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

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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 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 $^{15}NH_4$–$^{15}NO_3$). Soil inorganic N was measured using buried ion exchange membranes (PRS™-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.

After three years of treatment, there was no significant increase in soil nitrate (NO_3) or ammonium (NH_4) 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 an average 54 % increase in the forest floor available NH_4. No effect of treatments were observed on needle N or diameter growth, but an eight-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 forests (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 one-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. The 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; Strömgren 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; Strömgren 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 (Strömgren 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 increased even more the performance of *P. tabulaeformis* but reduced that of *P. asperata*, suggesting that the interaction 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 to 250 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$, although the average atmospheric N deposition in boreal ecosystems is estimated to be 2.34 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ (Holland et al., 1999). Obviously, 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 ^{15}N.

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 × natural N concentrations using $^{15}\mathrm{NH_4}$-$^{15}\mathrm{NO_3}$) 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 Quebec city (47°17′ N; 71°14′ O; 800 m a.s.l.). 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 charnorckitic gneiss. The C and the N content of the forest floor are 416.1 and 16.6 $\mathrm{g\,kg^{-1}}$, 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 ($NH_4 + NO_3$) averages 5.7 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ (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 precipitations 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).

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. Each block was divided in two 24 m × 12 m whole plots separated by a 12 m × 12 m buffer zone. Each whole plot 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 each block, and the soil warming treatment was randomly distributed within each whole plot.

2.3 Soil warming

Around each experimental tree, 70 m of heating cables were buried in a spiral pattern 5–10 cm belowground 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. 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 on the basis of projections for the site for the 2070–2100 period (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.

Storage of temperature data and control of warming were done with 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. In 2009, soil warming was started on 27 April with a remaining snowpack of 0.75 m, with snowmelt in control plots ending 19 days later. A system malfunction caused an early interruption of the soil warming in mid-August that year. In 2010, soil heating was started on 30 March because of a warm spring. 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 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 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. Deionized water in which were added Na (0.046 $\mathrm{mg\,L^{-1}}$), Ca (0.089 $\mathrm{mg\,L^{-1}}$), Mg (0.018 $\mathrm{mg\,L^{-1}}$), K (0.026 $\mathrm{mg\,L^{-1}}$), H (0.014 $\mathrm{mg\,L^{-1}}$), Cl (0.07 $\mathrm{mg\,L^{-1}}$) and SO_4 (1.01 $\mathrm{mg\,L^{-1}}$) was used as rain solution. 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 $\mathrm{mg\,L^{-1}}$ 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 liters of artificial precipitation was applied on every tree. The applications resulted in an increased N deposition of 1.544 $\mathrm{g\,N\,tree^{-1}\,yr^{-1}}$. 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 (PRS$^{\mathrm{TM}}$-probes, Western Ag Innovations Inc.; Saskatoon, Canada). Exchange membranes allow 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, three in the organic soil layer (approx. 5–10 cm deep) and three in the mineral soil layer (approx. 15–20 cm deep). The probes were buried on 12 May and 30 May in 2010 and 2011 respectively, following snowmelt, and replaced every six weeks. In autumn, 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). The values were reported as $\mathrm{\mu g\ 10\,cm^{-2}}$ 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 and mineral soil (first 30 cm). Samples were air-dried for a week and sieved to 2 mm. The homogenized soil samples were pooled by soil layer for each tree to form one bulk sample per horizon per tree. Soils were extracted with KCl for 12 h. Levels of NO_3 were measured by ion chromatography (Dionex 2120i) and NH_4 colorimetrically with a Technicon Autoanalyzer (Technicon AA2), 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 mg kg^{-1} for extractable NO_3; 31 % of samples and of < 2 µg 10 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: ±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 sub-sample of thirty needles for each tree was weighted to account for any change in the leaf specific mass of each tree. Needles were oven-dried at 65 °C and then ground at 250 µm. The total N content was determined with a Kjeldahl autoanalyser (Kjeltec Auto model 1030 Analyser, Tecator, UK) after digestion with H_2SO_4. The degree of isotopic N enrichment of the samples (^{15}N) was measured on sub-samples (5.8–6.1 mg) using isotope ratio mass spectrometry with a Isoprime100 IRMS continuous flow spectrometer (Isoprime Ltd, Cheadle, UK) at GEOTOP Research Center (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 (FH- and first 20 cm of B-horizon) was obtained by multiplying (i) the average level of extractable N ($NH_4 + NO_3$) 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 twelve soil samples cited earlier.

2.8 Calculation of ^{15}N abundance and recovery

The ^{15}N abundance was converted into the common per mill deviation from atmospheric standard of 0.3663 atom% ^{15}N and noted in $\delta^{15}N$ according to Eq. (1)

$$\delta^{15}\mathrm{N} = \left(\frac{R_\mathrm{sample}}{R_\mathrm{standard}} - 1\right) \times 1000 \tag{1}$$

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

$$^{15}\mathrm{N}_\mathrm{foliage} = m_\mathrm{foliage} \times \left(\frac{\mathrm{at.\%}^{15}\mathrm{N}_\mathrm{foliage} - \mathrm{at.\%}^{15}\mathrm{N}_\mathrm{ref}}{\mathrm{at.\%}^{15}\mathrm{N}_\mathrm{tracer} - \mathrm{at.\%}^{15}\mathrm{N}_\mathrm{ref}}\right) \tag{2}$$

where $m_{foliage}$ is the estimated N pool in the foliage, at.%$^{15}N_{tracer}$ is the at.%^{15}N in the fertilizer solution, at.%$^{15}N_{ref}$ is the at.%^{15}N in the foliage of non-fertilized trees, and at.%$^{15}N_{foliage}$ is the at.%^{15}N 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 was 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):

$$\mathrm{BAI}_t = \pi\left[(X+R_t)^2 - (X+R_\mathrm{i})^2\right] \tag{3}$$

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 modelled 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. 1a). 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:

$$Y = Y_0 + A \times \exp[-\exp(\beta - \kappa \times t)] \tag{4}$$

where Y is the maximal daily measured BAI, Y_0 is the lower asymptote, A is the upper asymptote, β is the rate of change of curve shape, κ is the abscissa of inflection point and t is the time in julian days. 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 ordinary least square 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. 1b). 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 $\mathrm{mm}^2\,\mathrm{day}^{-1}$, 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 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 × 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:

$$\mathrm{BAI}_{2008} = \pi\left[(X+R_\mathrm{i})^2 - (X+R_\mathrm{i}-R_{2008})^2\right] \tag{5}$$

and

$$\mathrm{BAI}_{2007} = \pi\left[(X+R_\mathrm{i}-R_{2008})^2 - (X+R_\mathrm{i}-R_{2008}-R_{2007})^2\right] \tag{6}$$

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.

2.11 Statistical methods

A linear mixed-effects analysis of variance (anova) with repeated measures was used to analyse 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 block as random factor. Soil, foliar and growth parameters were analyzed with temperature treatment, fertilization and year as fixed factors and block as random factors. Because SWC and pre-treatment BAI (average of BAI_{2007} and BAI_{2008}) tended to differ between treatments (Fig. 2 and Table 2), 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 dependant variables were linear. Due to the important variability of the growth-related response variables, a simulation approach was used to assess the statistical power of the experimental design, in other words the size of an actual difference between treatments that could have been missed. The minimum detectable difference between treatments 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). Statistical analysis, modelling and plots were done using the R software (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 18.4 to 42.1 % in 2011 compared to 12.8 to 34.9 % in 2010 ($p < 0.01$; Fig. 2). Heated plots tended to display higher average soil water content than control plots ($p = 0.14$), corresponding to a mean difference of 2 % between treatments (21.9 % and 19.5 % in 2010, and 27.5 % and 25.6 % in 2011, respectively).

3.2 Soil available and extractable N

Significant between-year differences were detected for both available and extractable N (Fig. 3 and Table 1). 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. 3). Extractable NH_4 decreased by 47 % in the mineral horizon in 2011 whereas extractable NO_3 showed a reverse trend (Fig. 3).

Available NH_4 levels were higher in the organic than the mineral horizon in 2010 (22.4 and 14.6 µg 10 cm^{-2}, respectively), but were similar in 2011 (Fig. 3). Available NH_4 decreased by 70 % and 54 % in the organic and mineral horizons in 2011, respectively ($p < 0.05$; Fig. 3). 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. 3).

In 2010 and 2011, the soil warming treatment increased available NH_4 in the organic soil horizon by 53.8 % in average ($p = 0.02$; Table 1 and Fig. 3). No such effect was observed for available NO_3, and extractable NH_4 and NO_3 in either soil horizon (Table 1). The effect of soil warming on forest floor available NH_4 tended to vary between years (warming × year: $p = 0.11$; Table 1) with increases of 74.3 % and 21.9 % in 2010 and 2011, respectively. Except for a likely increase in forest floor extractable NH_4 ($p = 0.09$; Table 1 and Fig. 3), 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 horizon and the first 20 cm of mineral soil (3.7 g extractable-N m^{-2}).

3.3 Average leaf weight and foliar N

Needle N concentrations were not affected significantly by any treatment and were stable over time (12.3 ± 0.4 g kg^{-1} in 2010 and 12.1 ± 0.4 g kg^{-1} in 2011; Fig. 4 and Table 1). Needle mass did not respond to treatments either averaging 3.6 mg needle^{-1} (data not shown).

Needle $\delta^{15}N$ concentrations measured in fertilized trees averaged 4.29 ± 0.71‰ and were significantly higher than those of control trees (-2.04 ± 0.17 ‰, $p < 0.01$; Fig. 4

and Table 1). With a calculated foliage N pool of 101 g tree^{-1}, an average of 1.1 % of the added N (1.54 g tree^{-1} yr^{-1}) was recovered in the foliage of fertilized trees.

3.4 Seasonal course of basal area increment

No effect of treatments on BAI ($A - Y_0$) was detected in either year with BAI averaging 740 ± 103 mm^2 and 700 ± 104 mm^2 in 2010 and 2011, respectively (Table 2). The onset of growth and maximum growth rate were reached on average one week earlier in 2010 compared to 2011 ($p < 0.01$; Table 2). 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, 8 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 was nine and seven days for growth onset, 50 and 40 days for growth ending, 700 and 500 mm^2 for total growth, 0.02 and 0.018 for the slope of growth curve, eight and six mm^2 day^{-1} for maximum daily growth and five and four days for the timing of maximum daily growth (Table 2). 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 NH_4 or NO_3 availability in the forest floor or mineral soil as measured by the two methods except for an increase (54 %) in NH_4 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 NH_4 measured in 2010 in heated plots compared to the control plots suggest a strong influence of the prevailing climatic conditions of 2010 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 NH_4 levels that year.

Given the influence of temperature on nitrification rates (Sabey et al., 1956; Malhi and McGill, 1982), an increase in NO_3 in the heated plots was expected. The lack of detectable effect of soil warming on NO_3 in the forest floor, despite an increase in NH_4, 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 NO_3 measured during a spruce budworm outbreak at the site in 1981–1984 (Houle et al., 2009). The absence of increased NO_3 in the mineral horizon of heated plots thus suggests that the increased NH_4 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 NO_3.

In contrast with available NH_4, extractable NH_4 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 NH_4 in the soil solution but not the larger pool of extractable NH_4 suggests that the effect of that treatment was relatively modest.

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 one 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 NH_4 (range 15–67 %) and 62 % less NO_3 (range 30–77 %) than the other three sites. A previous study conducted in the same watershed using ^{15}N isotopic pool dilutions showed that almost all of the NH_4 and NO_3 made available in the forest floor was 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 available inorganic N at our site – 0.8 % of the total N contained in the forest floor – maintain strong N sinks (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 ^{15}N levels, showing that a fraction of the inorganic ^{15}N 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).

Two factors could have hastened the BAI phenology: (i) increased availability of soil nutrients, which is supported by the +74.3 % available NH_4 measured that year in heated plots although the lack of foliar N differences between treatments suggests otherwise, and/or (ii) increased soil temperature, producing an earlier warming of the cold spring soils and hastening the period for uptake of water, nutrients and photosynthesis. 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), and 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 2). 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. A naturally higher water holding capacity and/or slower drainage in the randomly selected soil warming plots are likely to explain the higher soil water content in heated plots. This hypothesis is supported by the lack of relationship measured between soil temperature and soil water content ($p = 0.69$; data not shown). In a greenhouse study in Alaska, similar increases in moisture with warming were explained by pre-existing conditions (Shaver et al., 1998).

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.

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Table 1. Probability values from mixed-model anovas and ancovas applied to the soil and leaf N with warming, fertilization and year as fixed factors. SWC was included as covariable when significant (for soil analysis only). Significant p-values are in bold ($p < 0.05$).

	Soil N								Foliar N	
	Ion-exchange membranes				KCl extractions					
	FH horizon		B horizon		FH horizon		B horizon			
	NO_3	NH_4	NO_3	NH_4	NO_3	NH_4	NO_3^a	NH_4	Total N	^{15}N
SWC	0.08	0.07	**0.02**	**0.02**	0.72	0.97	< **0.01**	< **0.01**	–	–
Heating (H)	0.77	**0.02**	0.23	0.96	0.62	0.86	0.07	0.29	0.47	0.13
Fertilization (N)	0.84	0.43	0.94	0.31	0.41	0.09	0.52	0.81	0.85	< **0.01**
H × N	0.13	0.20	0.47	0.99	0.41	0.64	0.12	0.47	0.62	0.49
Year (Y)	< **0.01**	< **0.01**	< **0.01**	**0.05**	0.41	0.64	–	**0.01**	0.54	0.45
H × Y	0.82	0.11	0.55	0.33	0.15	0.25	–	0.63	0.22	0.23
N × Y	0.67	0.88	0.90	0.67	0.62	0.67	–	0.07	0.66	0.09
H × N × Y	0.19	0.65	0.67	0.79	0.25	0.94	–	0.67	0.44	0.13

[a] KCl-extracted NO_3 values in the mineral horizon were too low for detection in 2010. Therefore, only the 2011 data was analyzed and the factor "year" was removed.

Table 2. Mean 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 (average of 2007 and 2008 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

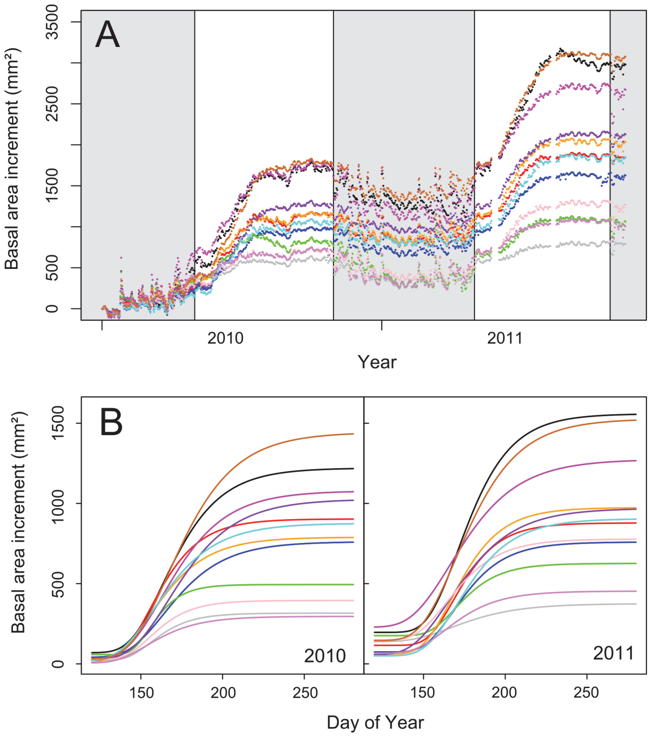

Fig. 1. (A) Average daily basal area increment of the 12 monitored balsam fir trees in 2010 and 2011 at the Lake Laflamme watershed (Québec, Canada). The non-shaded areas identify the periods used for growth modelling each year. **(B)** modeled seasonal basal area increment of each monitored balsam fir tree (12) in 2010 and 2011 using the Gompertz equation.

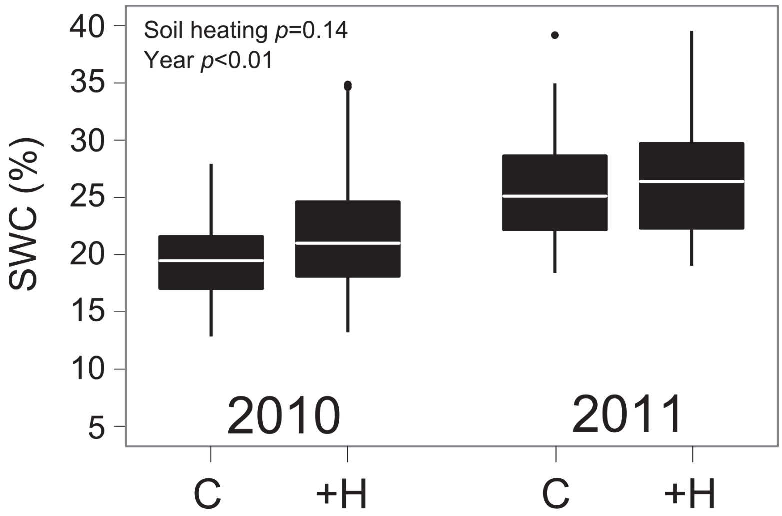

Fig. 2. Box plot of soil water content data for control (C; $n = 6$) and heated (+H; $n = 6$) plots.

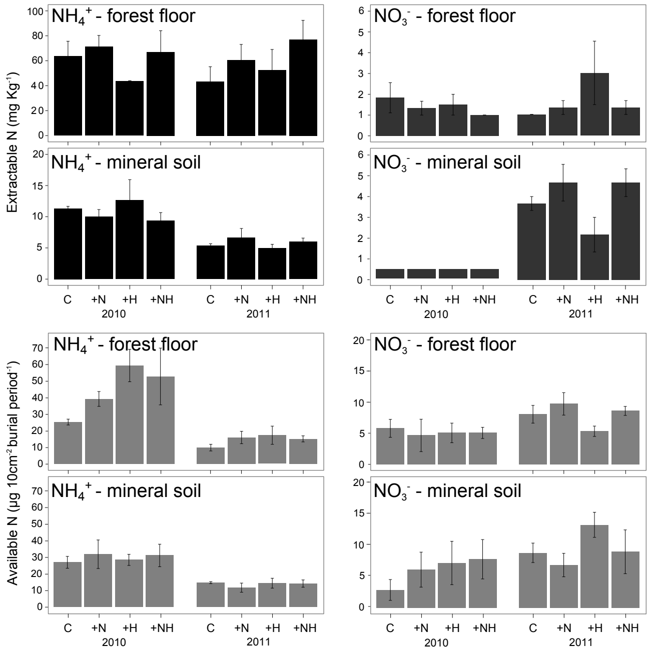

Fig. 3. Extractable and available NH_4 and NO_3 in the forest floor and mineral horizon in control (C), fertilized (+N), heated (+H) and heated-fertilized (+NH) plots in 2010 and 2011. Extractable N corresponds to inorganic N species measured on soil samples taken in September of each year and extracted with KCl 1 M. 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 ($< 1\,mg\,kg^{-1}$). Error bars are standard error.

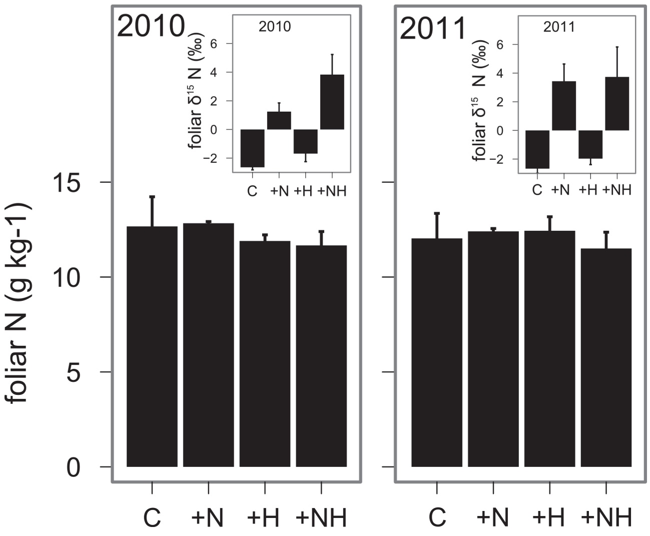

Fig. 4. Total N and ^{15}N concentration in the needles of balsam fir trees in 2010 and 2011. C: control trees (no heating, no fertilization); +N: fertilized trees; +H: heated trees; +NH: fertilized and heated trees. Error bars are standard error.