UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EFFECTS OF PALUDIFICATION AND WINTER PRECIPITATION CHANGES ON GROWTH OF BLACK SPRUCE (*PICEA MARIANA*) AND TREMBLING ASPEN (*POPULUS TREMULOIDES*)

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RÉSUMÉ

La forêt boréale du Québec pourrait être affectée par les changements climatiques. Dans cette étude, nous nous sommes concentrés sur les effets des changements des couvert de neige et de mousse, qui sont fortement touchés par le réchauffement climatique et peuvent affecter la croissance des arbres. Nous avons regardé l'effet sur la croissance de deux espèces commerciales des forêts du Québec - l'épinette noire (*Picea mariana*) et peuplier faux-tremble (*Populus tremuloides*). Au cours de deux années de suivis consécutives, des épinettes noires et des peupliers faux-tremble de 10 ans ont été sélectionnés pour des traitements : un couvert additionnel de neige pour retarder le dégel du sol (S+), l'enlèvement de la neige pour accélérer le dégel du sol (S-), un couvert additionnel de mousses (M+), sans couvert de mousses (M-), une fertilisation (F) et un contrôle (C). À la fin de la saison de croissance 2010, nous avons récolté tous les arbres échantillons pour analyser la répartition de la biomasse, les racines mycorrhizées et la composition ^{15}N du feuillage. Généralement, l'épinette noire a répondu plus fortement que le peuplier faux-tremble à la plupart des traitements, probablement parce que le système racinaire de l'épinette noire est peu profond et donc, plus sensible aux variations de température du sol dues aux perturbations du sol isolant. La fertilisation a augmenté la croissance des branches annuelles et le contenu 15N des aiguilles dans l'épinette noire et diminué le nombre des points d'infection mycorrhizienne dans le peuplier faux-tremble. Cependant, la répartition de la biomasse souterraine n'a pas été affectée de manière significative par la fertilisation. Les traitements S- et M- ont influencé positivement la croissance en diamètre basal et la croissance du volume des tiges d'arbres (seulement diamètre basal pour le tremble), qui pourrait être le résultat de la température plus chaude du sol avec S- et M- traitements. Les points d'infection mycorriziens sur les racines de peuplier faux-tremble ont été considérablement réduits par les traitements (S+, M+, M- et F), tandis que ceux de l'épinette ont été assez stables, ce qui indique que le peuplier faux-tremble pourrait être plus vulnérable aux changements climatiques futurs possibles. Nos résultats ont également suggéré que, dans le contexte du changement climatique, l'allocation de la biomasse des arbres (l'épinette noire et le peuplier faux-tremble) peut être attribuée à plus de détermination génétique et à l'adaptation à un sol froid et à la disponibilité en azote limitée.

Mots clés: épinette noire, peuplier faux-tremble, changement climatique, couvert de neige, couvert de mousse, répartition de la biomasse, infection mycorhizienne, ^{15}N, racines fines

General Introduction

The problem

It is generally accepted that average global temperature will increase throughout the 21st century. According to the last IPCC fourth assessment report, average global surface air temperature will increase from 1.9 to 4 °C in the 21st century. In North America the warming is expected to be larger during winter: an increase up to 10°C is projected, accompanied by up to 30% higher winter precipitation. Quebec is predicted to be warmer due to its location. In southern Quebec, temperatures have increased by 0.5-1.2°C from 1960 to 2003, whereas in northern Quebec temperatures has increased by about 2°C since 1993 (Bourque and Simonet 2008). Moreover, burn rate in the eastern Canadian boreal forest will increase by +0.2% during the 21st century in the context of climate change (Bergeron et al. 2010).

Due to the rapid and severe climate change, the boreal forests in eastern Canada are likely to be more vulnerable because of their sensitivity to warming. While summer processes have received some attention the effects of winter processes on forests are not well understood. Snow cover, the most important insulator of soils in winter will be affected directly by winter warming within boreal forest. Climate warming can induce to delayed snowfall in autumn and accelerated snowmelt in spring (Brown et Mote, 2009), which leaves bare soil to large air temperature changes and leads to increased numbers and severity soil freezing-thaw cycles. These can cause nutrient loss (Mitchell et al., 1996), water limitation (Zheng and Flerchinger, 2001), and reduced soil microbial community activity (Schieml and Clein, 1996).

Another important soil isolator in boreal forest is moss cover, which is also affected by climate change. Moss cover will keep soil temperature low level by creating a physical barrier over the forest floor (Hinzman et al., 1991). High moisture and cool summers are favorable for the development of moss cover and the enhance paludification. However, the increase of temperature and evapotranspiration caused by climate warming will exceed the increase of precipitation (Girardin and Mudelsee, 2008). Thus, less water availability would lead to more activity of forest fire; these conditions are unfavorable to the establishment and expansion of mosses (Lavoie et al., 2005).

Soil temperature plays a critical role for growth, distribution and composition of boreal forests. Low soil temperature affects several physiological and morphological attributes of trees (Day et al. 1990), restricts water uptake and root activity (Repo *et al.*, 2005), diminishes the growth of shoots and roots and the biomass allocation to roots (Lopushinsky and Max 1990) and reduces the photochemical efficiency (Fv/Fm) of the PSII of the current-year needles (Repo et al.2003). During Spring, low soil temperature plus high light intensities may enhance photoinhibition and delay the recovery of photosynthesis process (Repo et al. 2005). Therefore, soil temperature, affected directly by the changes of snow cover and moss cover, regulates the productivity of boreal forest. Black spruce (*Picea mariana (Mill.) BSP*) and trembling aspen (*Populus tremuloides Michx.*) are the two most widespread and economically important species in North America (Viereck and Johnson, 1990; Perala, 1990). It is reported that changes in temperature and precipitation regimes will affect the two species both within and outside the growing season (Gewehr et al., *submitted*). Thus, it is necessary to investigate the physiological responses of these two important species to the effects of climate change on snow and moss cover.

As shown in the following figure 1, the possible consequences of climate change, either delayed snowmelt or early snowmelt in spring, could adversely affect tree growth through different processes, such as damages of fine roots and soil microbe, limitation of nutrient and water uptake, onset of sapflow and photosynthesis in spring, etc. In this study, we measured stem, branch, height, roots, foliar $\delta^{15}N$ and root:shoot to explore the responses of trees to the possible future climate change.

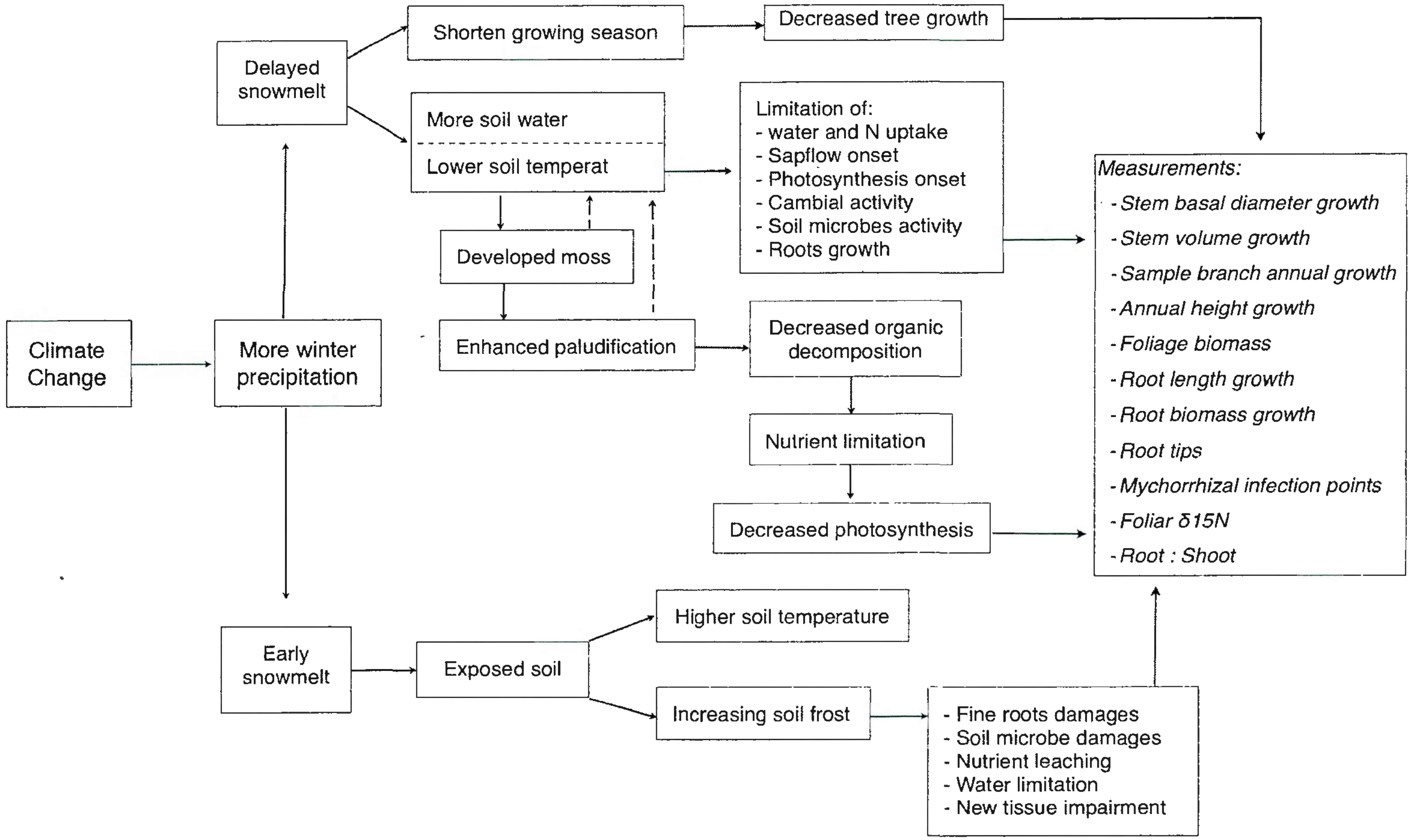

Figure 1: Possible negative consequences of climate change and variables measured to estimate the responses of trees.

State of knowledge

1) Winter precipitation

Impact of climate warming on boreal forest can cause a reduction of the duration and thickness of snow cover that directly affects the soil temperature beneath. Because of its low thermal conductivity, snow cover can effectively insulate the soil from cold air temperature and inhibit soil freezing during the winter and decrease soil heat loss (Hinkel and Hurd Jr 2006). Several field manipulations have demonstrated that soil temperature under snow cover is warmer and more stable than ambient temperature during most periods of winter (Walker et al. 1999, Schimel et al. 2004, Nobrega and Grogan 2007). Moderate deeper snow cover may also delay and decrease soil freeze-thaw cycles (Nobrega and Grogan 2007) and are hence favorable for fine root and soil nutrient dynamics. Nevertheless, warmer winter can be accompanied by less or more snow cover, which can increase or decrease the probability of frozen ground in winter, respectively (Venäläinen et al. 2001).

Climate warming can induce to early snowmelt in spring, although winter precipitation increases. Early melt of snow cover may lead to increases in soil frost and freeze-thaw effects which could be an important disturbance causing significant damage to fine roots (especially shallow-rooted species), stress on the soil microbial activity, losses of nutrient elements, limitation of water availability and affecting growth (Groffman et al. 2001). In early spring, when rising air temperature triggers the onset of photosynthesis of boreal conifer at the beginning of growing season (Tanja et al. 2003), insufficient soil water availability of frozen soil may slow down the recovery of photosynthesis. Furthermore, higher air temperature brings on the earlier development of buds that could make trees more vulnerable by repeated frosts in spring.

More snow cover may induce delayed snowmelt in spring which can delay or totally block the onset of sap flow, reduce or completely inhibit root growth and therefore reduce tree growth (Repo et al. 2008). Delayed snowmelt can also affect cambial activation, which may explain why snow plays an important role in determining the length of growing season (Vaganov et al. 1999).

2) Paludification

Paludification is a dynamic process that encompasses peat accumulation and leading usually to waterlogged conditions in the soil (Joosten 2002). In the Clay Belt of Ontario and Quebec, successional paludification has been shown to be associated with the abundance of Sphagnum spp., which can create coverage over a site and induce a raise in the water table. High water table can reduce tree biomass growth due to low oxygen in the root zone (Fenton and Bergeron 2006). Moreover, sphagnum mosses develop an environment that is cold, wet and acidic for decomposers. Also, the high C: N ratio of Sphagnum is resistant to decomposition (Hobbie 1996, Turetsky 2003) and hence reduces nutrient available for tree growth. The development of paludification is reducing soil temperature, decomposition rates, microbial activity and nutrient availability, which will further deteriorate tree growth conditions. For example, photosynthesis is affected because it requires large quantities of N for the synthesis of photosynthesis enzymes and chlorophyll (Billow et al. 1994). As a result both above- and below-ground growth therefore may be influenced. This process is one cause for the productivity decline of boreal forests during subsequent rotations without fire as stand replacing disturbance (Simard et al. 2007). Our previous study showed that thick moss cover could delay soil thawing for more than three weeks and induced to lower soil temperature throughout the whole study (Fréchette et al. 2011).

3) Carbon allocation and nitrogen uptake

Soil temperature is a key factor of tree growth. In early spring, low soil temperatures reduce the actual rate of recovery and delay the full recovery of photosynthesis capacity (Ensminger et al. 2008). During growing season, soil temperature can affect biomass allocation between shoots and roots (Ericsson et al. 1996). Low soil temperature can decrease flow of carbohydrates to roots and reduce new root elongation (Andersen et al. 1986). (Ryyppö et al. 1998) showed that low root zone temperature suppressed roots growth and necessary membrane changes for efficient water and nutrient uptake, which in turn limited net photosynthesis and therefore the availability of photosynthates for root growth. (Lippu 1998) found that low soil temperature can induce to an accumulation of photosynthates to shoots of Scots pine seedlings, while a decrease of photosyntheates to roots. But it has also been shown that seedling growth with increasing soil temperature (5, 10, 15, 20, 25, 30 and 35 °C) is different and dependent on tree species, trembling aspen allocated highest biomass to root and stem but lowest to leaf, jack pine allocated highest biomass to leaf but lowest to stem, black spruce allocated less biomass to roots but greater biomass to leaf than white spruce (Peng and Dang 2003).

The productivity of boreal forest is severely restrained by nitrogen limitation, which is deteriorated by low soil temperature. In field experiments in Alaskan black spruce forests, (Van Cleve et al. 1990) found that soil temperatures which were raised by average 8-10°C over two growing seasons (from May to September) significantly increased the availability of N, P, K and then caused a significant increase in tissue N and P concentration and leaf photosynthesis and therefore probably induce to faster growth. (Lahti et al. 2005)demonstrated that both roots growth and nutrient uptake of 5-year-old seedling of Norway spruce was reduced in lower soil temperature (9°C) treatments during the second growing season of the experiment. They suggested that the reduced nutrient uptake with lower soil temperature (9°C) in their study may be caused by the low activity of root nutrient transport, high soil water viscosity or lower water and nutrient-absorbing surface compared with seedlings in the higher soil temperature treatments.

In boreal forest and tundra, the proportional allocation of C to roots and mycorrhizas are high and C storage is great, thus surface soil temperatures must be important in determining the roots growth even the whole plant growth. However, the low soil temperature common in boreal forest inhibits uptake of water and nutrients (Lopushinsky and Kaufmann 1984), roots growth (Andersen et al. 1986, Lopushinsky and Max 1990) induces retarded growth and development of shoot by affecting many physiological processes (Vapaavuori et al. 1992).

4) Mycorrhizal fungal association

The nutrition of boreal forest trees generally depends on a symbiotic association of their roots with mycorrhizal fungi. Ecto-mycorrhizal (ECM) fungi are associated

The two dominant species in eastern Canadian boreal forest, black spruce and trembling aspen, are both associated with mycorrhizal fungi. The root system of black spruce symbioses with ecto-mycorrhizal (ECM) fungi, while trembling aspen is associated with both ECM and arbuscular mycorrhizal (AM) fungi. ECM fungi form a symbiotic relationship with plants by forming a sheath around fine root tips and then make Hartig net by fungal hyphae (Futai et al. 2008). Thus, ECM fungi increase the absorbing surface area of the host tree for water, mineral salts and metabolites uptake (Futai et al. 2008). AM fungi invade into the root cells and produce endo-mycorrhizal structures which can greatly increase the surface area of contact between the fungal hyphae and the cell cytoplasm to facilitate nutrient transfer between them (Smith and Read, 2008). The infection of mycorrhizal fungi may also protect the roots by repelling soil pathogens and thereby is favourable for root growth (Perrin 1990, Marschner and Dell 1994). It has been found that mycorrhizal fungal association have several roles: They transport fixed plant carbon below ground (Jakobsen and Rosendahl 1990); caused relatively high rates of hydraulic conductance when the root temperatures were low (Muhsin and Zwiazek 2002); induced to higher root: shoot than nonmycorrhizal ones at low soil temperatures (4°C) (Landh et al. 2002); influenced the natural abundance of ^{15}N of plant (Michelsen 1998); provided N for the host plants from soil pools of amino acids, amino sugar, protein, and chitin (Read and Perez-Moreno 2003), etc. Moreover, higher soil temperature can increase the length and tips of mycorrhizal roots (Domisch et al. 2002), and the number of infection points of mycorrhizal roots (Smith and Bowen 1979).

Objectives and Hypotheses

The objectives of this study were: 1) to exam the responses of the two species---black spruce and trembling aspen---to different thickness of snow cover and moss cover; 2) to predict the possible changes of forest composition and productivity within the study area by comparing the responses of these two species. Fertilization was used to test to what extent the changes could be explained by improved nutrition.

In this study we tested the following hypotheses depending upon the different treatments:

1) Fertilization (N addition) significantly increases the aboveground production of both species.
2) Snow added treatment (S+) affects both species negatively by leading to deeper soil freezing and later soil thawing, as snow cover is shoveled in the middle of winter and re-added to trees at the end of winter.
3) Both species grow better with snow removal treatment (S-), which accelerates soil thawing by shoveling snow cover to soil surface in early spring.
4) Moss added treatment (M+), by adding an additional moss layer onto the existing moss carpet, leads to colder and wet soil during growing season and therefore affect negatively on both species, especially trembling aspen that typically grows on warmer and well-drained soil.
5) Moss removal treatment (M-) affects positively in both species, since moss cover removal would lead to higher soil temperature during growing season and increase tree growth.
6) Reactions of plants occur mostly through changes in N concentrations and isotopic abundances.

Chapter 1

EFFECTS OF PALUDIFICATION AND WINTER PRECIPITATION CHANGES ON GROWTH OF BLACK SPRUCE (*PICEA MARIANA*) AND TREMBLING ASPEN (*POPULUS TREMULOIDES*)

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1.1 Abstract

The aim of this research is to get a more complete understanding of the effects of climate warming on boreal forests of eastern Canada. We focused on the effects of snow and moss cover changes, which are strongly affected by climate warming and can affect tree growth directly, on growth of the two commercial species of eastern Canada forests – black spruce (*Picea mariana*) and trembling aspen (*Populus tremuloides*). During two years consecutive study, the black spruce and trembling aspen of ten-year old have been selected to different treatments: more snow cover and soil frost (S+), early snow removal and accelerated soil thawing (S-), added moss cover (M+), removed moss cover (M-), fertilization (F) and control (C). At the end of the 2010 growing season, we harvested all sample trees to analyze their biomass allocation, mycorrhizal roots and foliar ^{15}N composition. Generally, black spruce responded stronger than trembling aspen to most of the treatments, probably because the shallow roots system of black spruce was more sensitive to soil temperature changes by soil insulator disturbances. Fertilization increased the annual branch growth and ^{15}N content of needles in black spruce, and decreased the mycorrhizal infection points in trembling aspen. However, above and underground biomass allocation wasn't affected significantly by fertilization. S- and M- treatments positively affect basal diameter growth and stem volume growth of trees (only basal diameter for aspen), which could result from the warmer soil temperature with S- and M- treatments. Mycorrizal infection points on the roots of trembling aspen were significantly lowered by treatments (S+, M+, M- and F), while those on spruce were quite stable, indicating that trembling aspen might be more vulnerable to possible future climate change. Our results also suggested that, in the context of climate change, the biomass allocation of trees may be more attributed to genetic determination and adaptation to cold soil and limited N availability.

Key words: black spruce, trembling aspen, climate change, snow cover, moss cover, biomass allocation, mycorrhizal infection, ^{15}N, fine roots

1.2 Introduction

Eastern Canadian forests have been affected significantly by climate warming. In southern Quebec, temperatures increased by 0.5-1.2°C from 1960 to 2003, whereas in northern Quebec, since 1993, temperatures has increased by about 2°C (Bourque and Simonet 2008). In the context of global warming, winter is being affected and will be affected especially. The trend of increasing winter precipitation of northern latitudes has resulted into an increased amount of snowfall over last century and is predicted to increase further in this century (Groisman and Easterling 1994, Vaganov et al. 1999, Giorgi et al. 2001). Deeper snow cover may lead to delayed snowmelt in spring which can delay the onset of growing season. Paradoxically, climate warming causes early snowmelt in spring, which can lead to deeper soil freezing, increase the number soil freeze-thaw cycles and therefore adversely affect tree growth by limited nutrient and water availability, affected sap flow and reduced soil microbial activity.

Furthermore, because of the low to moderate slopes and fine-textured soils, Clay Belt of Ontario and Quebec is prone to paludification (Bergeron et al. 2007), which is mainly caused by organic matter accumulation and accelerated by Sphagnum moss development (Fenton et al., 2005). As a result, soil temperature is lower under a continuous moss cover (Bonan 1991) and unfavorable to tree growth through many physiological processes in the growing season. For example, the soil microbial activity is limited by the lower soil temperature and thus reduces N mineralization and availability to roots. Reduced N availability in turn affects the above- and below-ground growth of trees. (Poorter and Nagel 2000) have confirmed the model of functional equilibrium hypothesis about carbon allocation which states that roots allocation increases when belowground resources are limiting whereas shoots allocation increases when limiting aboveground resources restricts carbon gain.

However, there is another possible consequence of moss cover in the context of climate warming. If the increase of temperature and evapotranspiration caused by climate warming exceeds the increase of precipitation (Girardin and Mudelsee 2008), less water availability would lead to more activity of forest fire, these conditions are unfavorable to the establishment and expansion of mosses (Lavoie et al. 2005).

Black spruce (*Picea mariana* (Mill.) BSP) and trembling aspen (*Populus tremuloides* Michx.)

are two key ecological and economical species in the boreal forest of eastern Canada. Trembling aspen grows better on warmer and well-drained soils than black spruce, which prefers cold and poorly-drained soils (Burns 1990). (Dang and Cheng 2004) reported that the photosynthetic capacity of black spruce is more sensitive to high soil temperature than trembling aspen. (Fréchette et al. 2011) found that reduced snow and moss cover caused lower rate of photosynthetic recovery and photosynthetic activity, especially in black spruce. In this study, we investigated the responses of above- and underground growth of black spruce and trembling aspen to changing snow and moss cover, which are altered directly by climate change.

1.3 Materials and Methods

1.3.1. Experimental areas

This study was carried out in the Abitibi-Témiscamingue region within the south-western boreal forest of eastern Canada (79°20'W, 49°44'N). Selected study areas are part of the black spruce (*Picea mariana* (Mill.) BSP.) - feather moss (*Pleurozium schreberi* (Bird) Mitt.) bioclimatic zone (Doucet 2009) and extend over the Clay Belt region of Quebec and Ontario, created by thick deposit left by proglacial Lakes Barlow and Ojibway after their maximum extension in the Wisconsinian glacial stage (Vincent and Hardy 1977). The clay soil within the area is classified as gleysol (Group 1998), which is typical of the Clay Belt and prone to paludification. The study areas are covered by continuous feathermoss and sphagnum moss cover with approximately 20 cm thick of raw humus layer beneath. According to the records nearest weather station at la Sarre, the mean annual temperature of the study areas was 0.7°C, with the lowest (-18.2°C) occurred in January and the highest (16.9°C) in July. The mean annual precipitation is 889.8 mm, with 246.30 mm as snow (Environment Canada 2011). Large stand replacing fires are the major disturbances in the study areas (Bergeron et al. 2004), inducing typical stand density with sparse seedlings and no canopy trees. After the recent large fire in 1997, the study areas were naturally generated by dominant black spruce, with trembling aspen as well.

1.3.2. Trees selection and treatments

The 84 healthy saplings of black spruce and trembling aspen were selected according to their size (1.2 to 2.5 m of height), 42 of each species. Seven experimental blocks were chosen randomly to conduct the experiments in an area of around 20 ha. Blocks were chosen to show homogenous growth condition and similar sized trees within a short distance from each other. Each block contained six spruce and six aspen, which were randomly assigned to one of the 6 treatments: added snow cover and soil frost (S+), early snow removal (S-), added moss cover (M+), removed moss cover (M-), fertilization (F) and control (C). The different treatments and trees were distributed homogeneously throughout the study areas. The treatments were conducted for two years consecutively, moss treatments were did in September 2009 and snow treatments in the winter of 2009/2010.

The purpose of the S+ treatment was to delay the soil thawing and keep the soil temperature at a lower level during the spring. For allowing deeply freeze of the soil, the snow cover of each selected tree was removed at the end of January to induce deep soil freezing. At the end of March 2010, 15 cm layer of hay with additional 60 cm snow upon were used to insulate the ground from warming air temperature. The hay layer was not removed until the end of May 2010. S- treatment was to accelerate the soil thawing and make a higher soil temperature in spring, thus at the end of March 2010, the snow cover was shoveled on a 1.5 m radius area around the tree.

The M+ treatment was to maintain the soil temperature at the lower level during the summer, by adding 15 cm thick of sphagnum moss cover with 1.5 m radius around the tree in September 2009. Meanwhile, the M- treatment was to raise the soil temperature throughout the growing season by removing all the sphagnum moss cover on a radius of 1.5 m around the tree.

For fertilization (F), an additional 140kg/ha slow release nitrogen fertilizer was added on a 2.0 m radius around the tree. No intervention was applied to the control (C) group. Snow cover and moss cover were kept intact and no fertilizer was added.

1.3.3 Ingrowth bags and mycorrhizal roots collection

Fine root production was estimated by ingrowth bag, made of plastic mesh with 40 cm length. The bags were filled with root-free garden soil mixed with sand which came from a nearby esker. In August 2009, two ingrowth bags were installed 50cm away from each sample tree, at a depth of 10cm. After installation, the removed moss cover was put back, excluding the M- treatment. In September 2010, all ingrowth bags were dug up and gently washed to separate the roots inside for measuring their length and dry mass. Besides, another fine roots (diameter ≤ 2mm) sample of each tree was collected to count the density of mycorrhizal infection points under microscope.

1.3.4 Destructive and non-destructive sampling

Tree height (H), DBH, D (Diameter at 5cm above ground) and D_0 (Diameter below the lowest branch) of 2009 and 2010 were measured. All trees were harvested in August 2010. The diameter of all branches was measured, as well as 10 sample branches per spruce and 6 sample branches per aspen were used for biomass analysis. Sample branches were selected systematically through the whole crown. Discs from stems were cut and sanded to estimate volume growth.

1.3.5 Foliar $\delta^{15}N$

Foliage samples of spruce were collected in May and August 2010, while aspen in the early July and at the end of August 2010.The shoots were oven-dried at 100°C for 48 hours in lab and then were milled for $\delta^{15}N$ analysis in the Stable Isotope Lab at GEOTOP.

1.3.6 Soil temperature measurements

Data loggers (iButton DS1990, Maxim electronics, Dallas, Texas, USA) were installed at a depth of 10cm and a distance of 20cm from 31 selected trees to record the soil temperature every four hours.

1.3.7 Pipe model ratio

Pipe model ratio equation (1) was used to estimate the foliar biomass of the trees:

$$R=\Sigma M_{SB}A_B / \Sigma A_{SB} \quad (1)$$

Where M_{SB} is the annual biomass of sample branch of a tree, A_B is the cross-sectional area of each living branch of the tree; A_{SB} is the cross-sectional area of a sample branch of the tree. Each tree was calculated separately.

1.3.8 Statistical analyses

Since the seven experimental blocks are chosen randomly over the study areas and sample trees in each block are also assigned randomly to one of the six different treatments, this study is expected to be the randomized complete block design (RCBD) using the following equation:

$$Y_{ij} = \mu + \alpha_i + \beta_j + \gamma x_{ij} + \varepsilon_{ij}$$

where Y is the response of the block and treatment effects, μ is the population mean across treatments, α_i is the effect for being in treatment i, β_j is the effect for being in block j, x_{ij} is the corresponding value for the concomitant variable and the coefficient of γ is the sum of squares of error obtained when an analysis of variance is carried out on the x_{ij}, i is the treatment factor, =1,2,...6, j is the block factor, =1,2,...7. Since some trees were died during the study, it makes the design unbalanced. (Tree death was not due to the treatments but due to animal damages). Thus we used a linear model with blocks and treatments as fixed effects. Variables included annual growth of sample branch, height growth, root length and biomass, root rips, mycorrhizal infection points and foliar $\delta^{15}N$. Covariates were DBH (diameter at breast height), D_0 (diameter at 5cm above ground) and D (diameter at the lowest living branch). The analysis was performed using the JMP 8 (SAS Institute Inc. Cary, NC, USA) statistical package with the GLM for generalized linear models. Tukey's tests were used to compare means and P<=0.05 was considered as significance.

1.4 Results

1.4.1 General Temperature Changes

The soil temperature in S+ treatment went down to -5.25°C in about two weeks since the snow was shoveled at the end of January 2010 and kept below freezing point about four weeks longer than S- treatment (figure 2a). After snowmelt, the soil of S+ treatment was cooler than S- treatment until the end of growing season (figure 2a). Similarly, the soil temperature in M+ treatment was also lower than M- treatment throughout the entire experiment, except during snow season, in which the mean soil temperature in M+ is slightly higher than M- treatment (figure 2b). From April to August 2010, the amplitude of diurnal temperature variation in S- and M- treatments was 1.58°C and 2.46°C greater than that in S+ and M+ treatments, respectively (figure 3a, 3b).

1.4.2 Response of Black Spruce

As shown in table 1 and figure 4, the growth of stem diameter at 5cm above ground and stem volume growth of black spruce showed significantly higher in S- and M- treatments than in the control. While annual height growth of black spruce was significantly increased by M+ treatment, fertilization significantly increased the annual growth of sample branches of black spruce, as well as significantly higher $\delta^{15}N$ of needle in both spring and autumn. Roots growth, such as length, biomass and root tips, and root: shoot ratio didn't show much difference between treatments. The mycorrhizal infection points of roots weren't significantly affected by treatments, neither.

1.4.3 Response of Trembling Aspen

Trembling Aspen were less sensitive to the treatments. As shown in table 2 and figure 5, the growth of stem diameter at 5cm above ground showed significantly higher in S- and M- treatments than in the control, accompanied by significantly lower in M+ and F treatments than control. All treatments, except S+, showed significantly lower mycorrhizal infection points of roots than control. Other above- and underground assimilation, such as sample branch annual growth, stem volume growth, roots length and biomass growth and root tips, didn't show significant influence by treatments, as well as root:shoot ratio. δ^{15}N of foliage in both spring and autumn didn't have significant responses neither.

1.5 Discussion

Our results confirmed, not surprisingly, that snow cover and moss cover affect soil condition beneath importantly, which was similar to our previous study (Fréchette et al. 2011). Removal of snow (S-) or moss (M-) cover treatment accelerated soil warming in spring and kept the soil temperature higher than in the control (C), added snow (S+) or added moss (M+) cover treatments throughout the growing season (figure 2a, 2b). In addition, the period of frozen soil in S+ treatment was prolonged by about one more month than S- treatment in spring. Generally, black spruce responded more sensitively than trembling aspen to most of the treatments and we observed most reactions to the treatments aboveground. This may be due to the fact that aboveground variables are more easily measured and have smaller measurement errors. On the other hand some below-ground variables like the percentage of mycorrhizally infected roots were well constrained and had low measurement errors.

We hypothesized that fertilization would increase the aboveground production of both species. In our study, the two species responded differently to nutrient addition. For black spruce, fertilization significantly increased the growth rate of sample branches and the ^{15}N portion of needles (figure 4c, i, j). For trembling aspen, trees with fertilization had significantly low mycorrhizal infection points (figure 5f), which is consistent with other studies (Alexander and Fairley 1983, Sun 2007). However, we didn't observe any increase in the growth of stem diameter, stem volume, foliage, annual sample branches (aspen) or height (table 1 and 2), indicating that biomass allocation to stem, foliage and branch wasn't affected significantly by fertilization. In addition, roots growth and root: shoot ratio in our study didn't show any significant difference by fertilization either. Also, Domenicano et al. (2011) studied hybrid poplar in Quebec and found that nitrogen availability or form didn't affect biomass allocation between aboveground and belowground fractions. Weih and Karlsson (1999) reported that the growth response of mountain birch cannot be explained simply by soil temperature and nitrogen availability, but genetic determination and cold environment adaptation. In the light of our results, we suggest that acclimatation of trees, both physiology and morphology, did not yet adapt to new soil conditions, in agreement with (King 1999) where nitrogen availability and soil temperature didn't control biomass allocation of trembling aspen and genetic had strong effect on allometric patterns of growth. .

Trees with disturbance a reduction of snow (S-) and moss cover (M-) showed significantly higher growth of basal diameter and stem volume for black spruce and only significantly high basal diameter growth for trembling aspen (table 1 and 2; figure 4a,b; figure 5a). The warmer soil caused by S- and M- treatment may contribute to the increment of stem growth. The positive effect of warmer soil on plant growth has been demonstrated by several studies. Norway spruce seedlings in heated plots showed remarkably high stem volume growth compared to unheated plots (StrÖMgren and Linder 2002). The same experiment of Norway spruce with heated soil showed higher rates of light-saturated photosynthesis (Bergh and Linder 1999). In this study, removal of snow cover at the end of March raised the soil temperature rapidly in spring, and the soil temperature was warmer than added snow treatment (S+) throughout the subsequent growing season (figure 2). Delayed snowmelt could shorten the length of growing season and reproductive period of boreal forest and therefore decline the forest productivity (Vaganov et al. 1999, Cooper et al. 2011). However, our added snow treatment (S+) didn't distinguish the effect of deep soil frost from late snow thaw, therefore obscured the corresponding results. Furthermore, other biomass allocation, such as branch, foliage and roots, wasn't affected significantly between treatments. One possibility is that the seedlings may adapt to the relative low soil temperature prevailing in boreal forest; the other is that the development of seedling was more controlled by genetic than environmental factor such as fluctuant soil temperature.

Mycorrhizal infection points on roots of aspen were affected significantly by different treatments. Moss cover changes (M+ and M-), add snow cover (S+) and fertilization significantly lower the mycorrhizal infection points on roots. However, the means of mycorrhizal infection points on the roots of black spruce by different treatments were close to each other. The influence of fertilization on mycorrhizal infection points is consistent with (Alexander and Fairley 1983) where nitrogen fertilization reduced mycorrhizal infection on the roots of sitka spruce (*Picea sitchensis*). Removal of moss and snow cover impacted the soil condition that affects directly or indirectly on mycorrhizal colonization. Removal of snow cover left the bared soil directly to cold air in spring and resulted in repeated freeze-thawing cycles of soil, which may adversely affect the physical characters of mycorrhizal fungi (Tibbett and Cairney 2007). It has been reported that ectomycorrhizal fungi, which associate with spruce and aspen (Marx 1975), establish directly below the moss cover and connect the host tree roots to the covering moss carpets by mycelial mats, so as to transfer nutrient from the moss shoot to the ectomycorrhizal roots of host trees (Carleton and Read 1991). Moreover, mosses contain abundant N-fixing cyanobacteria, which make mosses an important source of nitrogen (DeLuca et al. 2002). Thus, removal of moss cover completely disturbed this process and negatively affected the mycorrhizal colonization and nutrient transfer. Nevertheless, added moss cover treatment may also adversely impact mycorrhizal fungi since the lower soil temperature and high water table under thick moss cover are unfavorable to the development of aerobic ectomycorrhizal fungi (Marks 1973). The lower number of mycorrhizal infection points of trembling aspen, induced by changes of moss cover and removal of snow cover, indicated that aspen might be more vulnerable than black spruce in the context of climate change. The rate of mycorrhizal infection in black spruce on the other hand was remarkably stable (within a few percent of 11.22%), effects of the treatments on the infection of spruce were, therefore, likely to be small and not ecologically important.

$\delta^{15}N$ of foliage didn't vary much between treatments, except that fertilization increased foliar $\delta^{15}N$ of black spruce. Mycorrhizal fungi create ^{15}N-depleted organic nitrogen compounds and transfer them to the roots of host plant (Hobbie et al. 2008), depleting the ^{15}N of their host plan. Thus, the unfavorable condition to mycorrhizal fungi mentioned above may explain the small change of foliar $\delta^{15}N$, and longer term effects on mycorrhizal fungi could exacerbate N cycling of trees. The ambiguous results of fine roots (biomass, length and tips) may due to sampling procedure, since the effects of treatment were not significant and the data was quite noisy.

1.6 Conclusion

Snow and moss cover are recognized as very important factors in the boreal ecosystem since they play a key role in the thermal insulation of the soil. Snow cover can protect soil from extreme low air temperature and keep soil temperature around 0°C during winter. Moss cover act as a physical barrier covering the forest floor (Hinzman et al., 1991), so that it can absorb incoming solar energy for its own photosynthesis (Miller et al., 1980) and keep the soil temperature underneath lower. Thus, rapid climate warming predicted would affect the two important soil insulators of boreal forest, cause soil temperature variation and influence tree growth. In our experiment, reduction of snow and moss cover had positive effect on basal diameter growth of both species, indicated that low soil temperature restricted tree growth and delayed snowmelt had adverse effect on trees by shortening growing season, delaying onset of photosynthesis and sapflow, limiting nutrient and water availability. Fertilization and soil temperature changes didn't have much effect on the aboveground and belowground biomass allocation of both species, indicating that trees growth, at least in our study site, might be more attributed to genetic determination, rather than environmental influences (e.g. soil temperature variation, nitrogen availability).

Mycorrhizal fungi were also affected by changes of soil covers, mainly on trembling aspen. This may indicate that trembling aspen could be more vulnerable to the possible changes of soil insulators in the context of climate change.

1.7 Acknowledgements

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1.8 References

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1.9 Figures

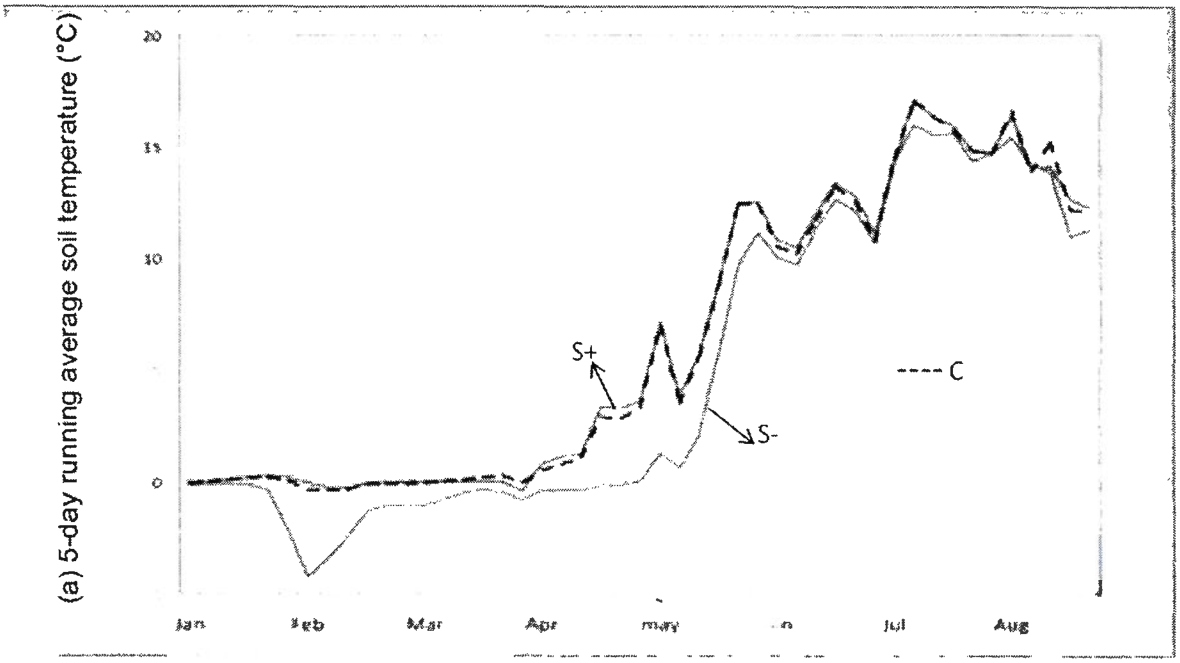


Figure 2a

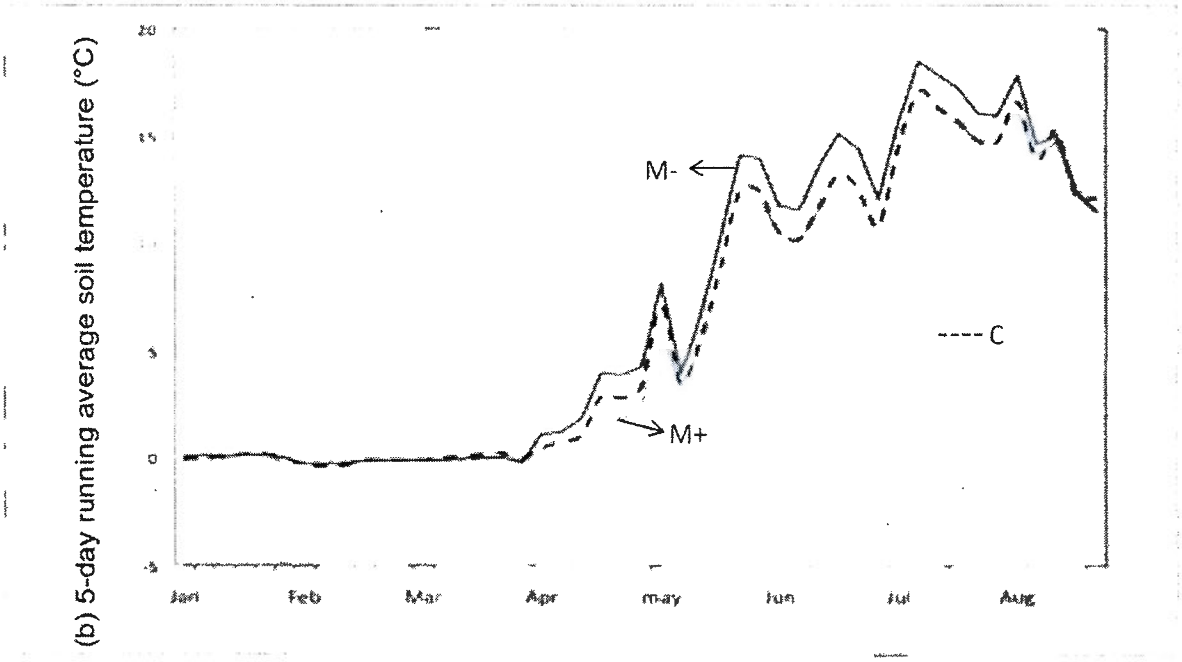


Figure 2b

Figure 2: 5-day running average soil temperature at a depth of 10cm in (a) additional snow treatment (S+, blue line), snow removal treatment (S-, red line), control (dashed black line); (b) additional moss treatment (M+, orange line), moss removal treatment (M-, green line), control (dashed black line).

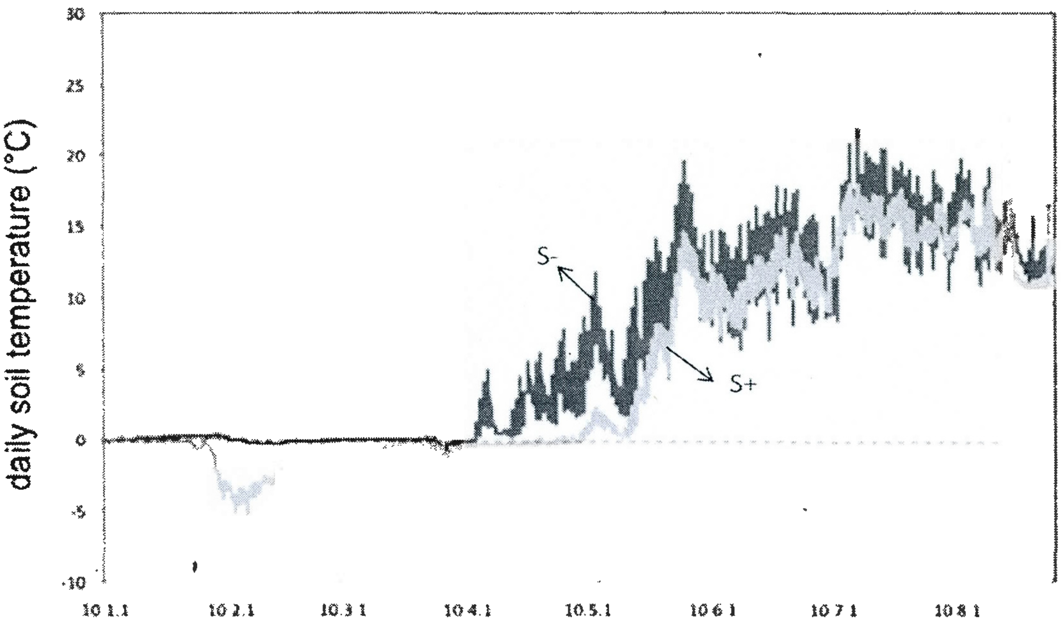


Figure 3a

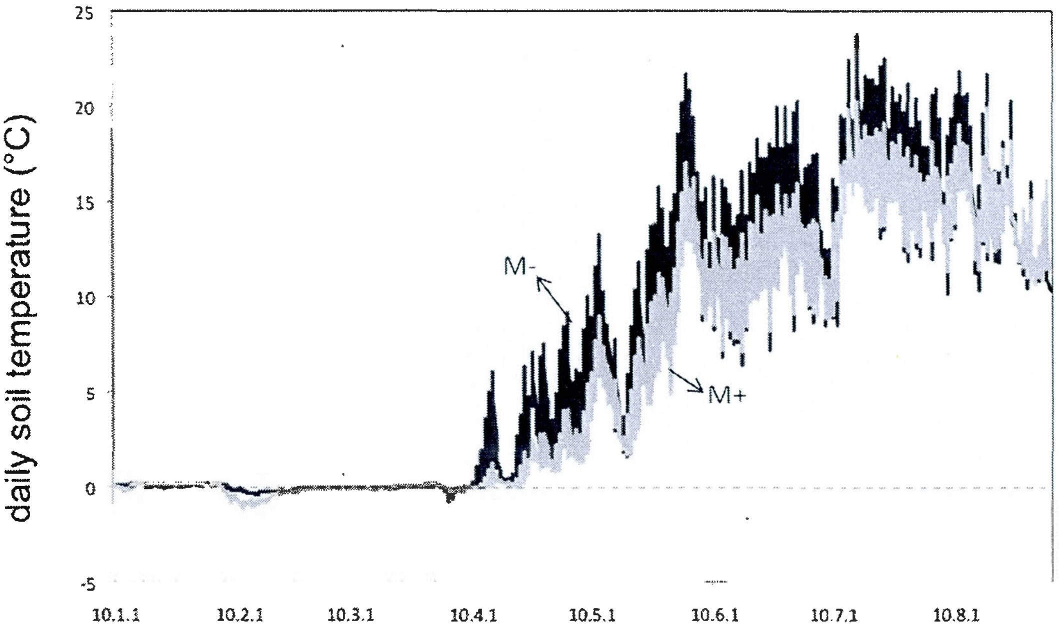
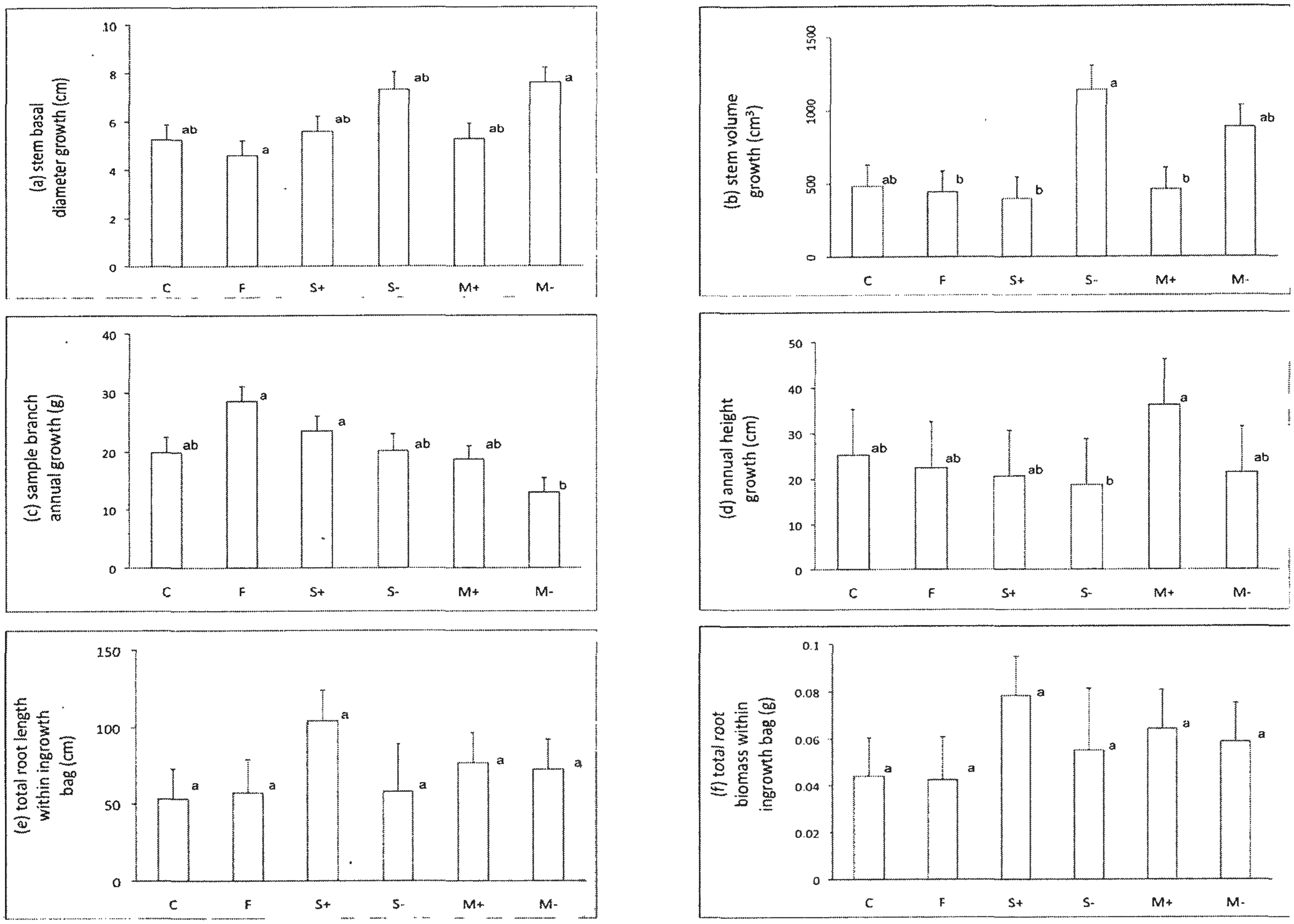


Figure 3b

Figure 3: Amplitude of diurnal temperature variation in additional snow treatment (S+, light red), snow removal treatment (S-, dark red), additional moss treatment (M+, light blue), moss removal treatment (M-, dark blue), at a soil depth of 10cm, from January to August 2010.


(a) stem basal diameter growth (cm)
0
2
4
6
8
10
C
F
S+
S-
M+
M-
ab
a
ab
ab
ab
a
(b) stem volume growth (cm³)
0
500
1000
1500
C
F
S+
S-
M+
M-
ab
b
b
a
b
ab
(c) sample branch annual growth (g)
0
10
20
30
40
C
F
S+
S-
M+
M-
ab
a
a
ab
ab
b
(d) annual height growth (cm)
0
10
20
30
40
50
C
F
S+
S-
M+
M-
ab
ab
ab
b
a
ab
(e) total root length within ingrowth bag (cm)
0
50
100
150
C
F
S+
S-
M+
M-
a
a
a
a
a
a
(f) total root biomass within ingrowth bag (g)
0
0.02
0.04
0.06
0.08
0.1
C
F
S+
S-
M+
M-
a
a
a
a
a
a

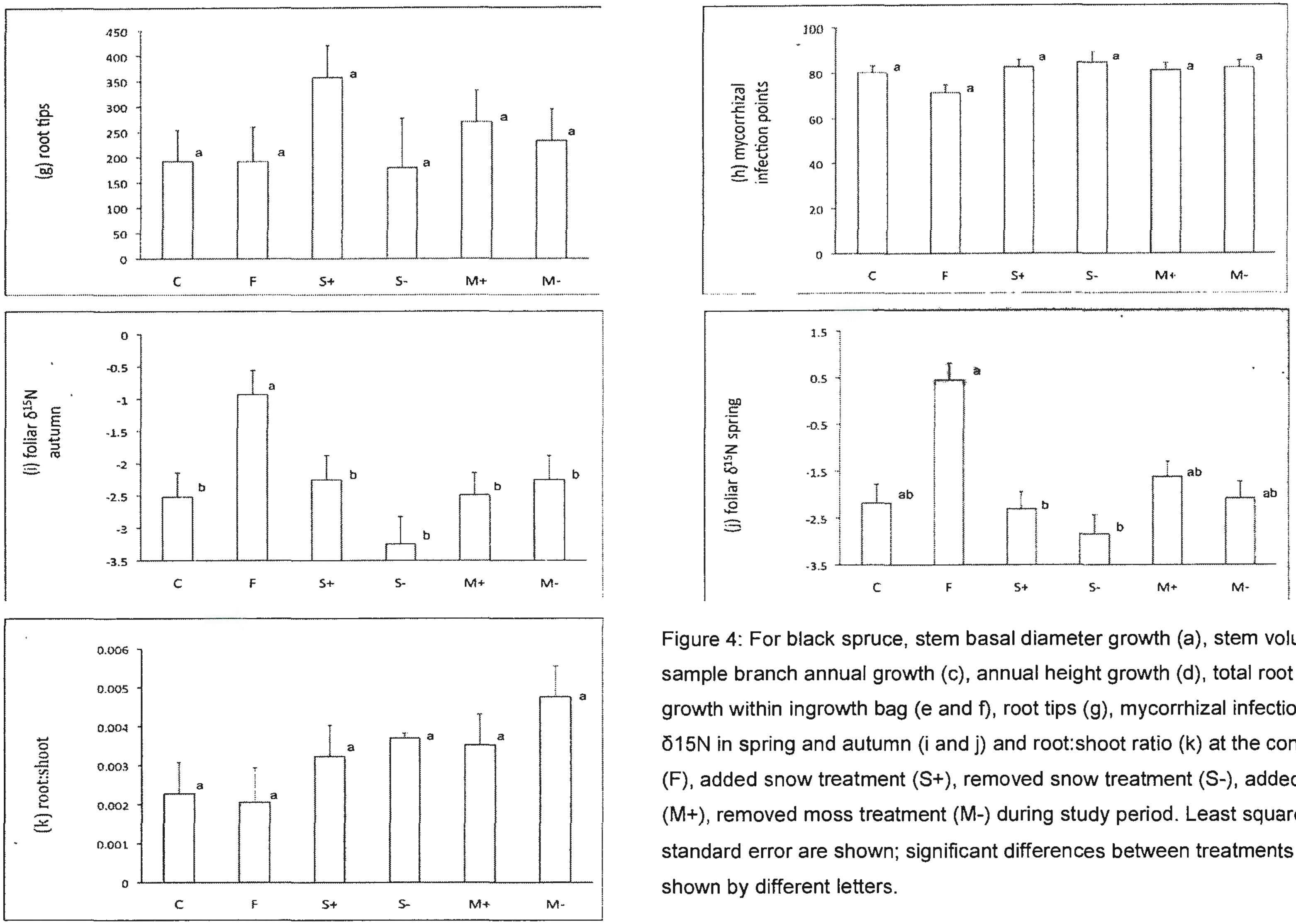
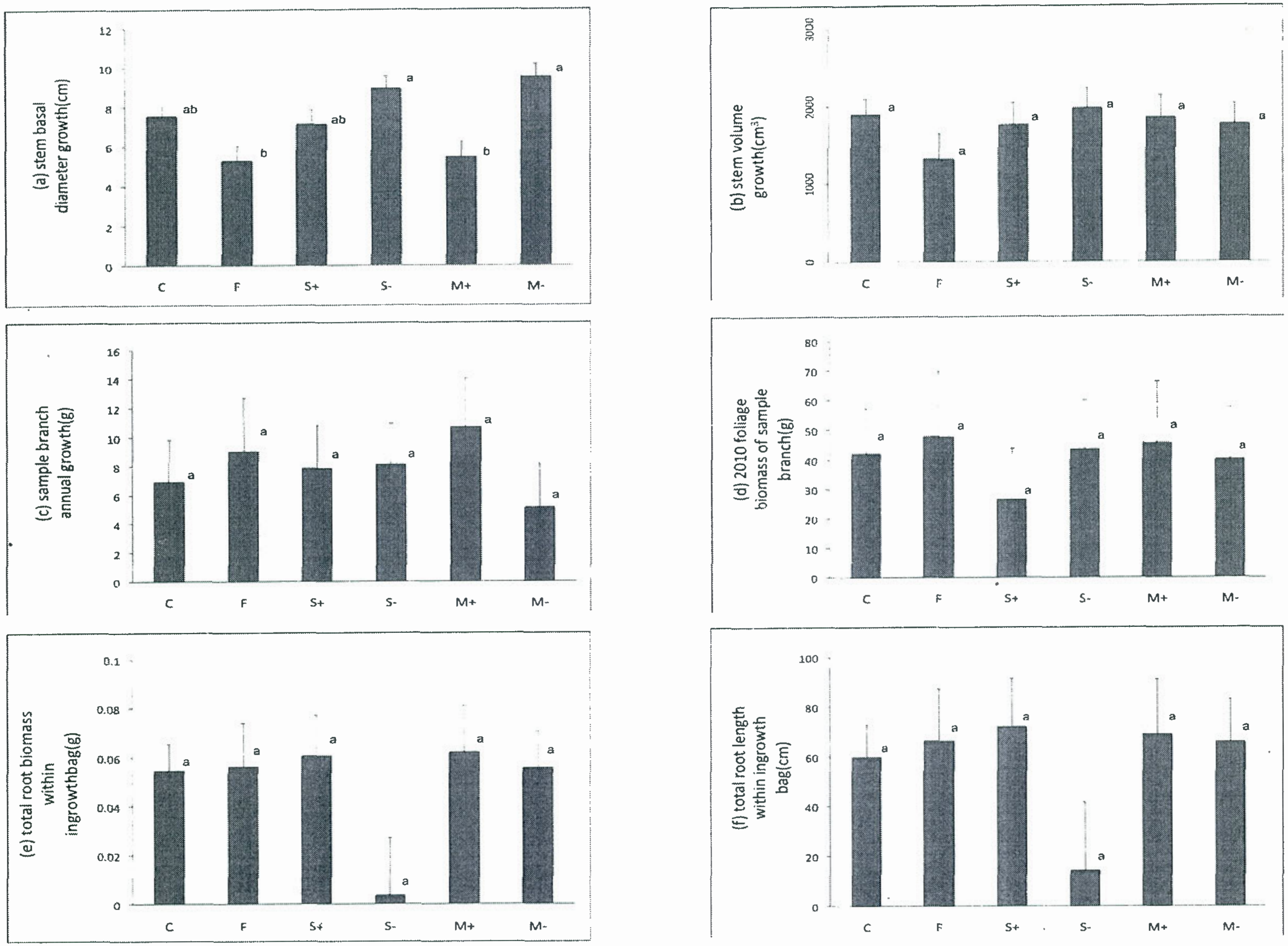
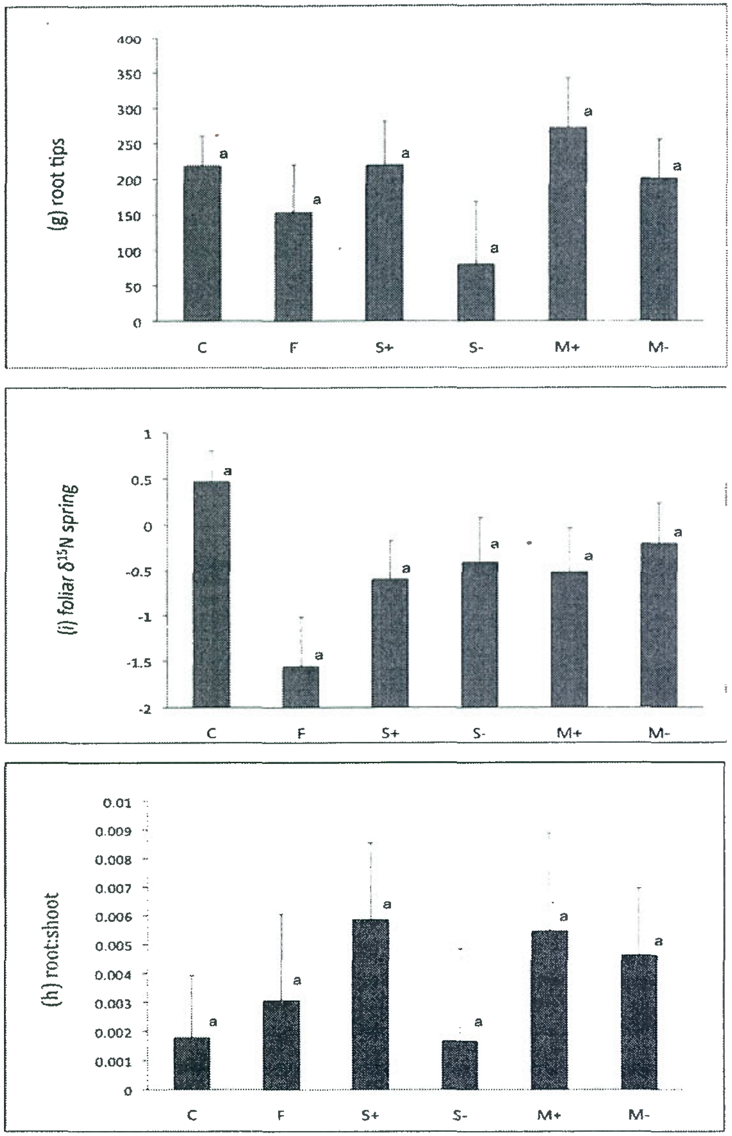


Figure 4: For black spruce, stem basal diameter growth (a), stem volume growth (b), sample branch annual growth (c), annual height growth (d), total root length and biomass growth within ingrowth bag (e and f), root tips (g), mycorrhizal infection points (h), foliar δ15N in spring and autumn (i and j) and root:shoot ratio (k) at the control (C), fertilization (F), added snow treatment (S+), removed snow treatment (S-), added moss treatment (M+), removed moss treatment (M-) during study period. Least square mean with standard error are shown; significant differences between treatments ($P \leq 0.05$) are shown by different letters.


(a) stem basal diameter growth(cm)
0
2
4
6
8
10
12
C
F
S+
S-
M+
M-
ab
b
ab
a
b
a
(b) stem volume growth(cm³)
0
1000
2000
3000
C
F
S+
S-
M+
M-
a
a
a
a
a
a
(c) sample branch annual growth(g)
0
2
4
6
8
10
12
14
16
C
F
S+
S-
M+
M-
a
a
a
a
a
a
(d) 2010 foliage biomass of sample branch(g)
0
10
20
30
40
50
60
70
80
C
F
S+
S-
M+
M-
a
a
a
a
a
a
(e) total root biomass within ingrowthbag(g)
0
0.02
0.04
0.06
0.08
0.1
C
F
S+
S-
M+
M-
a
a
a
a
a
a
(f) total root length within ingrowth bag(cm)
0
20
40
60
80
100
C
F
S+
S-
M+
M-
a
a
a
a
a
a



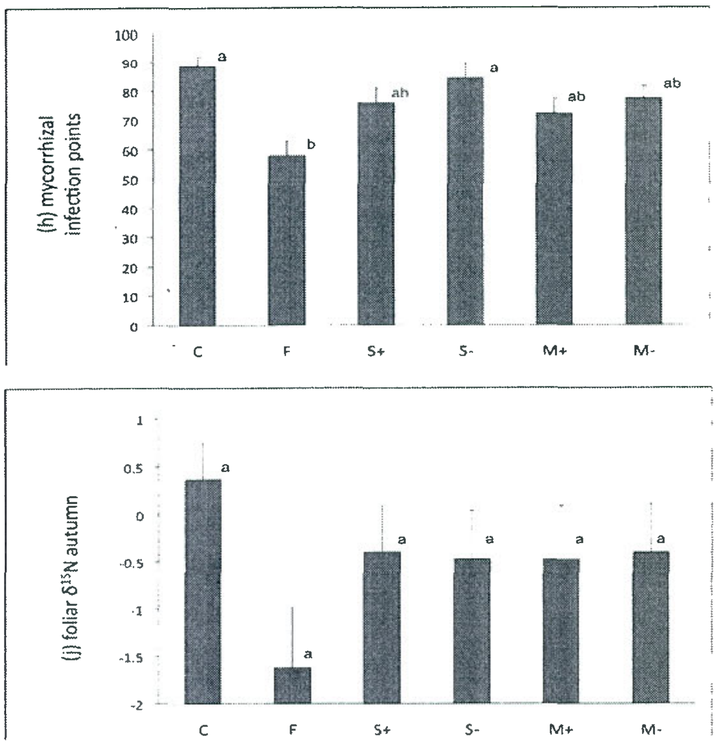


Figure 5: For trembling aspen, stem basal diameter growth (a), stem volume growth (b), sample branch annual growth (c), 2010 foliage biomass of sample branch (d), total root length and biomass growth within ingrowth bag (e and f), root tips (g), mycorrhizal infection points (h), foliar δ15N in spring and autumn (i and j) and root:shoot ratio (k) at the control (C), fertilization (F), added snow treatment (S+), removed snow treatment (S-), added moss treatment (M+), removed moss treatment (M-) during study period. Least square mean with standard error are shown; significant differences between treatments ($P \leq 0.05$) are shown by different letters.

1.10 Tables

Variable	treatment						SS model	SS	F-value	P-value	covariate
(Black Spruce)	C	F	S+	S-	M+	M-					
annual height growth	25.3617ab	22.5250ab	20.5699ab	18.6697b	36.1116a	21.3840ab	3322.1662	1142.0837	2.8905	0.0374*	DBH
stem diameter growth	5.2596ab	4.6093b	5.6072ab	7.3343ab	5.2861ab	7.6108a	244.9148	41.5131	3.7895	0.0126*	DBH
sample branch annual biomass growth	19.9307ab	28.5608a	23.4977a	20.1809ab	18.7157ab	12.9785b	4653.8216	1526.5907	4.199	0.0025*	D_0
stem volume growth	484.2632ab	443.9143b	398.2593b	1142.0768a	461.1070b	889.4342ab	14736465	2474260	4.1935	0.0079*	DBH
total root length within ingrowthbag	53.2515a	57.1507a	104.3831a	58.0128a	76.8175a	72.5087a	16613.077	9938.4687	0.8952	0.5041	D_0
total root biomass within ingrowthbag	0.0440a	0.0425a	0.0783a	0.0552a	0.0643a	0.0579a	0.011	0.0049	0.6352	0.6755	D_0
root tips	191.8931a	191.2885a	357.1126a	179.3901a	270.1201a	232.9446a	252510.2	109819.6	1.0879	0.3987	D_0
mycorrhizal infection points of roots	80.2980a	71.5088a	82.8373a	84.7108a	81.3877a	82.5478a	1860.3401	475.8754	1.8291	0.1552	D_0
δ^{15}N spring	-2.1811b	0.4436a	-2.3090b	-2.8540b	-1.6259b	-2.0840b	67.6732	35.6725	9.4821	<0.0001*	D_0
δ^{15}N autumn	-2.5218ab	-0.9343a	-3.2821b	-3.2467b	-2.4877ab	-2.2519ab	58.7379	19.8098	4.9425	0.0032*	D_0
root:shoot	0.00227a	0.00206a	0.00323a	0.00369a	0.00352a	0.00476a	0.000036	0.000026	1.452	0.2516	D_0

Table1: For black spruce, stem basal diameter growth, stem volume growth, sample branch annual growth, annual height growth, total root length and biomass growth within ingrowth bag, root tips, mycorrhizal infection points and foliar δ15N in spring and autumn at the control (C), fertilization (F), added snow treatment (S+), removed snow treatment (S-), added moss treatment (M+), removed moss treatment (M-) during study period. Covariates are DBH and D0 (Diameter at 5cm above ground). Within row, significant differences between treatments ($P \le 0.05$) are shown by different letters.

Variable	treatment						SS model	SS	F-value	P-value	covariate
(Trembling Aspen)	C	F	S+	S-	M+	M-					
2010 foliage biomass of sample branch	42.1018a	47.7489a	26.5066a	43.4319a	45.6399a	40.0607a	21910.198	1227.838	0.1994	0.9583	D
stem diameter growth	7.5493ab	5.2865b	7.1321ab	8.9378a	5.4627b	9.5277a	347.0872	43.418	4.9798	0.0236*	D
sample branch annual biomass growth	6.9202a	9.0270a	7.8724a	8.1197a	10.6557a	5.1326a	1470.9472	130.5148	0.4116	0.8381	D_0
stem volume growth	1898.4864a	1321.1548a	1761.4726a	1978.4050a	1854.0934a	1771.7242a	70414095	874851	0.6241	0.6836	D
total root length within ingrowthbag	59.9232a	66.4332a	72.0547a	14.1872a	69.1081a	65.9746a	14171.611	4356.264	0.7445	0.6041	DBH
total root biomass within ingrowthbag	0.0544a	0.0560a	0.0605a	0.0034a	0.0620a	0.0555a	0.0142	0.0045	1.0501	0.4302	DBH
root tips	218.7501a	153.4446a	219.3101a	80.0829a	271.6823a	200.1417a	166058.99	50681.29	0.8473	0.5404	DBH
mycorrhizal infection points of roots	88.5821a	57.9345b	75.9830ab	84.4164a	72.3873ab	77.5189ab	2910.8569	1373.236	4.6434	0.0137*	DBH
δ^{15}N spring	0.4675a	-1.5584a	-0.6046a	-0.4156a	-0.5233a	-0.2043a	36.659	8.6556	2.186	0.104	DBH
δ^{15}N autumn	0.3679a	-1.6224a	-0.3957a	-0.4697a	-0.4751a	-0.4026a	38.7721	7.87	1.494	0.2436	DBH
root:shoot	0.00178a	0.00306a	0.00586a	0.00166a	0.00545a	0.00461a	0.000326	0.0000591	0.5364	0.7454	D_0

Table2: For trembling aspen, 2010 foliage biomass of sample branch, stem basal diameter growth, stem volume growth, sample branch annual growth, total root length and biomass growth within ingrowth bag, root tips, mycorrhizal infection points and foliar δ^{15}N in spring and autumn at the control (C), fertilization (F), added snow treatment (S+), removed snow treatment (S-), added moss treatment (M+), removed moss treatment (M-) during study period. Covariates are DBH, D_0 (diameter at 5cm above ground) and D (diameter below the lowest living branch). Within row, significant differences between treatments ($P \leq 0.05$) are shown by different letters.

General Conclusion

Paludification and winter precipitation changes are two important ecological aspects affected strongly by climate change and in turn directly affect tree growth in boreal forests of eastern Canada. However, winter processes have been neglected for climate change research. In response to human-induced global change, high latitude ecosystems are predicted to warm significantly during this century (ACIA 2004) with more winter precipitation coming as snowfall. Deeper snow cover may lead to delayed snowmelt in spring which can delay the onset of growing season; or due to climate warming, early snowmelt can induce to frequent freeze-thaw cycles of soil which adversely affect tree growth. Due to the low to moderate slopes and fine-textured soils, Clay Belt of Ontario and Quebec is prone to paludification (Bergeron et al. 2007), which is mainly caused by organic matter accumulation and accelerated by Sphagnum moss development (Fenton et al. 2005). On the other hand, the increase of temperature and evapotranspiration caused by climate warming exceeds the increase of precipitation (Girardin and Mudelsee 2008), less water availability would lead to more activity of forest fire, these conditions are unfavorable to the establishment and expansion of mosses (Lavoie et al. 2005). The objective of this study was to investigate the impact of soil insulators changes on the above- and underground growth of the two key species in the eastern Canadian boreal forest, black spruce (*Picea mariana* (Mill.) BSP.) and trembling aspen (*Populus tremuloides* Michx.), using different treatments to simulate possible changes of snow cover and moss cover that would cause soil temperature variation.

S+ treatment kept soil temperature below freezing point for about one month longer than S- treatment. S- and M- treatment accelerated soil thawing in spring and induced soil temperature higher than control, S+ and M+ treatments during the subsequent growing season. Both species with S- and M- treatment showed significant higher basal diameter growth and stem volume growth (only spruce), indicating that warmer soil positively affected tree growth. Nevertheless, soil temperature didn't show any significant influence on branches, foliage and roots growth in both species. Fertilization had some significant influences on both species: increment of sample branches annual growth and ^{15}N of needles in black spruce, and decrease of mycorrhizal infection points on the roots of trembling aspen. However, other above and belowground biomass allocation, or root:shoot ratio, wasn't affected significantly by fertilization. The non-significant influence of fertilization and soil temperature on the growth and allometric pattern of trees suggested that the responses of trees to different treatments might be attributed to genetic determination and adaptation to cold soil and limited nitrogen availability, rather environmental factors such as soil temperature and nutrient addition. Furthermore, although black spruce showed more sensitivity to most of the treatments, the significant low mycorrhizal infection points on the roots of aspen with S-, M+ and M- treatments.

According to our results, in the context of climate change, black spruce may be affected stronger by the changes of snow cover and moss cover that bring variations of soil temperature and nutrient transfers. Accelerated snow thawing in spring and less moss cover may increase the basal diameter and volume growth of black spruce, while effects on biomass allocation may be more attributed to genetic determination. The different soil temperature induced by different treatments, and fertilization, appeared of little importance for trembling aspen. However, the low mycorrhizal infection points of trembling aspen indicated that this species may be more vulnerable to the possible future climate change, which may have profound influence on composition changes of eastern Canadian boreal forest.

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