



Increased soil temperature and atmospheric N deposition have no effect on the N status and growth of a mature balsam fir forest

L. D'Orangeville¹, D. Houle^{2,3}, B. Côté¹, L. Duchesne², and H. Morin⁴

¹Department of Natural Resource Sciences, McGill University, 21111 Lakeshore Road, Ste. Anne de Bellevue, Québec, H9X 3V9 Canada

²Ministère des Ressources naturelles et de la Faune, Direction de la recherche forestière, 2700 rue Einstein, Québec, G1P 3W8, Canada

³Consortium sur la climatologie régionale et l'adaptation aux changements climatiques (Ouranos), 550, rue Sherbrooke Ouest-Tour Ouest-19e étage, Montreal, Québec, H3A 1B9, Canada

⁴Département des sciences fondamentales, Université du Québec à Chicoutimi, 555 boul. de l'Université, Chicoutimi, Québec, G7H 2B1, Canada

Correspondence to: L. D'Orangeville (loic.dorangeville@mail.mcgill.ca)

Received: 14 December 2012 – Published in Biogeosciences Discuss.: 29 January 2013

Revised: 28 May 2013 – Accepted: 12 June 2013 – Published: 11 July 2013

Abstract. Nitrogen (N) is a major growth-limiting factor in boreal forest ecosystems. Increases of temperature and atmospheric N deposition are expected to affect forest growth directly and indirectly by increasing N availability due to higher rates of N mineralization. In order to understand the potential impacts of these changes, a mature balsam fir stand in Québec, Canada, was subjected during three consecutive growing seasons (2009–2011) to (i) experimentally increased soil temperature (4 °C) and earlier snowmelt (2–3 weeks) as well as (ii) increased inorganic N concentration in artificial precipitation (3 × current N concentrations using ¹⁵NH₄-¹⁵NO₃). Soil inorganic N was measured using buried ion-exchange membranes (PRSTM probes) and standard soil extractions. Dendrometers were used to monitor the variations in diameter growth and needles were analyzed annually for N to assess the nutritional response of trees. Results from the second (2010) and third (2011) year of treatment are reported.

After three years of treatment, there was no significant increase in soil nitrate (NO₃) or ammonium (NH₄) availability either in the organic or in the mineral soil as measured with standard soil extractions. Similar results were obtained with ion-exchange membranes, except for NH₄ in the forest floor, which increased by an average of 54 % over the two years. No effect of treatments were observed on needle N or diame-

ter growth, but an 8-day earlier peak in diameter growth was measured in heated plots in 2010.

We attributed the limited effects of our treatments to the acute soil competition for available N at the site. As a result, the projected modifications of the forest N cycle and concomitant increased forest growth due to an earlier snowmelt, increased soil temperature and N deposition should be considered with caution in similar cold N-poor ecosystems.

1 Introduction

The boreal forest of Canada accounts for one tenth of the world's forest (Burton et al., 2003). Recent simulations of the future climate from the Canadian Regional Climate Model (CRCM) for the eastern boreal forest of Canada suggest an average annual temperature increase of 3 °C by 2041–2060 relative to 1971–1990 (Plummer et al., 2006) and a 1-month earlier snowmelt by 2050 relative to 1971–2000 (Houle et al., 2012). Understanding the impact of climate change on boreal forest soils is of primary importance as recent studies show that the response of plants to climate in such biomes is limited by inorganic nitrogen (N) availability (Magnani et al., 2007; Melillo et al., 2011), which is in turn affected by temperature and water availability. A meta-analysis of 32 ecosystem warming studies, of which three were in boreal

forests, suggests a positive effect of increased soil temperature on soil inorganic N and plant productivity (Rustad et al., 2001). In addition, the start of snowmelt was found to coincide with the start of nutrient uptake and radial growth by conifer trees (Jarvis and Linder, 2000). Based on these relationships, many researchers expect the growth rates in boreal forests to increase in the future (Jarvis and Linder, 2000; Strömngren and Linder, 2002; Bronson et al., 2009).

Aside from soil N mineralization, atmospheric deposition of N represents an alternative and significant source of inorganic N in boreal forests. The amounts deposited in forest ecosystems through rain, fog or dry deposits strongly increased in the last century, especially in eastern North America (Driscoll et al., 2001), and an increase of 70 % is projected by 2050 (Galloway et al., 2004). The current impacts of N deposition on forests are well documented, with a generally positive effect on growth (Magnani et al., 2007) although its acidifying potential can also impair tree nutrition (Shortle and Smith, 1988).

The combination and likely interaction of increasing temperatures and N deposition on plants has garnered the attention of many researchers (Chapin et al., 1995; Mäkipää et al., 1999; Strömngren and Linder, 2002; Majdi and Öhrvik, 2004; Sager and Hutchinson, 2005; Zhao and Liu, 2009; Hutchison and Henry, 2010). Carbon sequestration models predict a positive impact on plant growth based primarily on increased organic matter decomposition and nutrient availability (Mäkipää et al., 1999), but our current understanding of the combined effect of climate change and increased N deposition on mature forest stands remains limited. In northern Sweden, Norway spruce stands subjected to soil warming and N fertilization increased stemwood production (Strömngren and Linder, 2002), but detrimental effects were measured on root longevity and elongation (Majdi and Öhrvik, 2004). In China, planted *Picea asperata* and *Pinus tabulaeformis* seedlings increased photosynthetic rates and grew faster when exposed to infrared warming or N additions (Zhao and Liu, 2009). When combined, the treatments further increased the performance of *P. tabulaeformis* but reduced that of *P. asperata*, suggesting that the interactive effects of increased soil temperature and N addition are complex and potentially species specific.

The amounts of N added in the experimental studies of soil warming and N deposition interactions cited earlier vary between 50 and 250 kg N ha⁻¹ yr⁻¹, although the average atmospheric N deposition in boreal ecosystems is estimated to be 2.34 kg N ha⁻¹ yr⁻¹ (Holland et al., 1999). Thus, these quantities do not accurately mimic the magnitude of the additional inputs of N to boreal forest ecosystems that can be expected in the future (Galloway et al., 2004). Furthermore, nutrients are generally added in one or two massive doses on the forest floor, avoiding the canopy and understory interactions that are likely to take place in forested ecosystems as well as the buffering role of natural N sinks (Hobbie et al., 2002; Gundale et al., 2011). These aboveground interactions

can be taken into account by adding N over the forest canopy, and the fate of the added N can be followed using traceable isotopic ¹⁵N.

In this paper, we report on the effect of experimentally increased soil temperature (+4 °C) by means of heat-resistance cables, increased inorganic N concentration in artificial precipitation (3 × current N concentrations using ¹⁵NH₄-¹⁵NO₃) and earlier onset of snowmelt (2–3 weeks) in a typical mature balsam fir stand growing in the boreal ecosystem of the Lake Laflamme watershed (Québec, Canada). We hypothesized that these treatments would increase soil N availability, needle N concentration and radial growth. The monitoring of tree growth and soil parameters was conducted over three growing seasons following the setup of the experiment. Significant changes in soil N availability associated with the burial of cables were detected until the end of the first year of treatment (data not shown). Therefore, the results presented in the present paper are limited to years two and three (2010 and 2011).

2 Materials and methods

2.1 Study area

The study site is located near the Lake Laflamme watershed, north of Québec city (47°17' N; 71°14' W; 800 m above sea level). The experimental plots were established in a 60 yr-old even-aged balsam fir (*Abies balsamea* (L.) Mill.) stand. The soil is an Orthic Ferro-Humic Podzol (Spodosol in the American classification system), laying on a bedrock of Precambrian charnockitic gneiss. The average thicknesses for LFH, Ae, Bhf and Bf horizons (based on the Canadian soil classification system) are 7.4, 3.6, 7.6 and 28.7 cm, respectively. The C and the N content of the forest floor are 416.1 and 16.6 g kg⁻¹, respectively, for a C:N ratio of 25. The forest floor and upper mineral horizon display a pH of 3.03 and 4.04, respectively. According to reference foliar nutrient levels for balsam fir (Michel, 2010), the study site displays no major nutrient deficit. A weather tower, located 200 m from the study area, records precipitation and air temperature. The climate is continental with cold winters and warm summers. From 1981 to 2006, mean annual air temperature and total precipitation were -0.3 °C and 1535 mm, respectively. Annual N deposition (NH₄ + NO₃) averages 5.7 kg N ha⁻¹ yr⁻¹ (Houle and Moore, 2008).

Contrasting weather conditions were observed in the two years of monitoring (2010–2011). In 2010, the summer was particularly dry with 58 % less precipitation and an average temperature 0.7 °C warmer in July–August relative to 2011. In 2011, precipitation was higher for the May to September growing season (747 mm compared to 596 mm in 2010). Relative to the average precipitation of 654 ± 47 mm received at the site from May to September 1975–2008, both monitoring

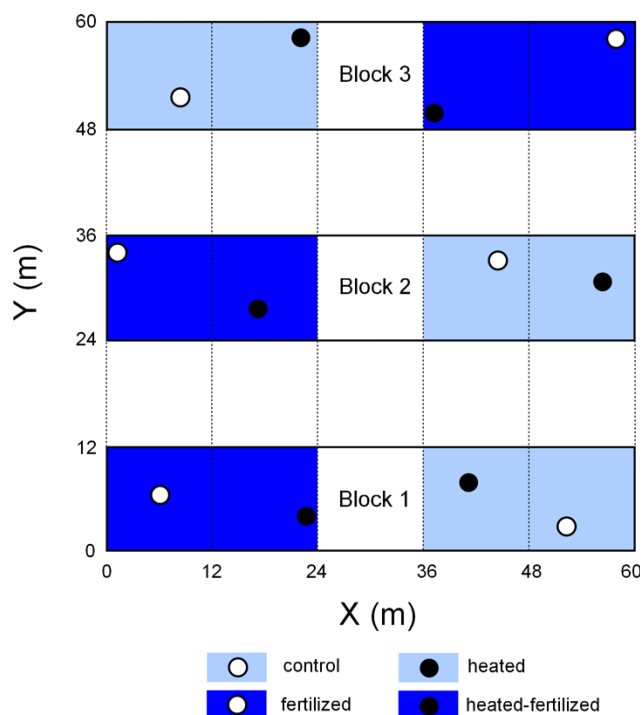


Fig. 1. Schematic description of the experimental design. Each circle corresponds to an experimental tree.

years were nonetheless representative of the normal precipitation regime during the growing season.

2.2 Experimental design

The experiment was set up in autumn 2008 and laid out according to a randomized split-plot design with two levels of soil warming (ambient and +4 °C) nested within two levels of artificial precipitation (no added NH_4NO_3 and three times the natural NH_4NO_3 concentration in ambient precipitation; details below). Because of the extensive manipulations and intensive sampling effort, we limited the experiment to twelve plots evenly distributed amongst three blocks. The blocks were 12 m × 60 m and laid out parallel to the slope with a 12 m buffer strip in between (Fig. 1). Each block was divided in two 24 m × 12 m sub-blocks separated by a 12 m × 12 m buffer zone. Each sub-block was divided into two 12 m × 12 m plots. Within each plot, a balsam fir tree was selected based on a visual estimation of good health and dominance or co-dominance in the canopy. The height and diameter of every selected tree was noted, ranging from 12.9 to 18.1 m and from 14.0 to 22.8 cm, respectively. The fertilization treatment was randomly distributed within the two sub-blocks of each block, and the soil-warming treatment was randomly distributed within the two plots of each sub-block (Fig. 1).

2.3 Soil warming

Heat-resistance cables were used to warm the soil as this method, relative to infrared warming, provides the most homogeneous warming throughout the soil strata (Aronson and McNulty, 2009). Around each experimental tree, 70 m of heating cables were buried in a spiral pattern 5–10 cm below-ground at the interface of the organic and mineral soil. To avoid potential bias between treatments due to cable burying, non-heating cables were also installed around control trees. The beginning and end of the cable were at 0.9 m and 2.5 m, respectively, from the base of the tree, with an average distance between cables of approximately 30 cm. Great care was taken to avoid root damage, and roots > 5 mm were bypassed. Soil temperature under the canopy of each tree was measured continuously with thermistors (precision: ± 0.2 °C; model 107-L from Campbell Scientific, Inc., Utah, USA) buried between cables. The warming cables were activated and deactivated when the average difference of soil temperature between heated and non-heated trees reached 3 °C and 5 °C, respectively, in order to maintain an average difference of 4 °C during the growing season on the basis of projections for the site for the 2070–2100 period (Houle et al., 2012). No warming was applied during winter as the soil, being insulated by a thick snowpack, is expected to experience only small temperature changes (Houle et al., 2012).

Soil heating was started in the spring of 2009. From the beginning of spring snow melt until the first autumn frost, the average soil temperature in treated plots was higher by 4.0 ± 0.4 °C, 4.1 ± 0.3 °C and 3.7 ± 0.9 °C in 2009, 2010 and 2011, respectively (Fig. 2). Storage of temperature data and control of warming were done with a CR1000 datalogger (Campbell Scientific, Inc., Utah, USA). At a depth of 31 cm (approximately 20 cm deep in the mineral soil), the soil temperature in heated plots was maintained approximately 2 °C above controls, as measured in July 2009 with 107-L thermistors linked to a CR1000 datalogger (Campbell Scientific, Inc., Utah, USA). In addition to the maintenance of a higher soil temperature during the growing season, the heating treatment was also designed to simulate an earlier snowmelt and an earlier snow-pack disappearance, as projected by Houle et al. (2012). In 2010, soil heating was started on March 30 because of a warm spring (Fig. 2). The snowpack was 0.85 m and the snowmelt in control plots was completed 28 days later. The treatment was stopped before the first freeze–thaw events, on 19 October. The cold spring of 2011 delayed the start of soil heating to 5 May. The snowpack was then 0.60 m and the snowmelt in control plots was completed 16 days after the beginning of treatment. Heating was terminated on 18 October.

2.4 Increasing atmospheric N deposition

The protocol used to increase atmospheric N deposition was designed to simulate how atmospheric N is deposited

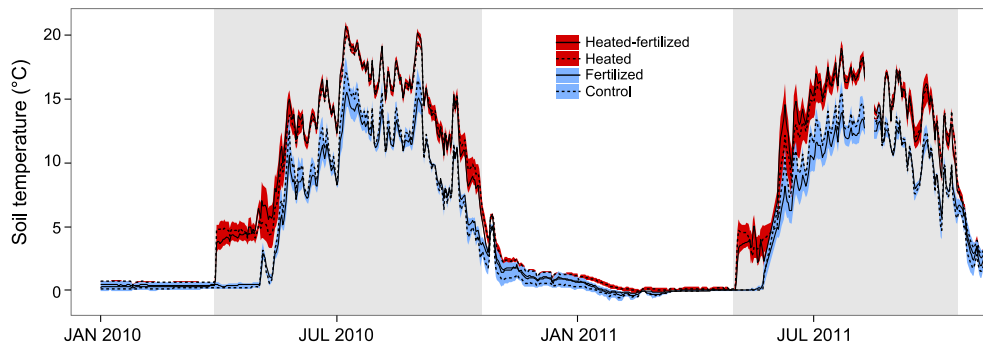


Fig. 2. Average soil temperature in control, fertilized, heated and heated-fertilized plots in 2010 and 2011. Colored ribbons are standard error. The periods of soil warming are represented by the shaded areas.

on forest ecosystems. The rain solution (control and N-enriched) was applied on the canopy using nozzles set up above each individual tree using a system of pumps and reservoirs. The composition of the artificial rain solution was based on the average ion concentration in incoming precipitation measured at the site in previous years. The concentration of the different elements added was as follows: Na (0.046 mg L^{-1}), Ca (0.089 mg L^{-1}), Mg (0.018 mg L^{-1}), K (0.026 mg L^{-1}), H (0.014 mg L^{-1}), Cl (0.07 mg L^{-1}) and SO_4 (1.01 mg L^{-1}). For the N treatment, NH_4NO_3 labelled with a 10% fraction of ^{15}N was added to reach a final rain concentration of 1.0 and 3.4 mg L^{-1} of NH_4^+ and NO_3^- , respectively, which corresponds to approximately three times the concentrations measured in the precipitation at the site. Each year and every week from mid-June to mid-September, 70 L of artificial precipitation was applied on every tree. The applications resulted in an increased N deposition of $1.544 \text{ g N tree}^{-1} \text{ yr}^{-1}$, which was dispersed over an area estimated to be $20\text{--}50 \text{ m}^2$, resulting in a rain event of $1.3\text{--}3.4 \text{ mm}$, or an additional $1.1\text{--}2.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Watering was rescheduled to the next day on rainy days.

2.5 Soil sampling and analysis

Soil N availability was monitored during the snow free period using ion-exchange membranes (PRSTM probes, Western Ag Innovations Inc., Saskatoon, Canada). Exchange membranes allow for the assessment of nutrients supply rates by continuously adsorbing free ions on charged surfaces similarly to plant roots. At first, the probes typically adsorb the labile pool of ions until depletion, followed by measurements of ion supply rates through mineralization, leaching or dissolution. The probe data will be referred to as “available” N hereafter. Avoiding direct contact with heating cables, six probes were evenly distributed around each tree at a distance of 1.5 m from the stem and inserted vertically, three in the organic soil layer (approximately 5–10 cm deep) and three in the mineral layer (approximately 15–20 cm deep). The probes were buried on 12 and 30 May in 2010 and 2011, respectively, following snowmelt, and replaced every six weeks. In au-

tumn, the last set of probes was removed on 30 September and 7 October in 2010 and 2011, respectively.

At the end of each burial period, the probes were sent to Western Ag Innovations for extraction after rinsing off the remaining soil from the membranes with deionized water. The probes were pooled per soil horizon for each tree. Membranes were eluted with 17.5 mL of 0.5 M HCl for 1 h. Concentrations of NH_4 and NO_3 in the extract were determined colorimetrically using a Technicon Autoanalyzer (Technicon AA2, Seal Analytical Inc., Mequon, USA). The values were reported as $\mu\text{g } 10 \text{ cm}^{-2}$ of resin surface and cumulated for each year.

Soils were sampled at the end of the growing season (September) for extractable N. Three evenly spaced cores around trees at a distance of 2 m from the stem were taken in the organic (FH horizon) and mineral horizons (first 20 cm of the B horizon) and pooled by soil horizon to form one bulk sample per horizon per plot. Being thin and discontinuous, the eluvial horizon (Ae) was not sampled. Samples were air-dried for a week (Carter and Gregorich, 2007) and sieved to 2 mm. Soils were extracted with KCl for 12 h. Levels of NO_3 were measured by ion chromatography (Dionex 2120i, Thermo Fisher Scientific Inc., Sunnyvale, USA) and NH_4 colorimetrically with a Technicon Autoanalyzer (Technicon AA2, Seal Analytical Inc., Mequon, USA), and will be referred to as “extractable” hereafter.

Levels of soil nitrates were close to the detection limit of the analytical devices used for the analyses (limit of $< 1 \text{ mg kg}^{-1}$ for extractable NO_3 ; 31% of samples and of $< 2 \mu\text{g } 10 \text{ cm}^{-2}$ for available NO_3 ; 51% of samples). Therefore, caution should be used when interpreting these results.

Volumetric soil water content (SWC) was measured weekly using a FieldScout TDR-300 device with 20 cm rods and standard calibration (accuracy: $\pm 3\%$ vol; Spectrum Technologies Inc., Plainfield, USA). For each plot, nine measurements were taken at a distance of 1.5 m from each tree and averaged.

2.6 Foliar sampling and analysis

The current-year foliage of experimental and reference trees was sampled from the upper third of the canopy on three branches. Sampling was done in September of both years at the end of each growing season. In 2010, a subsample of thirty needles for each tree was weighed to account for any change in the leaf-specific mass of each tree. Needles were oven-dried at 65 °C and then ground to 250 µm-sized fragments. The total N content was determined with a Kjeldahl autoanalyzer (Kjeltec Auto model 1030 Analyser, Tecator, UK) after digestion with H₂SO₄. The degree of isotopic N enrichment of the samples (¹⁵N) was measured on subsamples (5.8–6.1 mg) using isotope ratio mass spectrometry with a Isoprime100 IRMS continuous-flow spectrometer (Isoprime Ltd, Cheadle, UK) at GEOTOP Research Centre (Université du Québec à Montréal). The analytical error was ±0.2 ‰.

2.7 Calculation of N pools

Two labile N pools (foliage N and soil extractable N) were determined to assess the relative contribution of fertilization to N cycling in the plots. Foliage N of each tree was determined by multiplying the average foliar N concentrations measured in 2010 and 2011 with the total foliage mass estimated with the allometric equation of Lambert et al. (2005) for balsam fir using tree height and stem diameter as independent variables. The inorganic N pool of the forest floor (LFH horizon and first 20 cm of B horizon, excluding the Ae layer) was obtained by multiplying (i) the average level of extractable N (NH₄ + NO₃) of the organic and mineral horizons of plots in 2010 and 2011 by (ii) the horizon thickness, recorded using a soil corer at twelve sampling points next to the experimental site, and by (iii) the average bulk densities (mass of oven-dry soil divided by its volume) measured on the same 12 soil samples cited earlier. The Ae horizon was not included in the calculation as it was not analyzed for extractable N.

2.8 Calculation of ¹⁵N abundance and recovery

The ¹⁵N abundance was converted into the common per-mill deviation from atmospheric standard of 0.3663 atom % ¹⁵N and noted in δ¹⁵N according to Eq. (1)

$$\delta^{15}\text{N} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \cdot 1000, \quad (1)$$

where R is the ratio of ¹⁵N/¹⁴N. The ¹⁵N tracer recovery in the foliage was calculated using Eq. (2):

$$^{15}\text{N}_{\text{foliage}} = m_{\text{foliage}} \cdot \left(\frac{\text{at.}\%^{15}\text{N}_{\text{foliage}} - \text{at.}\%^{15}\text{N}_{\text{ref}}}{\text{at.}\%^{15}\text{N}_{\text{tracer}} - \text{at.}\%^{15}\text{N}_{\text{ref}}} \right), \quad (2)$$

where m_{foliage} is the estimated N pool in the foliage, at. % ¹⁵N_{tracer} is the at. % ¹⁵N in the fertilizer solution,

at. % ¹⁵N_{ref} is the at. % ¹⁵N in the foliage of non-fertilized trees and at. % ¹⁵N_{foliage} is the at. % ¹⁵N in the foliage of fertilized trees.

2.9 Seasonal course of basal area increment

Dendrometers (Ecomatik, Munich, Germany) were installed on every tree 2 m above ground to monitor radial variations with a precision of < 5 µm. Data were recorded every 15 min on the CR1000 datalogger and averaged to obtain hourly values. To account for the difference in stem size between trees, the recorded radial variations were converted to basal area increments (BAI) using Eq. (3):

$$\text{BAI}_t = \pi \left[(X + R_t)^2 - (X + R_i)^2 \right], \quad (3)$$

where R_t is the tree radius increment at time t of measurement, R_i is the initial radius read by the dendrometers upon their installation and X is the radius of the tree measured upon the installation of the dendrometers.

The Gompertz function provides a good description of seasonal tree growth patterns (Rossi et al., 2003). The seasonal BAI was modeled using data spanning from 1 May, a time when tree rehydration is expected to be completed (Turcotte et al., 2009), to the first frosts, characterized by large negative BAI values (Fig. 3a). Even during cambium dormancy, the changes in tree water potential produce significant day-to-day stem diameter variations confusing the identification of the start of the seasonal growth, i.e., the moment when the BAI values must be set to 0 (Duchesne et al., 2012). To avoid arbitrary choices, a formulation of the Gompertz model that includes a fourth parameter indicative of the initial stem size at the beginning of the growing season (Duchesne et al., 2012) was fitted to hourly BAI data for each tree:

$$Y = Y_0 + A \cdot \exp \left[-\exp(\beta - \kappa \cdot t) \right], \quad (4)$$

where Y is the maximal daily measured BAI, Y_0 is the lower asymptote, A is the upper asymptote, β is the abscissa of inflection point, κ is the rate of change of curve shape and t is the time in day of year (DOY). Therefore, $(A - Y_0)$ corresponds to the total annual BAI, while $(Y_t - Y_{t-1})$ corresponds to the daily BAI. All regressions had $R^2 > 0.92$ and normal distribution of the residuals (Motulsky and Ransnas, 1987). The “nlm” procedure from the R software was used with the ordinary least-squares method for parameter estimation (R Development Core Team, 2010). Gompertz growth curves were fitted for each tree (12) and each year (2), for a total of 24 models (Fig. 3b). The beginning and end of radial growth were determined as the day of year when modeled daily basal increment values went above and below 0.1 mm² day⁻¹, respectively.

2.10 Pre-treatment growth

Using a Trephor tool (Rossi et al., 2006), a wood microcore 15 mm in length and 1.9 mm in diameter was collected on

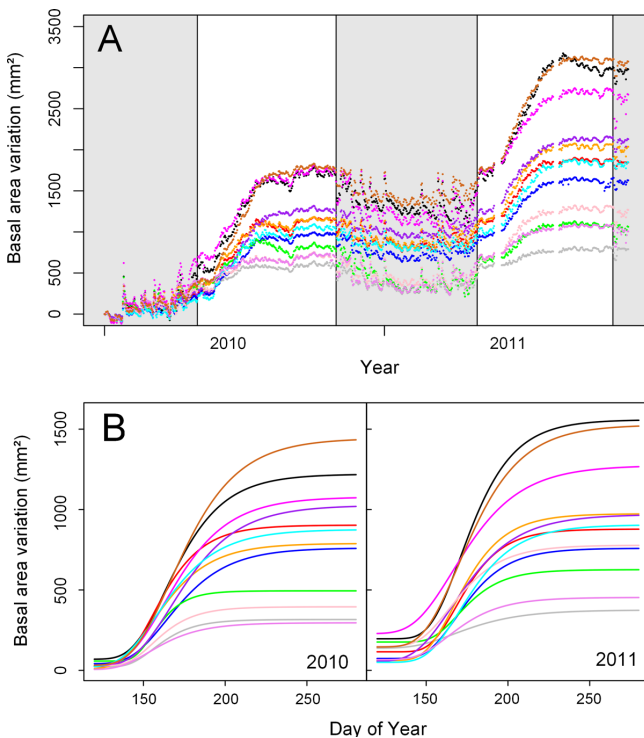


Fig. 3. (A) Average daily basal area variation of the 12 monitored balsam fir trees in 2010 and 2011 at the Lake Laflamme watershed (Québec, Canada). The non-shaded areas identify the periods used for growth modeling each year, and each monitored tree is represented by a different color. (B) Modeled seasonal basal area increment of each monitored balsam fir tree (12) in 2010 and 2011 using the Gompertz equation.

each tree next to the dendrometer to check for potential pre-treatment differences in BAI (Linares et al., 2009). The microcores were stored in a 10 % ethanol solution and embedded in paraffin (Rossi et al., 2006). Transverse sections were cut using a rotary microtome (6–10 μm in thickness), stained with safranin (1 : 100 with water) and fixed on slides. A camera linked to an optical microscope recorded numerical images at 400 \times magnification. The ring widths of 2007 and 2008 were measured along three radial rows using Wincell software (Regents Instruments Inc., Québec, Canada) and transformed into BAI with

$$\text{BAI}_{2008} = \pi \left[(X + R_i)^2 - (X + R_i - R_{2008})^2 \right] \quad (5)$$

and

$$\text{BAI}_{2007} = \pi \left[(X + R_i - R_{2008})^2 - (X + R_i - R_{2008} - R_{2007})^2 \right], \quad (6)$$

where R_i is the initial radius read by the dendrometers upon their installation, while R_{2008} and R_{2007} are the mean ring widths for the years 2008 and 2007.

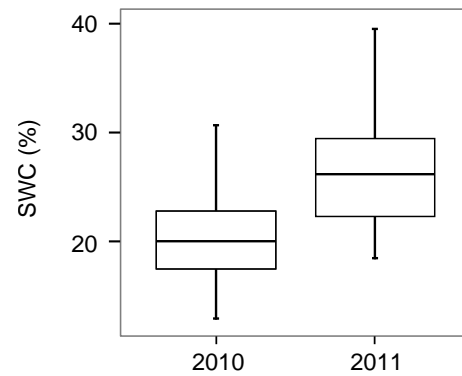


Fig. 4. Box plot of soil water content in 2010 and 2011 ($N = 12$). Soil warming was not significant ($P = 0.14$) and SWC was different between years ($P < 0.01$).

2.11 Statistical methods

A linear mixed-effects analysis of variance (anova) with repeated measures was used to analyze the effects of the treatments, assuming a compound symmetry variance-covariance structure. The effect of soil warming on soil water content (SWC) was tested with temperature treatment and year as fixed factors and plot, sub-block and block as random factors. Soil, foliar and growth parameters were analyzed with temperature treatment, fertilization and year as fixed factors and plot, sub-block and block as random factors. Because SWC and pretreatment BAI (average of BAI_{2007} and BAI_{2008}) tended to differ between treatments (Fig. 4 and Table 1), they were included as covariates in the anovas for soil and growth analysis, respectively, when significantly correlated with the response variable at $P < 0.05$. The relations between the covariates and the dependent variables were linear. KCl-extracted NO_3 values in the mineral horizon were too low for detection in 2010. Therefore, only the 2011 data were analyzed and the factor “year” was removed. Due to the large variability in the growth-related response variables, we assessed the statistical power of the experimental design to estimate the minimum detectable difference between treatments. This minimum detectable difference was calculated for the commonly used type I ($\alpha = 0.05$ and $\alpha = 0.10$) and type II ($\beta = 0.20$) error probabilities (Peterman, 1990; Stroup, 1999). Mixed-effects anovas were computed using the “lme” procedure in R (R Development Core Team, 2010), and statistical power was assessed using SAS statistical package (SAS version 9.2, SAS Institute, Cary, NC, USA).

3 Results

3.1 Soil water content

The average soil water content during the growing season was significantly higher in 2011 than in 2010, ranging from

Table 1. Mean basal area increment (BAI) parameters (and standard error) for balsam fir trees growing in control, heated, fertilized and heated-fertilized plots, and results from power analysis and mixed-model anovas applied to BAI parameters. Pre-BAI was included as covariable when significant. Significant P values are in bold ($P < 0.05$). Maximum daily growth corresponds to the highest ($Y_t - Y_{t-1}$) value.

		Pre-BAI (mm ²)	onset (DOY)	ending (DOY)	Annual BAI (mm ²)	Slope of growth curve	Maximum daily growth (mm ² day ⁻¹)	Timing of maximum daily growth (DOY)
2010	Control	818 (196)	119 (1)	297 (6)	894 (109)	0.046 (0.001)	15.4 (1.5)	165 (1)
	Fertilized (f)	1006 (102)	124 (5)	275 (28)	947 (297)	0.062 (0.015)	19.5 (2.4)	162 (3)
	Heated (h)	615 (121)	121 (4)	261 (15)	674 (169)	0.058 (0.006)	14.3 (2.8)	156 (1)
	h – f	473 (237)	121 (4)	250 (13)	444 (165)	0.059 (0.006)	9.4 (2.6)	155 (1)
2011	Control	818 (196)	124 (5)	294 (11)	785 (74)	0.046 (0.004)	15.3 (0.6)	167 (1)
	Fertilized (f)	1006 (102)	132 (4)	286 (16)	936 (325)	0.051 (0.005)	20.6 (5.0)	170 (1)
	Heated (h)	615 (121)	131 (3)	275 (7)	655 (98)	0.055 (0.003)	16.0 (1.5)	168 (2)
	h – f	473 (237)	128 (2)	270 (5)	430 (223)	0.050 (0.005)	10.3 (4.7)	165 (1)
ANOVA								
	Pre-BAI	–	0.68	0.03	< 0.01	0.22	< 0.01	< 0.01
	Heating (H)	< 0.01	0.81	0.45	0.85	0.39	0.89	0.03
	Fertilization (N)	0.82	0.75	0.32	0.60	0.41	0.75	0.47
	Year (Y)	–	< 0.01	0.08	0.35	0.20	0.45	< 0.01
	H × N	0.12	0.30	0.42	0.84	0.24	0.16	0.56
	H × Y	–	0.87	0.23	0.59	0.91	0.79	0.01
	N × Y	–	0.38	0.37	0.52	0.34	0.83	0.13
	H × N × Y	–	1.0	0.72	0.57	0.77	0.73	0.07
Power analysis (for $\beta = 0.2$)								
	Standard deviation (σ)	–	6	26	353	0.012	5.7	6
	Detectable delta (δ) at $\alpha = 0.05$	–	9	50	700	0.020	8.0	5
	Detectable delta (δ) at $\alpha = 0.10$	–	7	40	500	0.018	6.0	4

18.4 to 42.1 % in 2011 compared to 12.8 to 34.9 % in 2010 ($P < 0.01$; Fig. 4). There was no significant difference between heated and non-heated plots ($P = 0.14$).

3.2 Soil available and extractable N

Significant between-year differences ($P \leq 0.05$) were detected for available N (NH_4 and NO_3) in both horizons and for extractable NH_4 in the mineral horizon (Fig. 5). Extractable NH_4 decreased by 47 % in the mineral horizon in 2011 relative to 2010, whereas extractable NO_3 tended to show a reverse trend (Fig. 5). The forest floor was higher in extractable NH_4 than the mineral horizon in both years (60.6 and 8.3 mg kg⁻¹, respectively). Extractable NO_3 showed a different pattern with concentrations below the detection limit in the mineral horizon in 2010 but higher concentrations in the mineral horizon than in the organic horizon in 2011 (1.7 and 3.8 mg kg⁻¹ in 2011, respectively; Fig. 5).

Available NH_4 levels were higher in the organic than the mineral horizon in 2010 (22.4 and 14.6 $\mu\text{g } 10 \text{ cm}^{-2}$, respectively), but were similar in 2011 (Fig. 5). Available NH_4 decreased by 70 % and 54 % in the organic and mineral horizons, respectively, in 2011 relative to 2010 ($P < 0.05$; Fig. 5). No differences between horizons were observed for available NO_3 levels in both years. Levels of available NO_3 increased in 2011 relative to 2010 in both soil horizons ($P < 0.01$; Fig. 5).

In 2010 and 2011, the soil-warming treatment increased available NH_4 in the organic soil horizon by 53.8 % on average ($P = 0.02$; Fig. 5). No such effect was observed for available NO_3 , and extractable NH_4 and NO_3 in either soil horizon. Except for a likely increase in forest floor extractable NH_4 ($P = 0.09$; Fig. 5), the N deposition treatment did not have a significant effect on soil inorganic N. The annual input of N from the fertilization treatment represented 2.1 % of the inorganic N pool contained in the organic soil

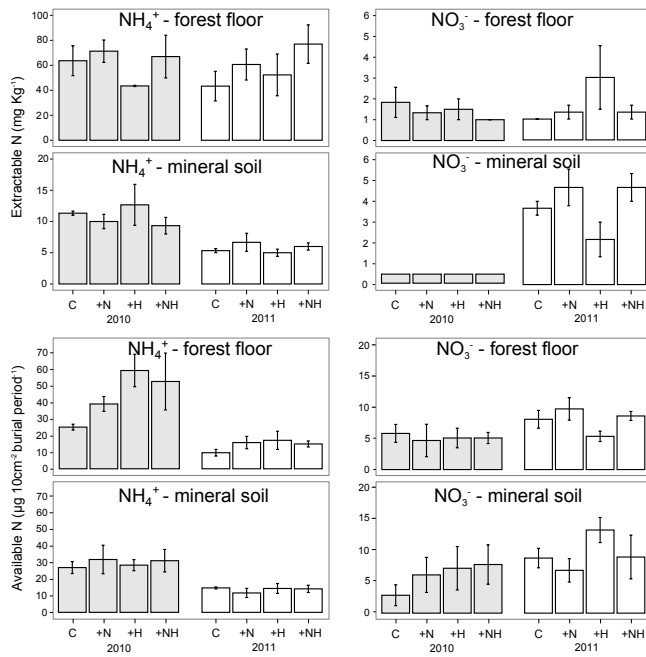


Fig. 5. Extractable and available NH_4 and NO_3 in the forest floor and mineral horizon in control (C), fertilized (+N), heated (+H) and heated-fertilized (+NH) plots in 2010 and 2011 ($N = 12$). Extractable N corresponds to inorganic N species measured on soil samples taken in September of each year and extracted with KCl 1M. Available N corresponds to the cumulative amount of inorganic N species measured with ion-exchange membranes (PRS probes) from 12 May to 30 September in 2010 and from 30 May to 7 October in 2011. Values of extractable NO_3 in the mineral horizon in 2010 were all below the detection limit of the analytic device ($< 1 \text{ mg kg}^{-1}$). Error bars are standard error. Significant between-year differences ($P \leq 0.05$) were detected for available N (NH_4 and NO_3) in both horizons and for extractable NH_4 in the mineral horizon. The only significant treatment effect was soil warming for available NH_4 in the organic horizon ($P = 0.02$) with no effect of years ($P = 0.11$).

horizon and the first 20 cm of mineral soil ($3.7 \text{ g extractable N m}^{-2}$).

3.3 Average leaf weight and foliar N

Needle N concentrations and needle mass did not respond significantly to any treatment nor did they vary significantly over time. Needle N concentration averaged $12.3 \pm 0.4 \text{ g N kg}^{-1}$ in 2010 and $12.1 \pm 0.4 \text{ g N kg}^{-1}$ in 2011 (Fig. 6), whereas needle mass averaged $3.6 \text{ mg needle}^{-1}$ over the two years of sampling (data not shown).

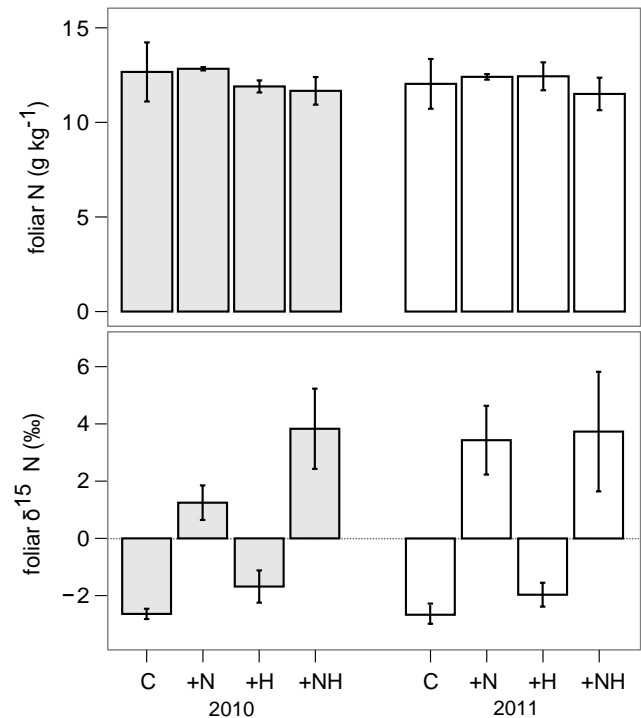


Fig. 6. Total N and ^{15}N concentration in the needles of balsam firs in 2010 and 2011 ($N = 12$). C: control trees (no heating, no fertilization); +N: fertilized trees; +H: heated trees; +NH: fertilized and heated trees. Error bars are standard error. Foliar N was not significantly affected by the treatments ($P \geq 0.47$). Levels of ^{15}N were significantly affected by fertilization ($P < 0.01$) but not by soil warming ($P = 0.13$). Foliar N and ^{15}N were not different between years ($P \geq 0.45$).

Needle $\delta^{15}\text{N}$ concentrations measured in fertilized trees averaged $4.29 \pm 0.71 \text{ ‰}$ and were significantly higher than those of control trees ($-2.04 \pm 0.17 \text{ ‰}$, $P < 0.01$; Fig. 6). With a calculated foliage N pool of 101 g tree^{-1} , an average of 1.1 % of the added N ($1.54 \text{ g tree}^{-1} \text{ yr}^{-1}$) was recovered in the foliage of fertilized trees.

3.4 Seasonal course of basal area increment (BAI)

The BAI was highly variable between trees, ranging from 191 to $1329 \text{ mm}^2 \text{ yr}^{-1}$ (Fig. 3). No effect of treatments on BAI ($A - Y_0$) was detected in either year, with BAI averaging $740 \pm 103 \text{ mm}^2$ and $700 \pm 104 \text{ mm}^2$ in 2010 and 2011, respectively (Table 1). BAI started to increase on 1 May 2010 and 9 May 2011 and reached a maximum on 28 September 2010 and 8 October 2011. The rate of growth increased steadily until mid-June (8 June in 2010 and 17 June in 2011) before decreasing until the end of the growing season (Table 1 and Fig. 3). The onset of growth and maximum growth rate were reached on average one week earlier in 2010 compared to 2011 ($P < 0.01$, Table 1). Heated trees reached their maximal growth rate significantly earlier than control trees

($P < 0.01$), although the significant warming-year interaction revealed that this effect was stronger in 2010 ($P < 0.01$), when the mean inflection point was reached on 4 June, eight days earlier than for non-heated trees.

The power analysis for growth variables revealed that for type I error probabilities of 0.05 and 0.1, respectively, the smallest detectable differences between treatments were 9 and 7 days for growth onset, 50 and 40 days for growth ending, 700 and 500 mm² for total growth, 0.02 and 0.018 for the slope of growth curve, 8 and 6 mm² day⁻¹ for maximum daily growth and 5 and 4 days for the timing of maximum daily growth (Table 1). Relative to the natural variance observed in the population of balsam fir trees, the power of our experimental design to detect true treatment effects was highest for the timing of maximum daily growth and lowest for annual BAI and ending of growth.

4 Discussion

4.1 Treatment effect on soil and foliar N

The hypothesis of increased soil N availability due to the treatments was rejected for N fertilization and verified in part for soil heating. Increased soil temperature did not raise NH₄ or NO₃ availability in the forest floor or mineral soil as measured by the two methods except for an increase (54 %) in NH₄ availability as measured with the ion-exchange membranes in the forest floor. The significant differences in available N observed in 2010 and 2011 as well as the three-fold increase in available NH₄ measured in 2010 in heated plots compared to the control plots suggest a strong influence of the prevailing climatic conditions of the 2010 growing season on the availability of soil N. Indeed, the warmer temperatures observed in 2010 prior to the August drought could have promoted N mineralization rates (Van Cleve et al., 1990; Rustad et al., 2001; Allison and Treseder, 2008; Brzostek et al., 2012) and increased the NH₄ levels that year.

Given the influence of temperature on nitrification rates (Sabey et al., 1956; Malhi and McGill, 1982), an increase in NO₃ in the heated plots was expected. The lack of detectable effect of soil warming on NO₃ in the forest floor, despite an increase in NH₄, could be explained by its low pH (3.03), a well-known nitrification inhibitor (Ste-Marie and Paré, 1999). In addition, the forest floor of balsam fir stands typically displays a high polyphenolic content, which can also inhibit nitrification (Olson and Reiners, 1983). However, conditions favorable to nitrification are encountered in the mineral soil (i.e., higher pH, lower polyphenolic content), as shown by a strong increase in NO₃ measured during a spruce budworm outbreak at the site in 1981–1984 (Houle et al., 2009). The absence of increased NO₃ in the mineral horizon of heated plots thus suggests that the increased NH₄ measured in the forest floor, although found on the buried

ion-exchange membranes, did not reach the underlying mineral soils where it could have been transformed to NO₃.

In contrast with available NH₄, extractable NH₄ in the forest floor did not respond to the soil-warming treatment. Adsorbing membranes interact with the inorganic ions present in the soil solution and are generally more sensitive to changes in the environment (Johnson et al., 2005), while soil extractions measure a larger pool of elements, which includes inorganic N bound to exchange sites. The fact that the soil-warming treatment increased the pool of NH₄ in the soil solution but not the larger pool of extractable NH₄ suggests that the effect of that treatment was relatively modest. Since the air drying of the samples prior to extraction may have resulted in some loss of labile N, data from ion-exchange membranes should be considered a more robust assessment of the potential changes in nutrient availability.

The limited effect of the soil heating on inorganic N availability could be due to the site condition. The levels of available N at the site were compared with published data from boreal forest soils of Canada sampled with identical ion-exchange membranes (PRS probes), including studies spanning over 1 to 11 growing seasons, monitoring unmanaged plots in a black spruce forest of Alberta (Jerabkova and Prescott, 2007), a wet spruce–fir forest of British Columbia (Hope, 2009), and another wet mixed-conifer forest in British Columbia (Bengtson et al., 2007). On a daily basis, the organic soil horizon sampled in the current study displayed 46 % less available NH₄ (range 15–67 %) and 62 % less NO₃ (range 30–77 %) than the other three sites. A previous study conducted in the same watershed using ¹⁵N isotopic pool dilutions showed that almost all of the NH₄ and NO₃ made available in the forest floor were immobilized in less than a day (Ste-Marie and Houle, 2006). In another experiment at the site, the addition of 3- and 10-fold the current atmospheric N deposition (17 and 57 kg N ha⁻¹ yr⁻¹, respectively) for three years did not have prolonged effects on inorganic N concentrations in the soil solution except for transitory increases that lasted less than a week, with the result that 95 % of the added N was immobilized above the rooting zone (Houle and Moore, 2008). All together, these results suggest that the low levels of extractable inorganic N at our site, 0.8 % of the total N contained in the forest floor, and the relatively high C : N ratio (25) maintain strong N sinks in the soil, including microbes and humus (Berg and Matzner, 1997; Nadelhoffer et al., 1999; Friedrich et al., 2011), which could be responsible for the relatively weak response of inorganic N after three years of soil warming.

There were no effects of the treatments on leaf N concentration although fertilized trees had significantly higher leaf ¹⁵N levels, showing that a fraction of the inorganic ¹⁵N in the artificial precipitation was immobilized in the foliage. In the long term, increased N deposition has been shown to have positive impacts on balsam fir N nutrition (McNeil et al., 2007) and carbon sequestration (Quinn Thomas et al., 2010). In the short term, however, the calculated 1.1 % recovery of

added N in the foliage of trees in the present study, while in good agreement with previous results (Bowden et al., 1989; Boyce et al., 1996; Bryan Dail et al., 2009), suggests a limited assimilation of deposited N through the leaf epidermis.

4.2 Treatment effect on growth

The phenology of radial growth was hastened by soil warming in 2010, when an earlier peak of growth was observed for heated trees. To our knowledge, this is the first study to detect an effect of soil warming on the phenology of basal area increment in conifers. The course of xylem production in black spruce trees growing in Québec, Canada, and subjected to an identical experimental design was not affected by three years of soil warming (Lupi et al., 2012). In a boreal Norway spruce stand of northern Sweden, six years of soil warming did not affect the phenology of basal area increment, although the maximum growth rate and seasonal production of wood were repeatedly higher for heated trees (Strömgren and Linder, 2002).

With a limited response in soil N availability and no changes in foliar N, there is little evidence to support that differences in N availability could account for the change in BAI phenology. An alternative explanation for this change in phenology could be an earlier uptake of water and nutrients induced by the early snowmelt and increase in soil temperature associated with the soil warming. The effect would have been more obvious in 2010 as the heated trees benefited from a longer additional growing season compared to 2011 (+12 days). Indeed, soil temperatures below 6 °C have been shown to significantly inhibit root activity in conifers (Alvarez-Uria and Körner, 2007). It is thus probable that trees growing in heated soils were able to start water and nutrient uptake earlier, as well as photosynthesis. Soil thaw is a prerequisite for the resumption of photosynthesis in balsam fir trees (Goodine et al., 2008), and higher rates of light-saturated photosynthesis were noted in boreal Norway spruce stands subject to soil warming (Bergh and Linder, 1999).

Although strong positive relationships have previously been established between rates of carbon sequestration in plants and increased levels of soil available N through increased natural atmospheric deposition (Magnani et al., 2007; Quinn Thomas et al., 2010), as well microbial mineralization (Rustad et al., 2001), fertilization (Tamm, 1991) or soil warming (Rustad et al., 2001), the beneficial effects of a higher rate of growth early in the season, in terms of carbon allocation and wood production, did not translate into higher annual BAI. This absence of effects is logical with the lack of changes in foliar N between treatments. However, it should be interpreted cautiously. Due to the important natural BAI variability between trees, treatment effects on annual BAI were less susceptible to be detected than for other growth variables (Table 1). Cumulating additional years of data will increase our confidence in the absence of effects. Nonetheless, it was previously observed that higher growth

rates at a certain point in a growing season do not necessarily enhance the annual stem growth (Deslauriers et al., 2003; Schmitt et al., 2004; Gruber et al., 2009). Four years of experimental warming of an entire pine–birch forest in Norway also resulted in similar radial growth between treatments (Rasmussen et al., 2002).

Most reported cases of null or negative effects of experimental soil warming on forest ecosystem productivity are related to water stress (Rustad et al., 2001). In the current study, soil water content and supply was not decreased by soil warming, which suggests that trees in the heated plots were not more water stressed than control trees. This is also supported by the lack of relationship measured between soil temperature and soil water content ($P = 0.69$; data not shown). Alternatively, there is little evidence that the soil disturbance associated with the burial of heating and control cables could have confounded our results. The impact of soil trenching on roots was minimized by running the cable below or above major roots. Disturbance was therefore restricted to fine roots, which have a relatively rapid turnover of ca. one year (Yuan and Chen, 2010). Given that cables were buried in fall 2008 and the data presented here span from April 2010 to October 2011, fine roots are highly likely to have recovered by the presented time period. The comparison of radial growth in treated trees with non-disturbed trees monitored during the entire experiment suggests no significant impairment of nutrient and water uptake capacity (D'Orangeville et al., 2013). As for the soil nutrient availability, disturbed nutrient levels in the soil following cable burial have been shown to return to normal within a year (Peterjohn et al., 1994; McHale and Mitchell, 1996).

5 Conclusions

Overall, and despite the changes in radial growth phenology, soil warming and/or additional N deposition did not significantly increase tree growth. This result, contrary to our hypothesis, suggests that some N-poor boreal forests could not respond as expected to increases in soil temperature and N availability when N is added in experimental conditions that mimic natural deposition and inorganic N concentrations. As a result, the modifications of the forest N cycle expected with climatic warming and increased N deposition (Rustad et al., 2001; Galloway et al., 2004) as well as the expected increases in forest growth and C sequestration (Jarvis and Linder, 2000; Magnani et al., 2007) may simply not happen in the short term for these sites. Given the crucial importance of the boreal forest in the global C cycle, more studies are necessary to better understand how these forest types will respond to climate change in order to improve the predictions of forest productivity and carbon sequestration models.

Acknowledgements. We would like to thank Mathieu Gélinas-Pouliot for the help with field maintenance and sampling, and Josianne De Blois for statistical advice. The costs associated with this research were covered by a Réal-Décoste doctoral research scholarship received by L. D'Orangeville (Ouranos and the Fonds Québécois de la recherche sur la nature et les technologies), the Ministère des Ressources naturelles et de la Faune du Québec and Le Fond Vert du Ministère du Développement Durable, Environnement, et Parc du Québec within the framework of the Action Plan 2006–2012 on climate change.

Edited by: F. Carswell

References

- Allison, S. D. and Treseder, K. K.: Warming and drying suppress microbial activity and carbon cycling in boreal forest soils, *Glob. Change Biol.*, 14, 2898–2909, 2008.
- Alvarez-Uria, P. and Körner, C.: Low temperature limits of root growth in deciduous and evergreen temperate tree species, *Funct. Ecol.*, 21, 211–218, 2007.
- Aronson, E. L. and McNulty, S. G.: Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality, *Agr. Forest Meteorol.*, 149, 1791–1799, 2009.
- Bengtson, P., Basiliko, N., and Prescott, C. E., and Grayston, S. J.: Spatial dependency of soil nutrient availability and microbial properties in a mixed forest of *Tsuga heterophylla* and *Pseudotsuga menziesii*, in coastal British Columbia, Canada, *Soil Biol. Biochem.*, 39, 2429–2435, 2007.
- Bergh, J. and Linder, S.: Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands, *Glob. Change Biol.*, 5, 245–253, 1999.
- Berg, B. and Matzner, E.: Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems, *Environ. Rev.*, 5, 1–25, 1997.
- Bowden, R. D., Geballe, G. T., and Bowden, W. B.: Foliar uptake of ^{15}N from simulated cloud water by red spruce (*Picea rubens*) seedlings, *Can. J. Forest Res.*, 19, 382–386, 1989.
- Boyce, R. L., Friedland, A. J., Chamberlain, C. P., and Poulson, S. R.: Direct canopy nitrogen uptake from ^{15}N -labeled wet deposition by mature red spruce, *Can. J. Forest Res.*, 26, 1539–1547, 1996.
- Bronson, D. R., Gower, S. T., Tanner, M., and Van Herk, I.: Effect of ecosystem warming on boreal black spruce bud burst and shoot growth, *Glob. Change Biol.*, 15, 1534–1543, 2009.
- Bryan Dail, D., Hollinger, D., Davidson, E., Fernandez, I., Sievering, H., Scott, N., and Gaige, E.: Distribution of nitrogen-15 tracers applied to the canopy of a mature spruce-hemlock stand, Howland, Maine, USA, *Oecologia*, 160, 589–599, 2009.
- Brzostek, E. R., Blair, J. M., Dukes, J. S., Frey, S. D., Hobbie, S. E., Melillo, J. M., Mitchell, R. J., Pendall, E., Reich, P. B., Shaver, G. R., Stefanski, A., Tjoelker, M. G., and Finzi, A. C.: The effect of experimental warming and precipitation change on proteolytic enzyme activity: positive feedbacks to nitrogen availability are not universal, *Glob. Change Biol.*, 18, 2617–2625, 2012.
- Burton, P. J., Messier, C., Weetman, G. F. Prepas, E. E., Adamowicz, W. L., and Tittler, R.: The current state of boreal forestry and the drive for change. Chapter 1. In: *Management of the Boreal Forest*. (eds Burton PJ, Messier C, Smith DW, Adamowicz WL), Ottawa, Ontario, Canada, NRC Research Press, 2003.
- Carter, M. R. and Gregorich, E. G.: *Soil sampling and methods of analysis*, 2nd Edn., CRC Press, Boca Raton, Florida, 2007.
- Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., and Laundre, J. A.: Responses of Arctic tundra to experimental and observed changes in climate, *Ecology*, 76, 694–712, 1995.
- Deslauriers, A., Morin, H., and Begin, Y.: Cellular phenology of annual ring formation of *Abies balsamea* in the Quebec boreal forest (Canada), *Can. J. Forest Res.*, 33, 190–200, 2003.
- D'Orangeville, L., Côté, B., Houle, D., Morin, H., and Duchesne, L.: A three-year increase in soil temperature and atmospheric N deposition has minor effects on the xylogenesis of mature balsam fir, *Trees*, in press, doi:10.1007/s00468-013-0899-4, 2013.
- Driscoll, C. T., Lawrence, G. B., Bulger, A. J., Butler, T. J., Cronan, C. S., Eagar, C., Lambert, K. F., Likens, G. E., Stoddard, J. L., and Weathers, K. C.: Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies, *Bioscience*, 51, 180–198, 2001.
- Duchesne, L., Houle, D., and D'Orangeville, L.: Influence of climate on seasonal patterns of stem increment of balsam fir in a boreal forest of Québec, Canada, *Agr. Forest Meteorol.*, 162–163, 108–114, 2012.
- Friedrich, U. T. A., Falk, K., Bahlmann, E., Marquardt, T., Meyer, H., Niemeier, T., Schemmel, S., von Oheimb, G., and Härdtle, W.: Fate of airborne nitrogen in heathland ecosystems: a ^{15}N tracer study, *Glob. Change Biol.*, 17, 1549–1559, 2011.
- Galloway, J. N., Dentener, F. J., Capone, D. G., Boyer, E. W., Howarth, R. W., Seitzinger, S. P., Asner, G. P., Cleveland, C. C., Green, P. A., Holland, E. A., Karl, D. M., Michaels, A. F., Porter, J. H., Townsend, A. R., and Vöosmarty, C. J.: Nitrogen cycles: past, present, and future. *Biogeochemistry*, 70, 153–226, 2004.
- Goodine, G. K., Lavigne, M. B., and Krasowski, M. J.: Springtime resumption of photosynthesis in balsam fir (*Abies balsamea*), *Tree Physiol.*, 28, 1069–1076, 2008.
- Gruber, A., Baumgartner, D., Zimmermann, J., and Oberhuber, W.: Temporal dynamic of wood formation in *Pinus cembra* along the alpine treeline ecotone and the effect of climate variables, *Trees*, 23, 623–635, 2009.
- Gundale, M. J., Deluca, T. H., and Nordin, A.: Bryophytes attenuate anthropogenic nitrogen inputs in boreal forests, *Glob. Change Biol.*, 17, 2743–2753, 2011.
- Hobbie, S. E., Nadelhoffer, K. J., and Högberg, P.: A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions, *Plant Soil*, 242, 163–170, 2002.
- Holland, E. A., Dentener, F. J., Braswell, B. H., and Sulzman, J. M.: Contemporary and pre-industrial global reactive nitrogen budgets, *Biogeochemistry*, 46, 7–43, 1999.
- Hope, G. D.: Clearcut harvesting effects on soil and creek inorganic nitrogen in high elevation forests of southern interior British Columbia, *Can. J. Soil Sci.*, 89, 35–44, 2009.
- Houle, D. and Moore, J.-D.: Soil solution, foliar concentrations and tree growth response to 3-year of ammonium-nitrate addition in two boreal forests of Québec, Canada, *Forest Ecol. Manage.*, 255, 2049–2060, 2008.
- Houle, D., Duchesne, L., and Boutin, R.: Effects of a spruce budworm outbreak on element export below the rooting zone: a case study for a balsam fir forest, *Ann. For. Sci.*, 66, p. 707, doi:10.1051/forest/2009057, 2009.

- Houle, D., Bouffard, A., Duchesne, L., Logan, T., and Harvey, R.: Projections of future soil temperature and water content for three southern Quebec forested sites, *J. Climate*, 25, 7609–7701, 2012.
- Hutchison, J. and Henry, H.: Additive effects of warming and increased nitrogen deposition in a temperate old field: plant productivity and the importance of winter, *Ecosystems*, 13, 661–672, 2010.
- Jarvis, P. and Linder, S.: Botany: constraints to growth of boreal forests. *Nature*, 405, 904–905, 2000.
- Jerabkova, L. and Prescott, C. E.: Post-harvest soil nitrate dynamics in aspen- and spruce-dominated boreal forests, *Forest Ecol. Manage.*, 242, 209–216, 2007.
- Johnson, D. W., Verburg, P. S. J., and Arnone, J. A.: Soil extraction, ion exchange resin, and ion exchange membrane measures of soil mineral nitrogen during incubation of a tallgrass prairie soil, *Soil Sci. Soc. Am. J.*, 69, 260–265, 2005.
- Lambert, M.-C., Ung, C.-H., and Raulier, F.: Canadian national tree aboveground biomass equations, *Can. J. Forest Res.*, 35, 1996–2018, 2005.
- Linares, J. C., Camamero, J. J., and Carreira, J. A.: Plastic responses of *Abies pinsapo* xylogenesis to drought and competition, *Tree Physiol.*, 29, 1525–1536, 2009.
- Lupi, C., Morin, H., Deslauriers, A., and Rossi, S.: Xylogenesis in black spruce: does soil temperature matter?, *Tree Physiol.*, 32, 74–82, 2012.
- Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S., Grelle, A., Hari, P., Jarvis, P. G., Kolar, P., Kowalski, A. S., Lankreijer, H., Law, B. E., Lindroth, A., Loustau, D., Manca, G., Moncrieff, J. B., Rayment, M., Tedeschi, V., Valentini, R., and Grace, J.: The human footprint in the carbon cycle of temperate and boreal forests, *Nature*, 447, 849–851, 2007.
- Majdi, H. and Öhrvik, J.: Interactive effects of soil warming and fertilization on root production, mortality, and longevity in a Norway spruce stand in Northern Sweden, *Glob. Change Biol.*, 10, 182–188, 2004.
- Mäkipää, R., Karjalainen, T., Pussinen, A., and Kellomäki, S.: Effects of climate change and nitrogen deposition on the carbon sequestration of a forest ecosystem in the boreal zone, *Can. J. Forest Res.*, 29, 1490–1501, 1999.
- Malhi, S. S. and McGill, W. B.: Nitrification in three Alberta soils: Effect of temperature, moisture and substrate concentration, *Soil Biol. Biochem.*, 14, 393–399, 1982.
- McHale, P. J. and Mitchell, M. J.: Disturbance effects on soil solution chemistry due to heating cable installation, *Biol. Fert. Soils*, 22, 40–44, 1996.
- McNeil, B. E., Read, J. M., and Driscoll, C. T.: Foliar nitrogen responses to elevated atmospheric nitrogen deposition in nine temperate forest canopy species, *Environ. Sci. Technol.*, 41, 5191–5197, 2007.
- Melillo, J. M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., Burrows, E., Bowles, F., Smith, R., Scott, L., Vario, C., Hill, T., Burton, A., Zhou, Y.-M., and Tang, J.: Soil warming, carbon-nitrogen interactions, and forest carbon budgets, *P. Natl. Acad. Sci.*, 108, 9508–9512, 2011.
- Michel, J. P.: Estimation opérationnelle de la fertilité des sols et évaluation des indices foliaires comme indicateur de suivi des réservoirs nutritifs des sols de la forêt boréale, M.Sc. thesis, Université du Québec à Montréal, Montreal, 116 pp., 2010.
- Motulsky, H. and Ransnas, L.: Fitting curves to data using nonlinear regression: a practical and nonmathematical review, *FASEB J.*, 1, 365–374, 1987.
- Nadelhoffer, K. J., Emmett, B. A., Gundersen, P., Kjonaas, O. J., Koopmans, C. J., Schleppei, P., Tietema, A., and Wright, R. F.: Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests, *Nature*, 398, 145–148, 1999.
- Olson, R. K. and Reiners, W. A.: Nitrification in subalpine balsam fir soils: Tests for inhibitory factors, *Soil Biol. Biochem.*, 15, 413–418, 1983.
- Peterjohn, W. T., Melillo, J. M., Steudler, P. A., Newkirk, K. M., Bowles, F. P., and Aber, J. D.: Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures, *Ecol. Appl.*, 4, 617–625, 1994.
- Peterman, R. M.: The Importance of Reporting Statistical Power: The Forest Decline and Acidic Deposition Example, *Ecology*, 71, 2024–2027, 1990.
- Plummer, D. A., Caya, D., Frigon, A., Côté, H., Giguère, M., Paquin, D., Biner, S., Harvey, R., and de Elia, R.: Climate and Climate Change over North America as Simulated by the Canadian RCM, *J. Climate*, 19, 3112–3132, 2006.
- Quinn Thomas, R., Canham, C. D., Weathers, K. C., and Goodale, C.: Increased tree carbon storage in response to nitrogen deposition in the US, *Nat. Geosci.*, 3, 13–17, 2010.
- R Development Core Team: R: A language and environment for statistical computing, Vienna, Austria, R Foundation for Statistical Computing, 2010.
- Rasmussen, L., Beier, C., and Bergstedt, A.: Experimental manipulations of old pine forest ecosystems to predict the potential tree growth effects of increased CO₂ and temperature in a future climate, *Forest Ecol. Manage.*, 158, 179–188, 2002.
- Rossi, S., Deslauriers, A., and Morin, H.: Application of the Gompertz equation for the study of xylem cell development, *Dendrochronologia*, 21, 33–39, 2003.
- Rossi, S., Anfodillo, T., and Menardi, R.: Trephor: a new tool for sampling microcores from tree stems, *IAWA J.*, 27, 89–97, 2006.
- Rustad, L. E., Campbell, J. L., Marion, G. M., Norby, R. J., Mitchell, M. J., Hartley, A. E., Cornelissen, J. H. C., Gurevitch, J., and GCTE-NEWS: A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming, *Oecologia*, 126, 543–562, 2001.
- Sabey, B. R., Bartholomew, W. V., Shaw, R., and Pesek, J.: Influence of Temperature on Nitrification in Soils, *Soil Sci. Soc. Am. J.*, 20, 357–360, 1956.
- Sager, E. P. S. and Hutchinson, T. C.: The effects of UV-B, nitrogen fertilization, and springtime warming on sugar maple seedlings and the soil chemistry of two central Ontario forests, *Can. J. Forest Res.*, 35, 2432–2446, 2005.
- Schimel, J. P. and Bennett, J.: Nitrogen mineralization: challenges of a changing paradigm, *Ecology*, 85, 591–602, 2004.
- Schmitt, U., Jalkanen, R., and Eckstein, D.: Cambium dynamics of *Pinus sylvestris* and *Betula* spp. in the northern boreal forest in Finland, *Silva Fenn.*, 38, 167–178, 2004.
- Shortle, W. C. and Smith, K. T.: Aluminum-induced calcium deficiency syndrome in declining red spruce, *Science*, 240, 1017–1018, 1988.
- Ste-Marie, C. and Houle, D.: Forest floor gross and net nitrogen mineralization in three forest types in Quebec, Canada, *Soil Biol.*

- Biochem., 38, 2135–2143, 2006.
- Ste-Marie, C. and Paré, D.: Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands, *Soil Biol. Biochem.*, 31, 1579–1589, 1999.
- Strömgren, M. and Linder, S.: Effects of nutrition and soil warming on stemwood production in a boreal Norway spruce stand, *Glob. Change Biol.*, 8, 1194–1204, 2002.
- Stroup, W. W.: Mixed model procedures to assess power, precision, and sample size in the design of experiments, *Proc. Biopharmaceutical Section*, 15–24, Am. Stat. Assoc., Baltimore, MD, 1999.
- Tamm, C.-O.: Nitrogen in terrestrial ecosystems, Berlin, Springer, 1991.
- Turcotte, A., Morin, H., Krause, C., Deslauriers, A., and Thibeault-Martel, M.: The timing of spring rehydration and its relation with the onset of wood formation in black spruce, *Agr. Forest Meteorol.*, 149, 1403–1409, 2009.
- Van Cleve, K., Oechel, W. C., and Hom, J. L.: Response of black spruce (*Picea mariana*) ecosystems to soil temperature modification in interior Alaska, *Can. J. Forest Res.*, 20, 1530–1535, 1990.
- Yuan, Z. Y. and Chen, H. Y. H.: Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses, *Crit. Rev. Plant Sci.*, 29, 204–221, 2010.
- Zhao, C. and Liu, Q.: Growth and photosynthetic response of two coniferous species to experimental warming and nitrogen fertilization, *Can. J. Forest Res.*, 39, 1–11, 2009.