}\text{C}$ (‰), (b) $\delta^{18}\text{O}$ (‰), (c) $\delta^{15}\text{N}$ (‰) in total foliar organic matter, (d) abundance of N relative to the dry weight and (e) carbon to nitrogen ratios (C/N) of black spruce needles from control (C), fertilized (F), moss addition (M+), moss removal (M-), delayed thawing (S+) and accelerated thawing (S-) treatments during spring (12 May), early summer (23 June) and late summer (13 August). Each data point represents the mean of $n = 7$ measurements \pm SD.

For instance, when warming soil with underground heating cables in a Norway spruce stand, Bergh and Linder (1999) observed higher rates of light-saturated photosynthesis on heated plots. Decreased photosynthetic activity in cold soil was reported in several growth chamber experiments (Ensminger et al. 2004, 2008, Repo et al. 2005). Our results thus suggest that a factor other than soil temperature interfered to suppress photosynthetic processes in spruce following the modification of moss cover. Lower foliar N in the spring in spruce without moss cover (Figure 4d, Table S4 available as Supplementary Data at *Tree Physiology* Online) suggests reduced nutrient uptake, which could have been caused either

by reduced water uptake by roots or by reduced nutrient availability in the soil following moss removal. The values of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ did not differ between the moss removal treatment and the control during spring (Figure 4a and b, Table S4 available as Supplementary Data at *Tree Physiology* Online), indicating that no change in water use efficiency and stomatal conductance occurred, thus suggesting the absence of water stress upon moss removal. Impaired water uptake caused by moss removal is, therefore, unlikely to explain our results. Instead, low foliar N (Figure 4d and Table S4 available as Supplementary Data at *Tree Physiology* Online) likely occurred as a result of reduced nutrient uptake.

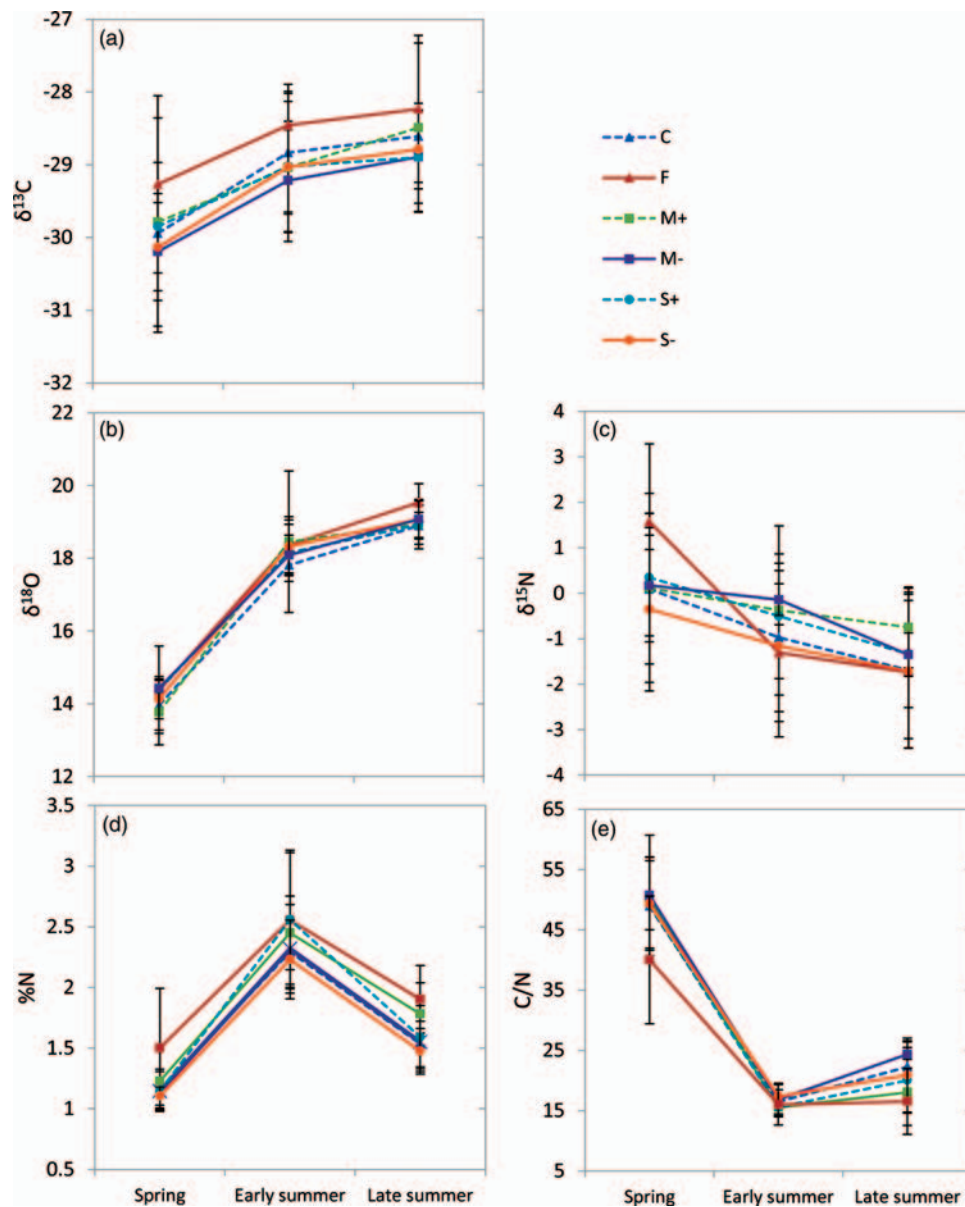


Figure 5. Effects of thermal insulation of soil on (a) $\delta^{13}\text{C}$ (‰), (b) $\delta^{18}\text{O}$ (‰), (c) $\delta^{15}\text{N}$ (‰) in total foliar organic matter, (d) abundance of N relative to the dry weight and (e) carbon to nitrogen ratios (C/N) of trembling aspen buds and leaves from control (C), fertilized (F), moss addition (M+), moss removal (M-), delayed thawing (S+) and accelerated thawing (S-) treatments during spring (12 May), early summer (23 June) and late summer (13 August). Each data point represents the mean of $n = 7$ measurements \pm SD.

Effects of snow cover on the spring recovery of photosynthesis

Under natural conditions, soil temperature under the snow-pack remained close to the freezing point during winter, whereas bare soil temperature in the snow removal treatment decreased within 1 week to temperatures ranging from -2.0 to -7.0 °C in February (Figure 1). In spring, additional snow and insulation extended the period of frozen soil by 3 weeks. Interestingly, photosynthetic recovery in spruce was less affected by the snow treatments than by the moss treatments (Figure 3 and Table S2 available as Supplementary Data at

Tree Physiology Online), while the recovery of aspen remained mostly unaffected by both moss and snow depth (Figure 3 and Table S3 available as Supplementary Data at Tree Physiology Online). However, snow cover had an effect on aspen, with earlier budbreak when soil thawing was accelerated through snow removal (Table 4). In spruce, warmer soil was associated with impaired photosynthetic recovery and reduced foliar N concentrations, especially in the spring. This suggests that the modification of snow cover affects soil N dynamics and/or the capacity of saplings for nutrient assimilation. Both could be explained by changes in soil biology

caused by modified soil temperature regimes in the spring. Snow removal in April 2008 resulted in direct exposure of the soil to the air, when night frosts were still frequent. Soil microbial populations are adversely affected by freeze–thaw cycles (Clein and Schimel 1995) but not to low temperatures in continuously frozen soil. A single freeze–thaw cycle killed 50% of soil microbial populations, and more than three cycles reduced the ability of microbial communities to decompose soil organic matter and mineralize N (Schimel and Clein 1996). This freeze–thaw cycle sensitivity might contribute to the lower foliar N concentrations observed in spruce without snow cover in the spring.

As is the case for the moss removal treatment, the absence of any differences in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values between the treatments makes restrictions in water supply and water stress unlikely. Water stress in the snow removal treatments can, therefore, be ruled out as a reason for slower photosynthetic recovery.

Accelerated thawing caused significantly lower N concentration in the leaves of spruce in spring (Figure 4d and Table S4 available as Supplementary Data at *Tree Physiology* Online), which likely explains the slower rate of recovery of F_v/F_m , ETR_{max} and PPFD_{sat} . In contrast, snow treatments had no effect on the photosynthetic activity of trembling aspen. This is probably a consequence of the deeper root system of aspen and its lower dependency on mycorrhizal associations for nutrient uptake (Bauhus and Messier 1999), which make the species less vulnerable to aboveground temperature variations. The fact that foliar N contents were not affected by the snow treatments in spring and early summer supports this hypothesis.

Snow treatments had either no or only minor effects on the phenology of bud development of the saplings in this study. In spruce, the timing of budburst was not affected, which is in accordance with previous studies with Scots pine, Norway spruce, silver fir (*Abies amabilis* (Dougl.)), noble fir (*Abies procera* Rehd) and black spruce (Van Cleve et al. 1990, Bergh and Linder 1999, Domisch et al. 2001, Repo et al. 2004). In contrast, in aspen accelerated soil thawing hastened the onset of budbreak (Table 4). Because the spring photosynthetic recovery of deciduous trees is conditional on leafing, earlier budburst in the spring might contribute to higher annual photosynthetic production (Richardson et al. 2009). However, early budburst can expose new leaves to a higher risk of frost damage in the spring (Saxe et al. 2001).

Effects of fertilizer treatment

The warming effect observed on soil following fertilization was most likely a result of metabolic heat generated by soil microbes in response to increased availability of soil nutrients (Carlyle and Norman 1941). The early photosynthetic recovery of saplings was generally not affected by fertilization,

likely due to the delay between fertilizer application and the release of readily available nutrients in the root zone. Fertilization had a stronger effect as the season progressed, and was reflected in higher photosynthetic capacities in both spruce and aspen. All moss and snow treatments generally affected photosynthetic processes to a greater extent than did fertilization, which suggests that nutrient assimilation itself was likely affected by alterations of moss and snow depths.

In conclusion, our results emphasize the importance of soil nutrient supply and assimilation during the spring recovery of photosynthesis in black spruce, which appears to be more limited by nutrient availability than by soil temperature. Moss plays a key role in soil N dynamics for its functions in soil insulation (Gornall et al. 2007), as well as in nutrient storage and transfer (Oechel and Van Cleve 1986). Snow cover during spring acts as a regulator of soil temperature, and might protect mycorrhizal fungi and decomposers against damaging freeze–thaw cycles. In the context of a possible shorter snow season, the role of moss as an insulator will become crucial, especially in the spring when reduced snow cover will be insufficient for insulating soil against extreme temperatures. Removal of soil insulation adversely affected the spring recovery in black spruce while having little or no effect on the recovery of trembling aspen. We cannot quantify losses in photosynthetic productivity in spruce or aspen from our data. Nonetheless, our data indicate that in Canada's black spruce–feather moss bioclimatic zone, a shorter snow season and concomitant reduced soil insulation can result in overall losses in the productivity of black spruce, whereas increased air temperature in the spring could partially counteract the adverse effects of reduced soil insulation.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* online.

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