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EFFECT OF CLIMATE CHANGE ON BOREAL FOREST SOILS: WILL SOIL CONDITIONS LIMIT THE ADAPTATION OF BOREAL ECOSYSTEMS TO CLIMATE CHANGE?

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ABSTRACT

Climate warming is expected to have particularly pronounced effects on boreal ecosystems. The functioning of the boreal forest species and their capacity to adapt to environmental changes appears to depend on soils condition. Climatic changes in boreal forest can alter current forest species composition and adaptation by changing soil conditions, moisture and temperature regimes, soil microbial activity and soil respiration. In this paper, we review various warming experiment studies that have been conducted to directly assess the effect of climatic warming on soil conditions. Results demonstrated that across a variety of experimental methodologies in boreal ecosystems, warming manipulations significantly increases rates of soil respiration, nitrogen mineralization often followed by increases in soil nutrient availability and decrease in microbial abundance. Despite these climatic change-induced increases in soil nutrient availability, most recent studies reported little or no change in soil organic matter decomposition. However, responses of decomposition to increased soil temperatures were highly variable and often site specific and were found to strongly depend on soil moisture. Thus, the prediction that global warming may increase decomposition rate must be considered in combination with its impact on soil moisture which appears to be a limiting factor.

Many studies have also provided evidence that local adaptation or acclimation to current climatic conditions is occurring, especially in unfragmented forests. In this paper, we argue that soil in unfragmented boreal forest is likely to be important for continued ecosystem stability in the context of climate change by delaying freeze-up in autumn and snow melt in spring.

The most commonly cited response of boreal forest species to global warming is a northward migration to track the climate and soil conditions (e.g. temperature and moisture) to which they are adapted to. Yet, there are some constraints that may influence this kind of adaptation such as water availability, genetic adaptation, changes in fire regimes, decomposers adaptation and paludification. In this study, we examined potential effect of climatic warming on future (period up to 2100) paludification changes through three different scenarios (increased temperature associated to increased precipitation (S1), increased temperature combined to decreased precipitation (2) and increased temperature with unchanged precipitation (S3)) in the Clay Belt lowland region. Precipitation was found to play a major role in the potential paludification response. For the 21st century, an increase in precipitations (~15-20%) will likely increase peat accumulation in boreal forest stands prone to paludification and facilitate forested peatlands expansion into upland forest while a diminution or unchanged precipitation combined to an increase in temperature (~4.7 °C) will probably favour succession of forested peatlands to upland boreal forests. Given the expected climate change in the Clay Belt lowland region, scenario 2 is less probable. For the more probable scenarios 1 and 3, summer clear-cut harvesting and prescribed burning followed by appropriate site preparation that removes the thick organic layers will have the potential to reduce or reverse paludification and consequently increase site productivity

Keywords: *Global boreal forest, boreal soils, climate change, adaptation, soil processes, temperature, soil warming experiments, precipitations, soil moisture, organic matter soils, decomposition rates, permafrost, soil respiration, mineralization, paludification, productivity.*

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1. INTRODUCTION

The boreal forest biome consists of a broad complex of forested and partially-forested ecosystems which form a circumpolar belt through northern Eurasia and North America (Fig.1) and account for about one-third of this planet's total forest area (Apps et al. 1993). Boreal forests cover about 9% (13.7 x 10^6 km^2) of the land between parallels 45˚ and 75˚ north (Czimczik et al. 2005) and consist of a mosaic of forests and wetlands reflecting adaptation of different plant species to harsh climatic conditions and past history of disturbances. Boreal forests have been the subject of significant research in recent years due to their link to cycle of global greenhouse gas concentrations (CO_2, CH_4) in the atmosphere (Gorham 1991; Glooschenko et al. 1994). They constitute large carbon reservoirs, which might play an important role in the feedback between the global carbon cycle and climate change (Dunn et al. 2007).

Structure, health, productivity and the distribution of tree species and forest ecosystems across boreal landscapes are mainly controlled by climate, soil conditions, relief and biota (Van Cleve and Powers 1995). Current climate models predict that changes in temperature, commonly termed global warming, and precipitations (regional decrease or increase) which expected to be more pronounced in the boreal regions (Gibbard et al. 2005; Houghton 2005; Wickland and Neff 2008), will result in a spatial redistribution of major forest types and potential loss of habitat for some important boreal species (Hamann and Wang 2006). For example, low relief lowland areas may lead to creation of peat-lands and favor wetland species over other forest species (Chapin et al. 2004). On the other hand, in areas with adequate drainage, forest may migrate northward into areas occupied currently by tundra (Reichstein 2007) if soil moisture does not limit tree growth (Chapin et al. 2004). In addition, under conditions of continued warming, drier soils may lead to replacement of certain forest species with steppe communities (Chapin et al. 2004).

The response of boreal forests to changes in temperature and precipitation is related to complex interactions between soil, nutrient availability, water table depth, soil biota and root respiration (Wurzburger et al. 2004). For instance, increasing temperature is likely to increase soil organic matter decomposition rates in warm dry conditions which may make nutrients more readily mineralized and available to plants (Kirschbaum 2000b). A better understanding of the effects of climate change on boreal forest soils is critically important, since the functioning of boreal forest tree species and their capacity to adapt to environmental changes appear to depend on soil conditions. The question that is addressed here is whether or not soil conditions (e.g. temperature, moisture, nutrients, and soil microorganisms) will limit the adaptation of boreal plant species to climate change? Consistent with the definition employed by Trainor et al. (2009), adaptation is defined here as an adjustment or acclimation in ecological systems in response to actual or expected climatic stimuli and their effects or impacts. For the purpose of this work, the term adaptation does not refer to any genotypic changes.

In this review, we synthesize results from reported studies in an attempt to understand the effects of climate changes on global boreal forest soils. We then analyzed studies showing modification of soil conditions as result of global warming and discuss the potential of boreal forest species to adapt to soil conditions under climate warming We will also discuss some processes (e.g. formation-paludification, moisture dynamic etc.) that will likely moderate or constrain the ability of boreal forest species to adapt to changing soil conditions. The potential effect of climate change on paludification process will be discussed through different climatic scenarios. For the purpose of this synthesis, we defined the study area as the circumpolar boreal forest that stretch mainly across Sweden, Finland, Norway, Russia, Alaska and northern Canada (Fig. 1).

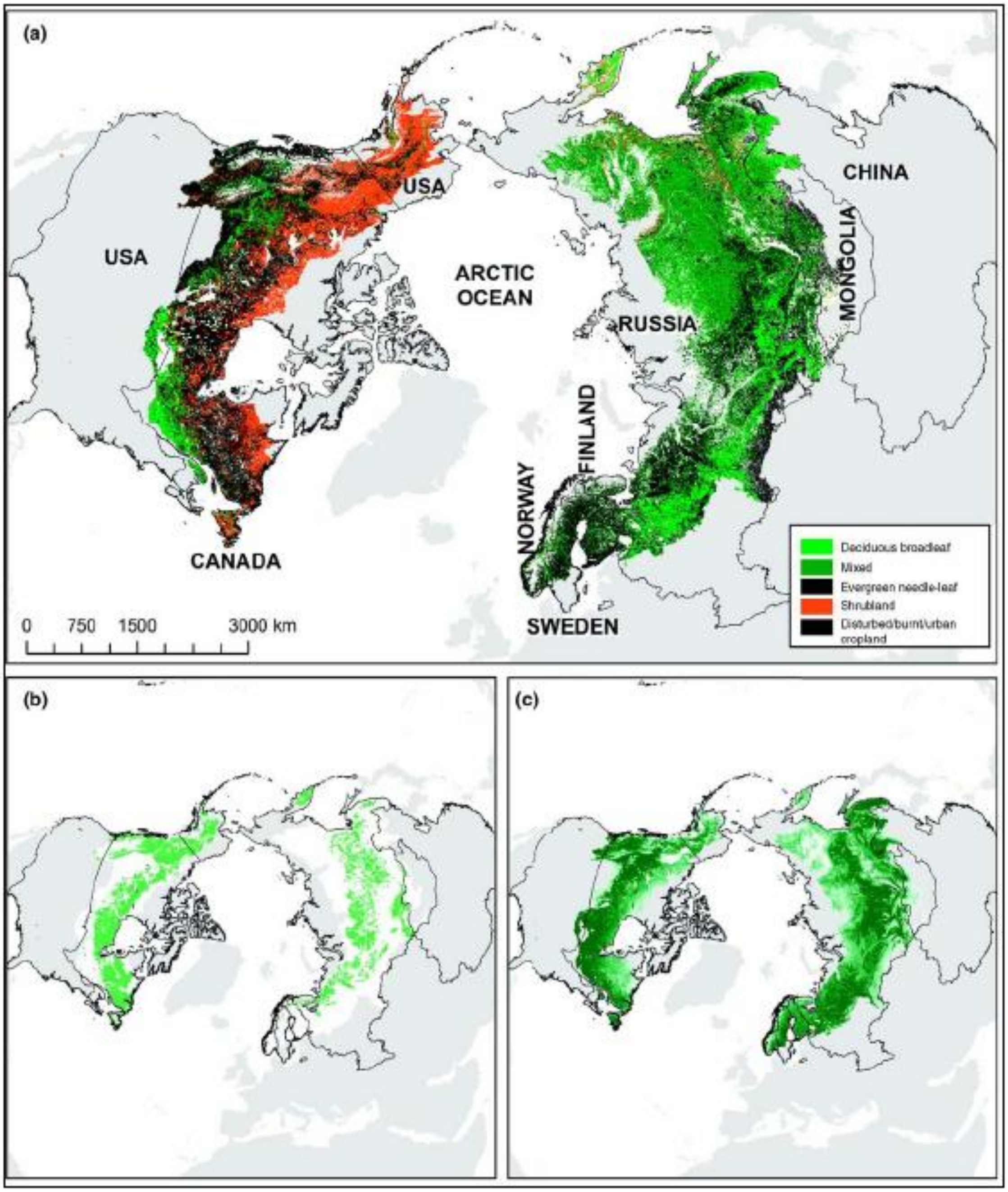

Fig. 1. Map of global extent and major classification of boreal forests (a), area of unfragmented boreal forests (b), and tree canopy density (c) (from Bradshaw et al. 2009).

2. BOREAL FOREST SOILS

Boreal forests contain substantial amounts of organic carbon, which have been accumulating since the last deglaciation (e.g. the retreat of the Laurentide ice sheet in North America, 6000 years ago, Hawkins 2004). These soils represent one-third of the world's soil organic carbon and are characterized by relatively cool temperatures that limit soil microorganism activity and therefore decomposition rates (Gorham 1991). Organic carbon plays a major role in nutrient cycling; as result, the characteristics and quantity of organic carbon in soils both reflect and control soil development and ultimately the productivity of boreal ecosystem. Boreal forests also have an acidic upper soil layer, low evaporation and an often wet soil conditions which tend to limit nutrient cycling (Bonan and Shugart 1989).

In boreal forests, soil forming processes such as organic matter accumulation, leaching, gleying, podzolization, and clay mineral transformations can be found. Among these, podozilation is a major soil forming process (Moore 1978). Podzols are therefore the typical soils of boreal forests (Stützer 1999). Podzolisation is a complex process (or number of sub-processes) in which organic material and soluble minerals (commonly Fe and Al) are leached from upper horizons (A and E) to lower B horizon (B) (Lundström et al. 2000). A detailed description of Podzolisation processes are reviewed in (Lundström et al. 2000; Sauer et al. 2007).

Boreal forest soils are generally young and developed on glacial deposits that vary from glacial till to thick sediments. The composition of boreal soils commonly ranged from sand, loamy sand, and sandy loam soils (typically moderately acid to neutral) to silty loam and clay loams (heavier soils). Boreal forests that occur over bedrock are often of similar bedrock origin (e.g. granitic) and characterized by shallow organic soils or more humus.

Seibert et al. (2007) indicated that the influence of topography on boreal soil properties is more important than other soil forming factors such as time or parent material. For instance, the flat topography (and thus low slopes) in the two major peatlands in the world (the Russian West Siberian Plain and the Canadian Hudson-Bay - James Bay Lowlands) illustrate the significance of this factor (Lavoie et al. 2005a). This leads to the important inference that such flat topography promotes the accumulation of organic matters, forming a thick forest floor layer in these regions.

Coniferous trees are widespread in the global boreal forest. Black spruce (*Picea mariana* (Mill) BSP), for instance, is one of the dominant tree species of the boreal forests of North America (O'Connell et al. 2003). Black spruce forests occupy both upland and lowland peat bogs sites and are well adapted to high soil moisture levels and cold, poorly aerated peat soils with low nutrient availability (Roy et al. 1999). These forests generate litter that is relatively resistant to decomposition processes and that promotes, in the absence of severe fire, the formation of a thick forest floor layer dominated by feather moss and sphagnum that immobilizes nutrients (Oechel and Van Cleve 1986).

In the context of global climate change, black spruce forests are important because of the substantial quantity of carbon accumulated in their soils, the occurrence of permafrost, and the tight relationship between the black spruce forest type and fire disturbance (e.g., Johnstone and Kasischke 2005; Vogel et al. 2005).

The expected climatic change in boreal forests (IPCC 2007) may accelerate decomposition rate of organic matter (Goulden et al. 1998; Serreze et al. 2000; Wickland and Neff 2008), increase soil moisture (Akinremi et al. 1999), soil temperatures (Osterkamp and Romanovsky 1999), water balance (Oechel et al. 1998), reduce the duration of snow cover (Beniston 1997), degrade permafrost (Osterkamp and Romanovsky 1999; Sazonova et al. 2004; Zhang et al. 2005) and increase the frequency of wildfires (Flannigan et al. 2005; Gillett et al. 2004). Collectively, all these effects may raise the release of carbon stored in boreal soils and have a significant positive feedback on global warming by rising atmospheric CO_2, and CH_4 (McGuire et al. 2001; Keyser et al. 2000). However, the loss of organic carbon caused by these positive feedbacks may be partially or entirely compensated by the gain in organic carbon stocks as result of the increased productivity or changes in the soil conditions that could include both wetting and drying trends (Wickland and Neff 2008).

There is no consensus about how the soil horizons are coded in different studies (e.g. Czimczik et al. 2005; Waldrop and Harden 2008). In general, one cannot expect to find standardized nomenclature because the boreal eco-region covers many countries that have their own soil classification. However, several studies from North America used different nomenclatures and occasionally, soil layers descriptions were almost similar. Table 1 provides examples of soil profile descriptions from Harden et al. (2006) and Waldrop and Harden (2008). Both classification are based on a simple nomenclature and separated soils to different horizons. In this paper we use Waldrop and Harden's (2008) description of soil horizons which appears to better reflect soil decomposition processes.

Table 1. Example of descriptions of boreal forest soil profiles. Data are from Harden et al. (2006) and Waldrop and Harden (2008).

Reference	Horizons	Important features
Harden et al. (2006)	LN	Lichen
	L	Live moss
	D	Dead moss, more moss than roots
	F	Fbric organics: more roots and amorphous material than moss
	M	Mmesic or moderately decomposed organics: amorphous organics
	H	Humic or highly decomposed organics: amorphous, unrecognizable organics
Waldrop & Harden (2008)	L/D	Live or dead moss
	O	Organic horizon: composed of slightly decomposed organic materiel mostly moss and rots
	A	Mineral horizon: typically a brown silt loam, sometimes grading into sandy loam or loam, occasionally with charcoal and/or rocks

3. EFFECT OF CLIMATE WARMING ON BOREAL SOIL PROCESSES

The Intergovernmental Panel on Climate Change (IPCC 2007) has arrived to the conclusion that climate change is no longer a subject for debate. It manifests its presence in many ways including increased temperature (generally warming) changes in precipitations trends and seasonality. Soil warming in boreal regions has the potential to create a very large positive feedback in the global cycle of carbon (Goulden et al. 1998).

Domisch et al. (2006) reported that soil temperature is a major factor affecting organic matter decomposition and consequently, global warming may accelerate decomposition processes. Other studies have reported that the rates of decomposition are directly linked to temperature and moisture or nutrient availability (Aerts 1997; Agren et al. 2001, Liski et al. 2003) and indirectly to substrate quality (Aerts 1997; Shaw and Harte 2001).

The effects of warmer climate on soil organic processes in cold biomes (from high latitude or high altitudes) have been the subject of many studies with a variety of substrates and under a variety of conditions (e.g. Aerts 1997; Agren et al. 2001; Liski et al. 2003; Van Cleve et al. (1990), Peterjohn et al. (1993, 1994), McHale and Mitchell (1996); Pajari (1995); Rustad and Fernandez (1998); Robinson et al. (1995). Yet, these studies have come to different conclusions regarding the effects of warming on important ecological processes (e.g. decomposition and mineralization rates, soil respiration and soil moistures). Responses to soil warming varied in the treated ecosystems (e.g. cold biomes as temperate) as reviewed by Zhang et al 2008, Aerts (2006) and Kirschbaum (2000a).

Van Cleve et al. (1990), Peterjohn et al. (1993), Peterjohn et al. (1994), McHale and Mitchell (1996) and Rustad and Fernandez (1998) showed that soil warming could increase litter decomposition and nitrogen and phosphorus mineralization rates. In contrast, other authors found no significant effect of warming on decomposition (Bergner et al. 2004; Aerts 2006; Dabros and Fyles 2009) or on soil respiration (Pajari 1995). Robinson et al. (1995) found that litter decomposition could even be reduced by soil warming; this effect was probably caused by increased drought of the litter. Over recent years, a number of studies found that respiration rate increases over the first years, but no significant increase in long-term (Luo et al. 2001; Rustad et al. 2001; Melillo et al. 2002; Eliasson et al. 2005).

In this review we focus on studies from global boreal forests, but studies from other forest regions or cold biomes are considered when they contribute to the understanding of the process. A summary of key boreal forest studies investigating the effects of warming on soil processes and vegetation from boreal ecosystem is given in table 2. These studies were done with a variety of substrates and under a variety of conditions and have come to different conclusions regarding the effects of climate warming on boreal soils. In this review we will explain in detail divergences and convergences between these studies.

Table 2. Summary of results from selected soil warming studies. The effects of warming on soil properties and vegetation was estimated with different methodologies (long and short term soil warming experiments, long and short term incubation studies and meta-analysis of soil warming experiments). Soil warming induced increases are indicated by ↑, significant increase by >↑, decreases by ↓, no significant effect by _ and parameter not measured by X.

Reference/sites	Soil warming experiments/method	soils responses			
		Decomposition rate	Nutriment availability	Soil Respiration	Soil microorganisms
Eliasson et al. (2005); Northern Sweden Flakaliden, norway spruce *(Picea abies (L.) Karst.)* on podozolic, sandy, glacial till.	10 years soil warming experiment using HC; 5°C. => Acclimation of the response of heterotrophic respiration (R_h) to soil temperature.	X	X	R_h: years 1-6: ↑44% R_h: years 7-10: ↓30%	X
Strömgren and Linder (2002); Northern Sweden, norway spruce; Irrigated (IRR) and fertilized sites (FER)	6 years soil warming experiment to study the impact of warming on stem volume growth, 5˚C => ↑ stem (115% IRR & 57 % IRR-FER).	X	X	↑ N & growing season	X
Niinistö et al. (2004); Eastern Finland, boreal stand of scots pine (*P. sylvestris L.*).	4 years soil warming experiment in situ using OTCs combined to increased CO_2 and air temperature; 4˚C.	X	X	↑CO_2=> ↑23-37% ; ↑T=>27-43%; ↑CO_2 & T =>35-59%	X
Robinson et al. (1995); Two contrasting European arctic systems	3 years soil warming experiment *in situ* using polythene tents (PT) combined to with ↑ 58% precipitation (P) and ↑ NPK, 1 ˚C.	↑ with ↑P, Fertilizer (N, P, K)	Small effect on the short term	↑	X
Dunn et al. (2009); Manitoba Canada, black spruce (Sph-dominated wetland & feather-moss on well to poorly drained sites.	3 years soil warming study.	↑	X	3 x > in wetland than upland soils	X
Van Cleve et al. (1990); Alaska, mature black spruce (Picea mariana [Mill.] BSP).	2 years soil warming experiment *in situ* heated plots by Heating tape (HC) in the rooting zone; 8-10˚C.	>↑	↑ [N, P, K], ↑ soil [N],	X	X

Table 2. (*continued)*

Verburg et al. (1999); Southern Norway, heather and scattered Scots pines.	2 years soil warming experiments using heating cables; 3-5˚C.	_	↑Nitrification	X	X
Bergner et al. (2004); East-central Alaska, burned black spruce forest site,	2 years soil warming experiment *in situ* using OTCs; 0.4-0.9˚C.	_	X	↑ 20% &↓ Root biomass	_
Alisson and Tresder (2008); Alaskan mature black spruce on well drained soils	2 years soil warming experiment in situ heated plots using OTCs; 0.5˚C; induced 22% ↓ in soil water content.	X	Slight ↑ of NH_4+ & NO_3−	↓ 50% only late in the growing season.	↓ 50%; ↑ activity of Fungi
Bronson et al. (2008); Manitoba, Canada, 12 years old black spruce on well-drained site	2 years soil warming experiment *in situ* heated plots using PT & HC; 1-5˚C. => earlier Shoot budburst (9-11 days); 3 years	X	X	↑ carbon uptake by black spruce	X
Bronson et al. (2009); Manitoba, Canada, 12 years old black spruce on well-drained site	2 years soil warming experiment *in situ* heated plots using HC; 5˚C.	X	X	Year1:↑24% Year2:↑11%	X
Dabros and Fyles (2009); North-western Quebec, Canada, black spruce (BS), Aspen trembling (AT) and Sphagnum (Sph),litters From moderately to well drained sites.	2 years soil warming experiment *in situ* heated plots using OTCs; 2.3°C.	decomposition rate: AT: lower BS and Sph: no significant.	AT: ↑ C:N; Sph: ↓ [Ca]; control plots: [N]>↑	X	X
Lükewille and Wright (1997); Southern Norway, norway spruce.	15 months soil warming experiment *in situ* using electrical cables; 3-5˚C.	↑	↑[N]	↑	X
Robinson et al. (1997); High arctic polar south tree line, Abisko (Sweeden).	13 months soil warming experiment *in situ* using OTPT combined to with ↑58% P; 1 ˚C.	_	X	X	X
Peterjohn et al. (1994); Massachusetts, mixed deciduous (MD), Harvard forest	6 months soil warming experiment *in situ* heated plots by HC; 5 ˚C.	X	↑ N rate	↑	X

Table 2. *(concluded)*

Dorrepaal et al. (2005); Leaf litter collected from several Sphagnum dominated peatlands along a latitudinal gradient (68° N to 52° N).	20 months outdoor litter incubation under field conditions.	Sphagnum litter decomposed slower than other litters in all regions	↑ [Lignin, N & C] ; ↓C:N & C:P	X	X
Neff and hooper (2002); Alaskan Sagwon Station, northern latitude soils.	Long-term Laboratory incubation (1 year) at 10 and 30˚C.	↑	X	↑	X
Paré et al. (2006); Five experimental sites representing three biomes of eastern Canada, black spruce (BS), Sugar maple (SM), balsam fir (BF).	Long term laboratory soil incubation (46 weeks) at four temperatures (3, 10, 15, and 22 ˚C).	X	C mineraliz.: BF> SM >BS	CO_2 efflux: BS > SM at any T	X
Wickland and Neff (2008); Central Alaska, Mature black spruce on well-drained site (no permafrost), moderately well drained and poorly drained (with permafrost at 0.5 m)	Long-term soil incubation (57 days) at five moisture content (2, 25, 50, 75 and 100% saturation) and two temperatures (10˚C and 20˚C).	≠ SOM chemistry => ≠ decomposition rate within and among forest sites	Mineralization >↑ in well-drained sites	X	X
Rustad et al. (2001); 32 research sites representing different biomes including cold biomes (high latitude or altitude).	Meta-analysis of soil warming experiments. 2-9 years of experimental warming; 0.3-6°C.	X	X	Average ↑ of 20%, with greater ↑ over the first years, but no significant increase in long-term	X
Aerts (2006); 34 research sites representing cold biomes, deciduous, coniferous, shrub.	Meta-analysis of soil warming experiments. 1-3 years of experimental warming using different methods OTCs, PT, HC and HL; 0.1-5 ˚C.	Slight ↑	X	X	X

Warming methods, OTCs: Open-toped chambers, HC: heated cables, HL: heated lamps, PT: polythene tent, OPPT: Open-toped polythene tent. SOM: soil organic matter, T: temperature, CO_2: carbon dioxide, N: nitrogen, P: phosphorus, C: carbon, Ratio C: N, Ratio C: P, Mineraliz.: mineralization

3.1. Effects of temperature and moisture on decomposition process

The effects of temperature and moisture on soil organic matter decomposition have been widely examined in experimental studies and field measurement. It is generally accepted that experimentally warming soil has similar effects on organic matter decomposition as global warming does (Smith et al. 2008). Similarly, Aerts (2006) reported that experimental warming methods (e.g. Open-top chambers, polythene tents, heating cables in the soil, infrared heaters, etc.) have the potential to raise temperatures within realistic limits for this century (1.5–5 °C for this century; Houghton et al.2001). However, these methods may generate artefacts especially with regards to soil moisture reduction.

In a very recent study, Dabros and Fyles (2009) used an Open-top chamber (OTC, as described by Marion et al. 1997) climate change simulation to predict the potential effect of climate warming on soil decomposition of three litter types (aspen, black spruce and Sphagnum moss) in the northwest boreal forest of Quebec. This two-year experiment was marked by: a)- higher air temperature of 2-3 ˚C, which is within realistic limits of the predicable temperature increase for this century by IPCC (2007) and Houghton et al. (2001), b)- lower relative humidity (1 to 3%), drier soil volumetric content and cooler soil (up to 2.3 ˚C) in comparison to Dabros's (2008) control plots. The authors found that the OTC treatment caused little or no change to decomposition of litters and led to lower soil moisture. They concluded that the impact of climatic warming, as simulated by their OTC treatment, on decomposition process may be minimal.

In another recent study, Wickland and Neff (2008) conducted a series of incubation studies on the decomposition of boreal soil under various moisture and temperature conditions. Results from this study, as showed in figure 2, indicate that soil moisture had a strong effect on decomposition at various temperatures. Indeed, they found that the effect of temperature on decomposition is significant between 50 and 75 % saturation and negligibly small at the lowest percent (Fig. 2). Wickland and Neff (2008) also reported that decomposition was inhibited at both low and high moisture content. As a result, if soils become very dry or very wet in the context of climatic warming then it will affect future carbon dynamics in boreal soils.

While these two studies have highlighted the effect of moisture on decomposition, they obtained different decomposition rates on similar black spruce forest substrate. One possible explanation of this difference could be due to the experimental methods used in both studies. In fact, Aerts (2006) reported that the responses of soil processes to simulated climate change are expected to vary according to the experimental methods (OTC vs. incubation) and that OTC generally led to a drying of the soils and reduced decomposition rates compared to other methods (e.g. infrared lamps). This confirmation was consistent with other authors' explanation regarding the observed reduced decomposition rates in some warming experiments (e.g. Kirschbaum 2000a and 2006).

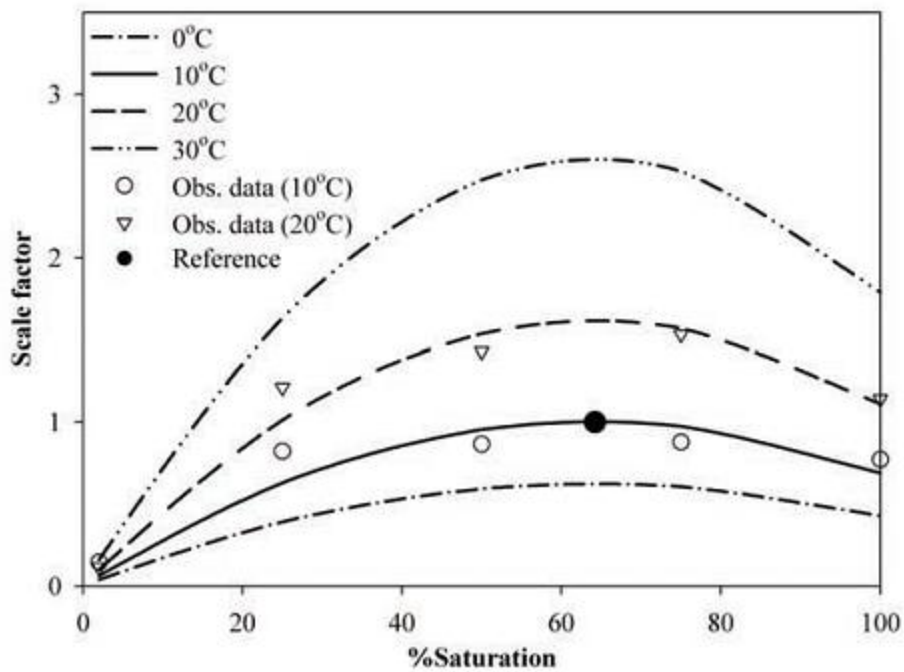

Fig. 2. The decomposition rates determined on the basis of the work of (Wickland and Neff 2008). The decomposition rates were shown as scale factors (from Fan et al. 2008).

Other studies have focused on temperature as the major factor affecting boreal organic matter decomposition and assumed that the effects of temperature and moisture on decomposition to be independent (Van Cleve et al. 1990; Robinson et al. 1995; Robinson et al. 1997; Verburg et al. 1999; Bergner et al. 2004). Van Cleve et al. (1990) showed that soil warming increased significantly the decomposition of the forest floor in an Alaskan black spruce. In contrast, Bergner et al. (2004), and Lükewille and Wright (1997) found no significant effect on decomposition process in response to elevated soil temperatures in an Alaskan black spruce and

Norwegian Norway spruce forests respectively. Similarly, another warming study has found that warming reduces soil moisture which may restrain decomposition rate (Verburg et al. 1999).

In a recent meta-analysis of experimental warming studies from 34 cold biomes sites including boreal ecosystems, Aerts (2006) found that warming treatments resulted in slightly increased decomposition rates and that litter decomposition was controlled by both temperature and moisture. This was corroborated by natural latitudinal gradient study by Dorrepaal et al. (2005). This study found that decomposition rates varied with latitudes, between 68˚N and 52˚N, in several Sphagnum-dominated peatlands of NW Europe where Sphagnum was found to decompose slower than other litter.

Aerts (2006) also suggested that both temperature and soil moisture and their interaction (both as experimental treatment and as explanatory variables) have to be considered in soil warming experimental studies. We believe that not taking into account these factors may explain the low responsiveness of boreal soils decomposition found in some of the reviewed studies. Table 2 shows a summary of global boreal forest studies examining impacts of soil warming on decomposition rate.

Temperature sensitivity of organic carbon soil

In the scientific literature, the term of temperature sensitivity (or dependence) of soil organic matter remains a topic of debate (Davidson and Janssens, 2006; Paré et al. 2006). The temperature sensitivity is the change in the decomposition rate of soil organic matter to variable temperature under constant conditions. It's often referred to as Q_{10}, the factor by which the respiration is multiplied when temperature increases by 10 ˚C (Davidson et al. 2006).

Giardina and Ryan (2000) found that recalcitrant carbon (resistant to decomposition) is not sensitive to temperature variation, while Fierer et al. (2006) and Knorr et al. (2005) reported that non labile organic matter is more sensitive to temperature than labile pools. Other studies suggested that recalcitrant and labile pools have similar temperature sensitivity (Conen et al. 2006, Fang et al. 2005). Conen et al. (2006a) compared the stable isotopic signature of organic carbon soil and reported that the difference in temperature sensitivity between young and old carbon are negligible under field conditions and that the feedbacks of the carbon cycle on climate change are driven equally by young and old organic carbon soil. This was supported by another experimental study (Fierer et al. 2006). Given the approach they used, it appears that Conen's view appears to prevail.

Davidson and Janssens, (2006) reported that most studies of the temperature sensitivity of decomposition were conducted primarily on organic matter in upland mineral soils where conditions (good drainage and aeration) are generally favourable for decomposition. They suggested that future studies should be expanded to include wetlands, peatlands and permafrost soils where current constraints on decomposition are likely to change consequently of climatic warming. The authors concluded that a high research priority should be devoted to the demonstration, if any, to the constraints sensitive to climate.

In the light of the results discussed above, it's obvious that there is still no concusses on an agreed effect of future global warming on boreal soils. We believe that this disagreement is largely due to the omission of the consideration of important confounding effects.

3.2. Effects of site conditions on decomposition process in boreal ecosystems

The effect of site conditions (e.g. substrate type, drainage, permafrost, earlier snowmelt, topography) on decomposition processes in boreal soils has recently received considerable interest in the context of global warming. Subsequently, several experimental warming studies have acknowledged the great importance of site conditions on boreal soils decomposition (Van Cleve et al. 1990; Verburg et al. 1999; Niinistö et al. 2004; Alisson and Tresder, 2008; Bronson et al. 2008; Wickland and Neff 2008; Dabros and Fyles 2009; Dunn et al. 2009).

3.2.1 Substrate type

Dabros and Fyles 2009 found that soil warming has shown to have a little or no effect on the litter decomposition regardless the substrate type (aspen, black spruce or Sphagnum moss) or the site (well-drained vs. moderately drained sites). In fact, their OTC treatment resulted in lower decomposition of aspen litter and no effect on decomposition rates for spruce and Sphagnum litter which had the highest moisture content. In contrast to this study, a recent study found that decomposition rates were significantly greater for well drained site compared to moderately and poorly drained sites (Wickland and Neff 2008). Since well-drained sites from both studies were located in North American boreal black spruce forests, Bronson et al. (2008) reported that some of the variation in warming responses across different studies could have been due to methodological differences. In another recent study, Paré et al. (2006) examined the effect of temperature on soil organic matter decomposition along a latitudinal gradient encompassing deciduous and coniferous forest types in three forest biomes of eastern Canada. Contrary to what was commonly believed, Paré et al. (2006) found that soil organic matter contained in coniferous boreal soils are not more resistant than deciduous forests to increasing their specific rates of soil heterotrophic respiration under warming conditions. In addition, in boreal forest soils the presence or absence of permafrost in sites may explain the observed variation in warming responses.

3.2.2 Permafrost soil and earlier snowmelt

Permafrost is defined as soil that remains frozen or below zero degrees continuously for at least two years. Approximately 20% of the earth's land surface area and over 50% of Canada and Russia are underlain by permafrost. Substantial amount of carbon is stored under the perennially frozen permafrost through a slow freeze-thaw process that progressively moves organic matter deeper into the ground where it is sealed off from decomposition by the cold temperature.

Several studies reported a trend toward earlier snowmelt of the snow cover in the boreal forest. Dabros and Fyles (2009) reported in their experiment that the presence of frozen soil patches in the OTC was caused by the earlier disappearance of the insulating snow cover when compared to the control plots. These frozen patches may have contributed to cooler and drier spring soils and the presence of snow cover have led to higher moisture in control plot than in the OTC. This paradox "cooler soils in a warmer world" that Dabros and Fyles (2009) referred to has been expressed before by Groffman et al. (2001b) and then has been reported in experimental studies (Hardy et al. 2001; Decker et al. 2003). This explanation is consistent with the findings of Mellander et al. 2005, who reported that the largest spatial variability in the timing of soil warming in spring between different sites occurred through the years with a thin snow layer, which is a possible consequence of climate warming in the boreal landscape of northern Sweden. Another study of snow cover in Alaska also found a trend toward earlier spring snowmelt (Stone et al., 2002). Additionally, Serreze et al., 2000 reported that satellite measurements indicate that snow cover area decreased over the period 1972 to 1988 in both North America and Eurasia. Consequently, these changes will have impacts on soil respiration, moisture content, air and soil temperatures as well as the degradation of soil carbon.

3.2.3. Topography and drainage

Topography is a major factor controlling both hydrological and soil processes at the boreal landscape scale (Van Cleve and Powers 1995; Seibert et al. 2007). Van Cleve and Powers (1995) reported that topography plays a major role in modifying the regional climate of the northern boreal forest and therefore the accumulation of mineral soil organic carbon in interior Alaska (Fig. 9-14 in Van Cleve and Powers 1995). Similarly, Fisher and Binkley, (2000) observed a strong relationship between topographical position, soil chemistry, vegetation composition, and forest productivity in young boreal forest soils, as result of the downslope transport of water and nutrients. To illustrate the importance of topography on soil properties, Seibert et al., (2007) reported:

"The direction of the slope (i.e. the aspect) influences the amount and intensity of solar radiation to which a location is exposed and subsequently the temperature regime, which affects soil biological and chemical processes as well as evaporation. The local slope determines not only the intensity of such processes as erosion and sediment redistribution, but also local drainage capacity. However, the most important effect of topography on soils in, for instance, boreal regions is its influence on water flow patterns at the landscape level. Topographical features such as curvature, slope, and upslope area influence the hydrological conditions of a location and generate different soil moisture conditions and flow patterns".

Changes in topography have been also found to affect soil microbial (Fisk et al. 1998). In an extensive study in Fennoscandian boreal forests, Högberg et al. (2007) has found that changing edaphic conditions along a topographic gradient match with differently structured forest floor microbial communities.

3.3. Effect of Soil respiration, nutrient availability and microorganism on soil decomposition in boreal forests

As the boreal soil experiences warming, the elevated temperature may lead to an increase in soil respiration (efflux of CO_2 soil) as well as to accelerated nitrogen mineralization which in its turn will increase nutrient availability (Peterjohn et al. 1994). This was confirmed by results from field and laboratory experiments.

3.3.1. Soil respiration

Soil respiration refers to the total carbon dioxide (CO_2) efflux at the soil surface. It comprises biotic, chemical and physical processes. Previous studies have concluded that soil respiration is highly enhanced by temperature (Krischbaum 1995; Liski et al. 2003). Soil respiration has been estimated with different methodologies (Fig. 3)

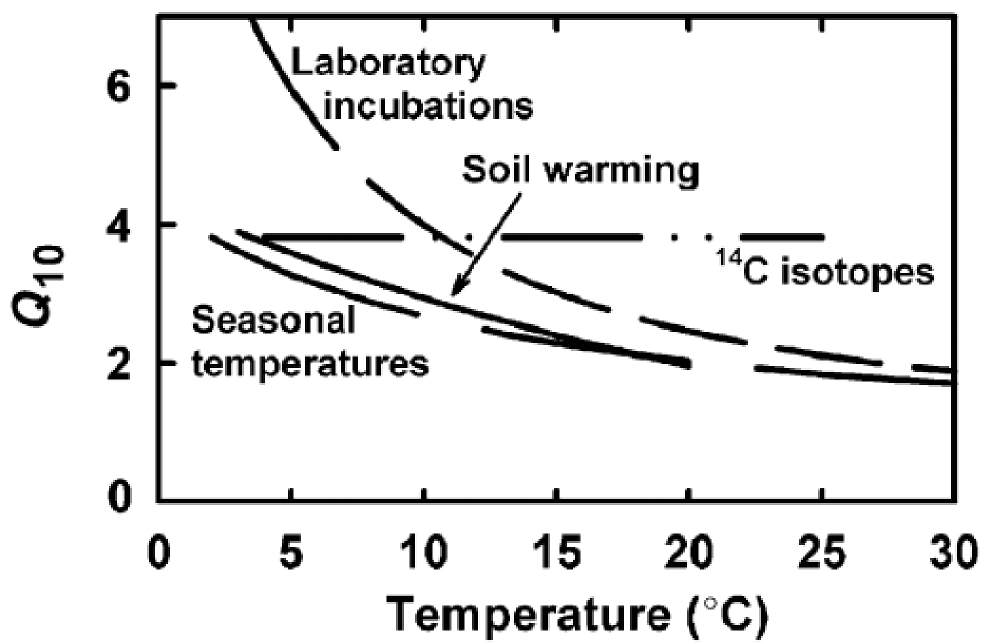

Fig. 3. Temperature sensitivity of soil respiration rates estimated with different methodologies. Short-term soil warming data summarized based on the work of Peterjohn et al. (1993, 1994), McHale et al. (1996) and Rustad and Fernandez (1998); data on seasonal temperature summarized by Lloyd and Taylor (1994) and laboratory incubations by Krischbaum (1995); ^{14}C isotope analyses based on Trumbore et al. (1996). Figure from Krischbaum (2004).

In one of the rare field experiments where soil temperature of Alaskan boreal black spruce forests were increased by on average 8-10 ˚C over two growing seasons, Van Cleve et al. (1990) found that the forest floor biomass declined with warming, suggesting an increase in carbon mineralization. In a recent study in a black spruce forest in Manitoba, soil respiration increased in response to warming by heating cables, but decreased if the air above the cables was heated (Bronson et al. 2008). In contrast to these studies, a recent field experimental study in the Alaskan boreal forests found that 0.5 ˚C soil warming decreased soil respiration up to 50% (Allison and Treseder 2008). Similarly soil water content and bacterial and fungal abundance were declined by 22%, 50% and 50 % respectively. As for decomposition, the difference in warming responses between these studies could have been due to methodological differences (Bronson et al. 2008), even though this justification is not in accord with the finding of a larger meta-analysis study by Rustad et al. (2001) who found that response to warming was not affected by the warming techniques.

In another four year growing season field experiment in young boreal forest of Finland, Niinistö et al. (2004) found that forest soil CO_2 efflux increase as response to elevated atmospheric concentration of CO_2, air temperature and their combination by 23-37%, 27-43% and 35-59% respectively (Fig. 4). The authors reported that emissions of CO_2 from forest soil were greater in response to elevated temperature than under ambient conditions over the four year experiment and hence temperature came out as a significant factor for mean CO_2 efflux in ANOVA when combined data was used for that period. Nevertheless, after the first year of experiment, the authors observed decrease in the temperature sensitivity of soil CO_2 efflux in the elevated temperature treatment. Instead of giving a clear reason behind the observed decrease in the temperature sensitivity, the authors provided a number of possible factors such as depletion of the labile carbon pool in the soil, lowered soil water content, acclimation of the roots and microbes to higher temperatures, or decreases in respiring microbial biomass in the soil due to various warming-induced stresses. As with soil organic matter decomposition, we highly believe that the observed decrease in the temperature sensitivity in Niinistö et al.'s (2004) experiment could be a consequence of soil moisture which has been shown in previous study to constrain the respiration response to temperature in boreal soils (Gulledge and Schimel 2000). This is supported by

Davidson et al. (1998) who found that below a certain threshold, soil moisture may constrain soil respiration more strongly than temperature.

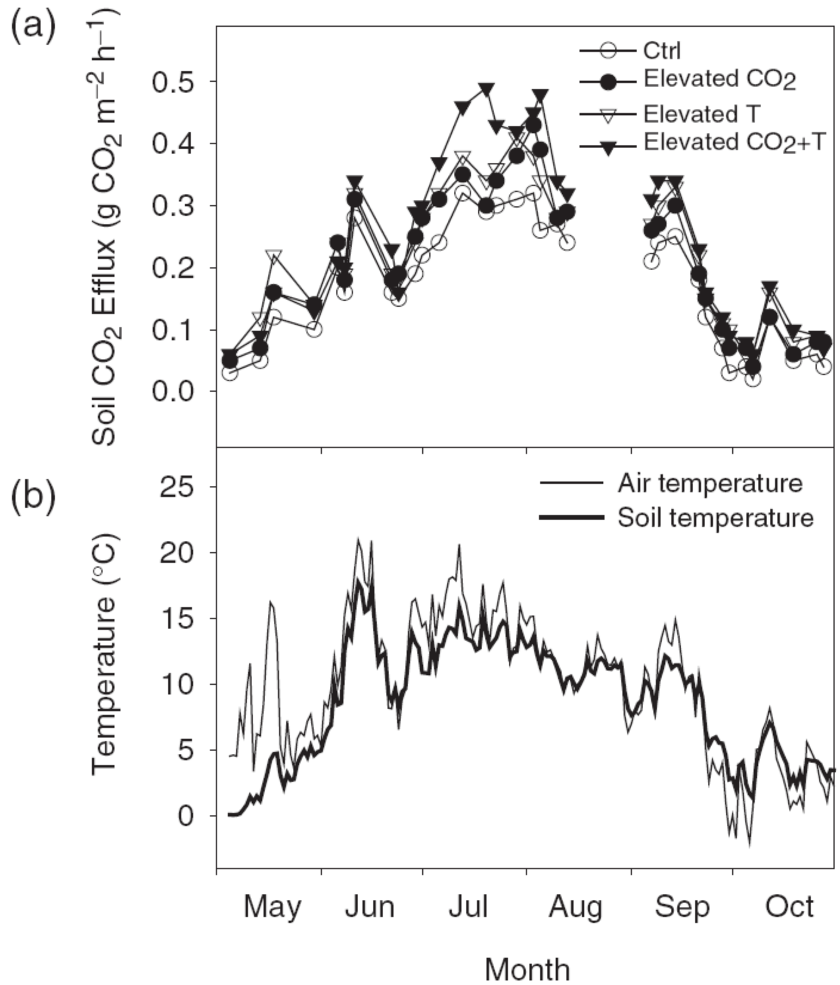

Fig. 4. (a): Soil surface CO2 efflux in the closed chambers. (b): Air and soil temperatures measured 5 cm below moss surface. Figure from Niinistö et al. (2004).

The variation in warming responses between discussed studies mentioned above suggests that soil respiration is affected by other edaphic factors, such as the absence or presence of permafrost and soil moisture. Indeed, Allison and Treseder's (2008) experiment was conducted in boreal forest sites with well-drained soils without permafrost. Under such site conditions, warming treatment may decrease carbon cycling if microbial activity becomes more limited by moisture than by temperature. On the other hand, Van Cleve et al.'s (1990) site was underlain by permafrost, Bronsons et al. (2008) and Niinistö et al.'s (2004) sites in Manitoba and Finland were irrigated. Allison and Treseder (2008) suggested that at these sites, temperature probably limited microbial activity more than moisture in accord with positive effect on warming soil respiration.Under climate warming, Allison and Treseder's (2008) suggested that soil respiration in drier boreal ecosystems may not increase, whereas Van Cleve et al. (1990) and Niinistö et al. (2004) found that some boreal systems with wet soils may experience an increase in soil respiration.

In one of the long-term soil warming experiments (10 years), Eliasson et al. (2005) examined the effect of elevated soil temperature in an N-limited boreal ecosystem where soil moisture was nonlimiting factor. Eliasson et al. (2005) found that the ecosystem warming experiments typically show greater increase in soil respiration over the first 6 years of warming and a decline over the last 3 years of a 10-year study. These findings are similar to those of other studies (Luo et al. 2001; Rustad et al. 2001; Mellilo et al. 2002; Bronson et al. 2008) who found that elevated respiration rates under soil warming in field experiments return to pre-warming values within the first few years. This temporal change of soil respiration, when viewed at the ecosystem or stand level, was described as acclimation of the response of heterotrophic respiration to soil temperature (Luo et al. 2001; Rustad et al. 2001; Mellilo et al. 2002) and thermal adaptation of microbial respiration rates (knorr et al. 2005). In other words this transient response is attributed to rapid decomposition of labile C compounds in the first years of soil warming (Luo et al. 2001; Rustad et al. 2001; Mellilo et al. 2002; Eliasson et al. 2005; Davidson and Janssens 2006). Studies that attributed these observations to acclimation (e.g. Luo et al. 2001) were criticized by Kirschbaum (2004) because acclimation implied a physiological adjustment by decomposer organisms to their altered environment. The author added that such acclimation would stop a long-term response of soil-carbon efflux to changing temperature and thus would not lead to any significant loss of soil carbon in the long term and no positive feedback on atmospheric CO_2 concentrations.

We believe that Luo's et al. (2001) results were confounded by a more rapid decrease in easily available substrate at higher temperatures than at lower ones. Kirschbaum (2004) and Eliasson et al., (2005) reported that the transitory response was more likely caused by substrate depletion of labile carbon rather than acclimation.

Although there is general recognition of the potential of elevated temperatures as consequence of the expected global warming to enhance soil respiration, we observed through the reviewed papers that there have been few attempts to separate soil decomposers' respiration from that of roots. A question can then be raised concerning the mixing of soil and roots respiration responses to soil warming. Could the mixing of these two parameters induce some artefacts regarding the soil responses? It is beyond the scope of this review to answer to this question.

3.3.2. Nutrient availability

Nitrogen (N) and Phosphorus (P) are the most important forest nutrient (Kreutzweizer et al. 2008) and boreal forests in general tend to be strongly nutrient-limited (Rustad et al. 2001). Most N is derived from the decomposition of soil organic matter (Kirschbaum 2000b). Overview of N cycling process and the biogeochemistry of P in forest soils are provided in Attiwill and Adams (1993).

Most warming experiments have resulted in higher soil nutrient availability at different levels. In a meta-analysis of the response of N mineralization to experimental ecosystem warming, Rustad et al. (2001) found that warming increased mineralization by 46%. Van Cleve et al. (1990) reported that the availability of N, P and K was significantly increased by soil warming manipulation. In this experiment, Van Cleve et al. 1990 found that concentrations of total soil N and exchangeable N (mainly NH_4) of the organic soil layers of the experimentally warmed plot increased by more than twofold and 3-15-fold respectively (Fig.5), whereas NO_3^-N concentrations declined significantly probably as result of enhanced denitrification (loss of NO_2 and N2 gas to the atmosphere) potential. Similarly, in another warming experiment by Peterjhon et al. (1994), heated plots showed twofold higher rates of N-mineralization in both forest floor and mineral soil layers (Fig. 5). The authors did not observed any increase in the NO_2 efflux from the heated plot with no increase in nitrification or soil N water suggesting that the only alternative explanation appears to be an increase N uptake by plant.

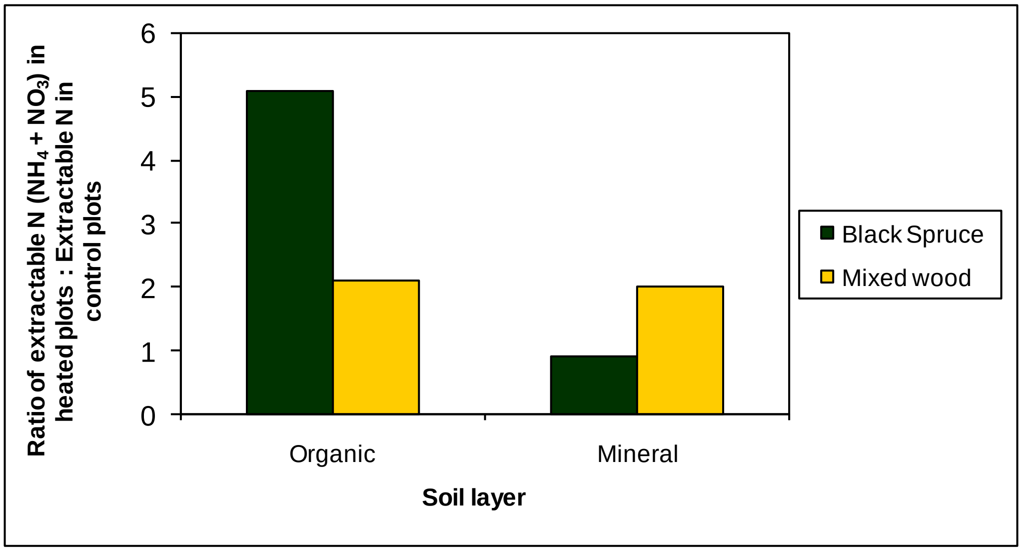

Fig.5. The ratio of total extractable N ($NH_4 + NO_3$) in the heated plots to the total extractable N in control plots from in situ experimental manipulations of soil temperature in the organic and mineral soil layers of black spruce and mixed deciduous forests. Data are from Van Cleve et al. (1990) and Peterjohn et al. (1994) respectively. Figure modified after Saxe et al. (2001).

The only whole-ecosystem experiment with mature trees in situ where temperature of boreal Norwegian sparse pine-spruce forests were raised on average 3-5 ˚C (Lükewille and Wright 1997), soil warming resulted in increased release of N which appears as significant concentrations of both NH_4 and NO_3. In contrast, in more recent studies, Dabros and Fyles (2009) found no significant effect of the OTC treatments of nutrient supply rates for any of the tested nutrients (available N, NH_4, P, K, Ca and Mg), whereas Allison and Treseder (2008) found slight increase in soil N availability.

We believe that interaction between soil moisture and temperature could create the complex patterns of N availability observed in the different discussed studies. Overall, increased temperature coupled with a decline in soil moisture is anticipated to cause an increase in mineralization in boreal soils**.**

3.3.3. Soil microorganism

Microbial communities play a major role in regulating climate response to the carbon cycle. They are involved in the degradation and mineralization of organic matter, thus warming effects on microbial communities may alter ecosystem carbon and nutrient balance (Bergner et al. 2004).

Högber et al. (2007) demonstrated that fungi are particularly important drivers of carbon and nutrient balance in boreal ecosystems because of their adaptation to low soil pH. Fungi were also found to commonly form mycorrhizal associations that assist boreal vegetation to obtain nutrient (Read et al. 2004). Fungal communities have been shown to respond to changes in temperature (Robinson et al. 2004).

Many other studies have examined the effect of warming on microbial communities in boreal soils with permafrost (Van Cleve et al. 1990), following fire (Bergner et al. 2004) or on a well drained boreal site (Allison and Treseder 2008).

While Bergner et al. (2004) found that warming (0.4 ˚C - 0.9 ˚C) did not affect bacterial or fungal biomass in Alaskan burned boreal forest (Fig. 6), Allison and Treseder (2008) concluded that bacterial and fungal abundance decreased by over 50% in well-drained boreal soils suggesting that this decline in microbial process may be more strongly limited by decreasing in water content than by temperature (Allison and Treseder 2008).

Allison and Treseder (2008) also observed a significant shift in the community structure of active fungi in response to warming. Because they assessed fungal community structure only once during their experiment, we believe that more research is needed to determine whether the shift in the community structure in the drier boreal soil as result of warming will persist over many years and under different soil conditions. Another, recent study in arctic tundra found that warming increased fungal biomass (Clemmensen et al., 2006).

Overall, results from most reviewed studies demonstrated that across a variety of experimental methodologies in the boreal ecosystems, warming manipulations significantly increase rates of soil respiration and N mineralization. Results also suggested that warming may affect microbial abundance and biomass in different ways and will depend on site specification.

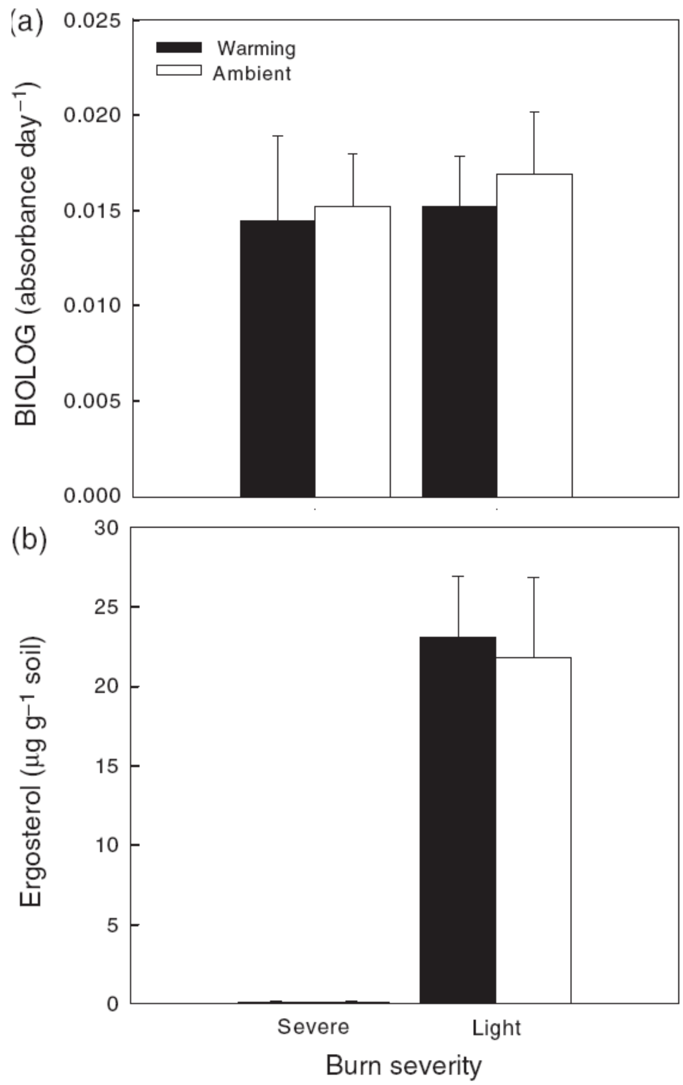

Fig.6. Effect of burn severity on bacterial (a) and fungal (b) abundances in soil. Biolog and Ergosterol was used as indexes of bacterial abundance and live fungal biomass respectively. Bars represent means (±SE) of six plots. Figure from Bergner et al. (2004).

4. EFFECT OF FIRE ON BOREAL SOIL PROPERTIES

Fire is a major and natural element of the boreal ecosystem (Flannigan et al. (2006, 2009); Bond-Lamberty et al. 2007) and broader changes are expected to occur in boreal forests as result of climate warming. In general, fire frequency is expected to increase (Flannigan et al. 2001) partly as result of global warming. Yet, the level of change depends on the climate model used and the investigated boreal region (Flannigan et al. 2005).

A certain number of studies have examined the effect of fire on soil properties of the boreal region (O'Neill et al. 2002; Bergner et al. 2004; Czimczik et al. 2005; Kasischke and Johnstone 2005; Neff et al. 2005; Ping et al. 2005; Harden et al. 2006; Waldrop and Harden 2008; Bond-Lamberty et al. 2009; O'Donnell et al. 2009). It is primordial to mention that climate change was not a studied factor in most of the reviewed studies. However, fire has the capacity to alter soil conditions through changes in soil temperature and create trends similar to warming experiments at least within a few years following fire.

O'Neill et al. (2002) reported that fire modified soil conditions of Alaskan boreal burned forest which may affect carbon exchange for decades following the burn. Several studies have documented post-fire changes in soil properties by affecting decomposition (Viereck et al. 1983), soil moisture (O'Neill et al. (2002), microbial communities (Hart et al. 2005; Waldrop and Harden 2008), and organic matter content and quality (Johnson and Curtis 2001). Yet, the post-fire changes in thermal conditions, organic matter quality and ecosystem respiration are less clear (O'Neill et al. 2003). O'Donnell et al. (2009) suggested that this lack of clarity is largely due to the complex interactions among burning, soil organic matter quality, soil temperature, soil moisture, and soil microbial communities.

In recent laboratory incubations soils from burned black spruce forest in Alaska, O'Donnell et al. (2009) found that burning decreased the sensitivity of decomposition to warmer soil conditions in both upland forest and sphagnum peatland sites. Although, they suggested that decomposition of organic matter in burned sites is moisture limited, they concluded: *"However, it is not clear from these incubation results whether fire altered the chemical composition of organic matter, the biological properties of soil, or both*".

Neff et al. (2005) reported that the decomposability of organic matter substrates was decreased by fire during the selective burning of labile compounds. Other studies have found a reduction of microbial biomass in near surface soils (Certini 2005, Waldrop and Harden 2008; Hart et al. 2005) which can largely reduce the response of microbial respiration to increased temperature.

The combustion and regrowth of northern boreal ecosystems following fire can have large impact on soil temperature and moisture conditions (O'Neill et al. 2003; Kasischke and Johnstone 2005). However, O'Donnell et al. (2009) and Yoshikawa et al. (2003) observed, contrary to general expectations, cooler summer soil temperature in the second year following fire, which may be due, in part, to a quick recovery with higher albedo (the ratio of radiation reflected into space relative to total radiation intercepted by an ecosystem) and soil temperature.

In addition to the effect of albedo and soil moisture, the role of topography (Ping et al. 2005) and permafrost (Waldrop and Harden 2008, Harden et al. 2006) are also important in controlling soil temperatures following fire. For example, Ping et al. (2005) reported that soils in boreal forest of Alaska, with permafrost in potentially warmer/drier slopes are most likely to show major changes in moisture and temperature regimes after fire whereas soils within the coldest and wettest sites are less affected by fire because most the saturated organic layer and permafrost are preserved after fire. Another three year warming experiment showed that elevated temperature increased CO_2 and reduced root biomass, but had no effect on microorganism biomass or soil organic matter content (Bergner et al. 2004). A summary of the effects of fires on properties of forest soils (table 3) is provided by Certini (2005).

Table 3. Summary of the effects of fires on properties of forest soils (table from Certini 2005).

Physical, physico-chemical, and mineralogical properties

Water repellence: the natural water repellence of soil often increases because of the formation of a continuous water-repellent layer a few cm beneath the surface. It implies limitations in soil permeability and, thus, increased runoff and erosion

Structure stability: complexity decreases as a result of the combustion of organic cements

Bulk density: increases because of the collapse of aggregates and the clogging of voids by the ash and the dispersed clay minerals; as a consequence, soil porosity and permeability decrease

Particle-size distribution: does not change directly, but the increased erosion can remove selectively the fine fraction

pH: in noncalcareous soils increases, although ephemerally, because of the release of the alkaline cations (Ca, Mg, K, Na) bound to the organic matter

Mineralogical assemblage: changes, but only at temperatures higher than 500°C

Colour: darkens, due to charring, and reddens, due to formation of iron oxides

Temperature regime: changes temporarily because of both the disappearing of the vegetable mantle and the darkening of ground (decreased albedo)

Chemical properties

Quantity of organic matter: decreases immediately after fire, but in the long run generally exceeds the pre-fire level

Quality of organic matter: changes remarkably, with a relative enrichment of the fraction more recalcitrant to biochemical attack. This is due to both selective burning of fresh residues (leaves, twigs, etc.), and neoformation of aromatic and highly polymerised (humic-like) compounds. Charred material, an exclusive product of incomplete combustion, shows residence times of centuries or even millennia

Availability of nutrients: increases, often remarkably, but ephemerally

Organic N (unavailable, often almost coinciding with total N) in part volatilises and in part mineralises to ammonium, a form available to biota. Ammonium adsorbs on negative charges of mineral and organic surfaces but, with time, is destined to be biochemically transformed to nitrate, which is leached soon if not taken up by cells. Nitrogen availability lowers to pre-fire levels in a few years

Organic P mineralises to orthophosphate and the loss through volatilisation is negligible; orthophosphate is not leached out of soil but if not promptly taken up, it precipitates as slightly available mineral forms

Calcium, magnesium and potassium often increase remarkably but ephemerally

Exchange capacity: decreases proportionally to the loss of organic matter

Base saturation: increases as a consequence of the prevailing release of bases from the combusting organic matter

Biological properties

Microbial biomass: decreases; the recovery of the pre-fire level depends chiefly on promptness of plant recolonisation

Composition of microbial community: changes as a consequence of the selective effect of fire on some groups of microorganisms and the modification imposed to vegetation; generally, fungi diminish more than bacteria

Soil-dwelling invertebrates biomass: decreases, but less than that of microorganisms thanks to the higher mobility of the invertebrates

Composition of soil-dwelling invertebrates community: changes, the time of recovery of the pre-fire assemblage differs highly among the various phyla

5. FOREST SOILS AND SPECIES DISTRIBUTION RESPONSES TO GLOBAL WARMING: CONSTRAINTS AND ADAPTATION

One of the anticipated responses of boreal forests to global warming is the migration of plant species to higher latitudes as the climate and soil conditions to which they are adapted do. Will such forest movement be realized as suggested by many Dynamic Global Vegetation Models? Some vegetation models project that forests may eventually replace between 11 and 50% of Tundra under doubling atmospheric [CO_2] scenario (Harding et al. 2002; Kaplan et al. 2003). However, such migration is likely to be moderated or constrained in reality by many processes such as soil formation-paludification, moisture dynamic, genetic local adaptation or topographic gradients not yet considered in most models (e.g. Gamache and Payette 2005).

In the context of warming climate, soil temperature and decomposition would increase in upland areas of boreal forests where drying occurs as a result of drought or adequate drainage. For instance, Dunn et al. (2009) demonstrated that under drier future climate, natural regeneration of conifers could be significantly reduced in the southern boreal forest of western Canada. Therefore, the expected increase of boreal soil temperature may cause an adaptation of boreal vegetation by a shift from coniferous to deciduous tree species (Kellomaki and Kolstrom 1992). In addition, (Côté et al. 2000) found a greater nitrogen mineralization for deciduous than coniferous stands both in the mineral soil and forest soil in the northeastern boreal mixed wood forest of Canada. As the rate of decomposition is higher in boreal deciduous forests (because of both litter and site conditions), this may further raise nitrogen availability, leading to increase in productivity.

In boreal lowland peat bogs forests where the water table is maintained, soil warming may have little or no significant impact on decomposition rate of the soil organic matter as suggested by some reviewed studies (e.g. Verburg et al. 1999; Bergner et al. 2004; Aerts 2006; Dabros and Fyles 2009). Higher water tables would increase soil heat capacity, possibly protecting soil organic against heterotrophic respiration (Dunn et al. 2009). Thus, climatic warming will have a slight or no effect on decomposition in these low relief lowland areas, which in turn will not affect the adaptation of boreal tree species to the elevated air temperature. Therefore, current soil conditions may persist for many decades in response to increasing and climate change. Similarly, Dabros and Fyles (2009) concluded: *"It is possible that the threshold for changes in soil* *conditions required to significantly impact decomposition of northern plant species is high enough that at least within the mixed wood-boreal regions, climatic changes will have a slight or no impact on decomposition anytime in a foreseeable future."*

Unfragmented boreal forest is likely to be important for continued ecosystem stability in the context of changing climate. The soil in unfragmented forests is generally several degrees cooler in late spring and summer and several degrees warmer in late fall and winter than in open areas, delaying freeze-up in autumn and snow melt in spring (Rivers and Lynch 2004). In addition to the moderated microclimate, maintenance of high genetic diversity and the presence of productive mature trees are likely to enhance adaptive responses of unfragmented forests landscapes to climate change. As temperature increases, the current climatic conditions that characterize the boreal biome will move northwards. For boreal species to migrate north, unfragmented forests patches have to be closely connected to allow gene migration between them (Jump and Penuelas 2005). In this case, unfragmented boreal forests landscapes will be best adapted to keep-up with rapidly changing soil conditions, provided that moisture is not a limiting factor.

Under warming change, fire frequency and severity are expected to increase in northern boreal forests. One of the consequences of severe fires may lead to the formation of reddened mineral horizons. These reddish horizons frequently occur in upland soils at the surface and occasionally as a buried horizon. These horizons may negatively affect tree growth because of the water repellency and soil firmness (Certini 2005; Ping et al. 2005). There is little work in the scientific literature with regards to soil water repellency formation of reddened mineral horizons in boreal regions (e.g. Certini 2005; Ping et al. 2005). Overall, the studies reviewed indicate that the temperature response of post-fire of boreal soils is likely to be variable and site specific. For instance, in some areas, such as the eastern boreal region of North America, fire frequency may decrease due to increased precipitation (Flannigan et al. 2005; IPCC 2007). This would likely allow these forests to grow and continue to be adapted to its current soil conditions and consequently accumulate additional carbon over time.

In the context of climate warming, soil responses will likely to also vary with site topography. Boreal uplands areas with sufficient drainage may experience more droughts than lowland peat bogs areas which may limit growth and forest productivity. For instance, Grant et al. (2009) found that the 2001–2003 drought effects on net ecosystem productivity at several boreal sites were largely determined by topography. Ultimately, we believe that topography will play a major role in determining the microclimate, snow accumulation, the growing season length, soil water availability and the forest species distribution as well as adaptation across the boreal landscapes.

In areas of the northern boreal forest, global warming may lead to higher soil and permafrost temperatures and possibly a deeper active layer (Serreze et al. 2000). As permafrost melts, the exposed soil becomes increasingly saturated with water (Chapin et al. 2000). One particularly consequence of the increasingly saturated soil, in the absence of the high demand of trees, is forest bogs and process known as paludification. Paludification is the accumulation of organic matter over time, and is generally thought to be caused by increasing soil moisture (Crawford et al. 2003; Lavoie et al. 2005a and 2005b; Vygodskaya et al. 2007). It reduces soil temperature, decomposition rates, microbial activity, and nutrient availability (Lavoie et al. 2005a). This process creates wetter conditions, which promote the growth of Sphagnum mosses (Fenton et al. 2005; Fenton and Bergeron 2007) and the conversion of potentially forested areas to large bog landscapes largely resistant to forest establishment and growth (Crawford et al. 2003).

If paludification occurs as result of climate warming, boreal plant adaptation (move toward higher latitudes) will be restrained by predicted changing soil conditions. Indeed, Crawford et al. (2003) reported that paludification may lead to a retreat rather than an advance in the northern limit of the boreal forest contrary to general expectations. This was corroborated by Skre et al. (2002) who reported that climatic warming may result in a retreat southwards of the boreal forest due to increased bog development northwards.

We’ve observed that the issue of paludification as possible consequence of climatic warming and its effects on boreal soils has been rarely discussed in the scientific literature (e.g. Crawford et al. 2003; Skre et al. 2002; Lavoie et al. 2005a,b; Vygodskaya et al. 2007). Therefore, we believe that the question of whether global warming will cause the northern boreal forest to paludify as well as the magnitude of this process should be a high research priority in the future.

6. POTENTIAL EFFECT OF CLIMATE WARMING ON PLADUFICATION: EXEMPLE OF THE CLAY BELT REGION OF EASTERN NORTH AMERICA

The Clay Belt, a boreal region of eastern North America, is part of the Canadian Hudston Bay – James Bay lowlands. In this region the mineral substrate is mostly composed of clay deposits (resistant to water penetration) left by pro-glacial Lake Ojibway (Veillette 1994) with generally flat topography (plains broken by gentle undulations or ridges) which promotes the accumulation of organic matters and landscape paludification (Lavoie et al. 2005a) as well as increase in water availability. The later is related to precipitation (P) being greater than evapotranspiration (ET). In this region the hydrological balance (P minus ET and minus runoff) is critical for the initiation of peat formation (paludification) especially in forested peatlands.

As part of the eastern Canada, summer temperature and precipitation are expected to increase in the Clay Belt region by 1-5°C and 20%, respectively (Flannigan et al. 1998). For this region, MacIver and Isaac (1989) reported that annual mean temperature, precipitation and potential maximum annual evapotranspiration are projected to increase by 4.7°C, 15% and ~12%, respectively, for the period 1951-2099. Based on many model scenarios (e.g. Houghton et al. 2001) we do have rather accurate prediction of future warming trends of the clay belt region. However, there is much uncertainty in the precipitation and evapotranspiration projections as this region was identified to have insufficient data to provide reliable and accurate precipitations trends (IPCC 2007).

Within the framework of this study, the effects of climate warming on paludification processes in the clay belt region will be analyzed using one temperature scenario (increase) and three precipitation scenarios (increased, decreased or unchanged) for the period up to 2100. To do so, we asked the following questions: (1) how does paludification change across the clay belt landscape under climate changes? (2) Given these changes in paludification amplitude, do we also see changes in vegetation composition? (3) Finally, what are the relative effects of changes in future silvicultural treatments?

The effects of the expected climate warming on paludification processes under three different proposed scenarios are illustrated in Table 4.

Scenario 1: Increased temperature combined with greater precipitation to offset evapotranspiration (ET) in forested peatlands would not lead to significant soil moisture content alterations, water-table level (WTL) would be maintained and peat accumulation should remain unchanged or be favored. As a result, current paludified sites may persist for many decades in response to climate warming and in the absence of fire. Under such conditions, mixedwood (MW) and white spruce will eventually replace black spruce (BS) in upland areas while black spruce stands will likely remain dominant in low relief lowlands areas (Bonan et al. 1990).

Scenario 2: Under increased temperature and decreased precipitation (P) scenario, soil moisture content in forest peatland is expected to undergo a signification alteration with a much lower WTL and higher ET. Consequently, this would result in an increase in organic matter decomposition and a reduction in sphagnum growth and therefore a decrease in the abundance paludified sites in the Clay Belt. Under such conditions, increased ET associated with warming may result in excessive soil moisture stress and conversion of upland to steppe and peatland forested sites to aspen and white spruce dominated forests.

Scenario 3: is quite similar to scenario 2 with increased ET and decreased WTL but lower than S2. As a result, the thick organic layers are expected to dry up and bring about a decline of sphagnum growth within stands prone to paludification. Consequently, mixedwood and white spruce will eventually replace black spruce dominated sites in lowlands and dry well-drained uplands respectively.

At the light of the expected paludification response to climatic warming (Table 4), here we suggest different silvicultural treatment options for each of our three scenarios (S1, S2 and S3): For S1 and S3, summer clear-cut harvesting (CT: total clear-cutting) and prescribed burning (PB) combined with appropriate site preparation that removes the thick organic layers will have the potential to reduce or reverse paludification and consequently increase site productivity (Lavoie et al. 2005a). Partial harvesting would be not an appropriate option for these scenarios (1 and 3). Indeed, recent research suggests that partial harvesting in lowland black spruce stands of the Clay Belt may increase the rate of paludification, development of a thick, waterlogged forest floor layer that reduces stand productivity (Fenton and Bergeron, 2007).

Under scenarios 2, nutrient availability should increase (e.g. N) because of enhanced decomposition rates and drought conditions of the thick organic layers. Therefore, in this case silvicultural treatments such as partial harvesting (CP: partial cutting) followed by site replanting with non N-limited boreal species adapted to dry soil conditions (e.g. poplar, birch, jack pine (JP), white spruce (WS)) should be more appropriate in the context of a decline of paludification.

Table 4. Response of paludification to predicted climate change under three different scenarios (S1, S2 and S3) in the Clay Belt region. Increases are indicated by ↑, decreases by ↓ and significant increases and decreases by ↑↑ and ↓↓ respectively.

Scenarios	Paludification response		Expected vegetation changes	Recommended silvicultural treatments
	Indicators	Response		
(S1) ↑Temperature, ↑ Precipitation	ET and WTL remain unchanged	Paludification unchanged or slightly favored	BS + MW+ WS	CT + PB
(S2) ↑Temperature, ↓Precipitation	↑↑ ET and ↓↓WTL ↑↑ decomposition rate ↓↓ sphagnum growth	Decline in paludification ↑ soil fertilization	Aspen + JP	CT + CP + replanting (e.g. JP, WS, poplar)
(S3) ↑Temperature, Precipitation unchanged	↑ ET and ↓WTL, ↑ decomposition rate ↓ sphagnum growth	Decrease of stands prone to paludification	Aspen + MW + BS	CT + B + replanting (e.g. JP, WS, poplar)

In conclusion, the precipitation is likely to play a major role in the boreal forested region located on the Clay Belt. For the 21st century, increased precipitations (~15-20%) will likely increase peat accumulation in boreal forest stands prone to paludification and facilitate the expansion of forested peatlands into upland forests, while reduced or unchanged precipitations combined to increased temperatures (~4.7 °C) should favour succession of forested peatlands to upland boreal forests (Lavoie et al. 2005b).

In the future, the growing demand for wood products will increase pressure to harvest sites undergoing paludification in the Clay Belt region. Forest management practices should be planned in context with the adaptation of forests to expected climate changes, and eventually under one of the more probable scenarios (1 or 3). Although, this analysis was an attempt to predict paludification responses through three hypothetical scenarios for the Clay belt lowland region, some site specificities such as topographic depressions with higher peat accumulation should be taken into consideration. In this case, paludification is an edaphic process that will not be reversed. For a better understanding of the impact of climate change on boreal forest stands prone to paludification, further research is needed to improve these predictions (e.g. quantitative relationship between precipitation and ET).

7. CONCLUSION

Expected climatic warming in boreal forests can clearly alter process in soils by changing forest composition, vegetation uptake rates, soil conditions, moisture and temperature regimes and soil microbial activity. Among the studies that we reviewed, these alterations in soil conditions often led to increase in CO_2 emissions, nutrient availability (N and P). Warming may affect microbial abundance and biomass in different ways and will depend on site specification (e.g. drier vs. wetland boreal ecosystems). It is also apparent that soil responses to warming can be highly variable and will depend on site specification. The extent and magnitude of warming on boreal soils conditions will depend on soil types and site (e.g. well-drained site, permafrost, etc.) with strong regional differences. In addition, some of the variability among reported results of the studies we reviewed could have arisen from differences in used methods and sampling designs.

Many of the warming soil studies reviewed have been short term, usually less than three years with emphasis on the first year or two. Because some impacts of soil could be prolonged or delayed beyond many years, long term warming experiments in boreal forest are necessary to evaluate transient responses, to determine longer-trends and to give the boreal ecosystem the time necessary to respond to climate-induced changes. Indeed, a number of soil warming experiment studies found that respiration rate increases over the first years, but there was no significant increase in long-term.

Most of the studies reviewed indicated or inferred that under soil warming conditions, boreal forests may respond positively to increased CO_2 levels and temperature provided that water does not act as inhibitor at high and low levels. The most cited response of boreal forest species to global warming is a northward migration to track soil conditions (e.g. temperature and moisture) to which they are adapted to. Yet, there are some constraints that may influence this kind of adaptation (migration) such as water availability, changes in fire regimes, decomposers adaptation and paludification. In this study, we examined potential effect of climatic warming on future (period up to 2100) paludification changes under three different scenarios (increased temperature associated to increased precipitation (S1), increased temperature combined to decreased precipitation (2) and increased temperature with unchanged precipitation (S3)) the Clay Belt lowland region. Precipitation was found to play a major role in the potential paludification response. Indeed, an increase in precipitations (~15-20%) would likely increase peat accumulation in boreal forest stands prone to paludification and facilitate the expansion of forested peatlands into upland forests, while reduced or unchanged precipitations combined to increased temperatures (~4.7 °C) should probably favour succession of forested peatlands to upland boreal forests. Given the expected climate change in the studied region, where precipitation is expected to increase, S2 is less probable. Summer clear harvesting and prescribed burning followed by an appropriate site preparation have been suggested for the more probable scenarios S1 and S3 while partial harvesting followed by site replanting with adapted boreal species to dry soil conditions.

Because climate changes are expected to be more pronounced in the boreal regions, efforts to maintain or enhance the ability of the boreal forests to adapt to climate are essential. An overview of possible approaches for adapting forests to climate change are provided in Spittlehouse and Stewart (2003), Spittlehouse (2005) and Bernier and Schoene (2009). There is now more evidence that maintaining a certain number of unfragmented forests is important in resisting to global climate change by local adaptation.

Finally, despite the fact that boreal soils will not constrain adaptation of boreal forests, some consequences of climatic warming may reduce the ability of certain species to respond to natural disturbances such as pest and disease outbreaks and extreme weather events. Under such conditions, Jump and Penuelas (2005) predicted an extinction risk among a number of species and that the rapid rate at which climate change is expected to occur may also increase the pressure on many species to adapt to their new northern soil conditions.

REFERENCES

Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. Oikos 79(3): 439-449.

Aerts, R. 2006. The freezer defrosting: Global warming and litter decomposition rates in cold biomes. Journal of Ecology 94(4): 713-724.

Agren, G.I., Bosatta, E., and Magill, A.H. 2001. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. Oecologia 128(1): 94-98.

Akinremi, O.O., McGinn, S.M., and Cutforth, H.W. 1999. Precipitation trends on the Canadian prairies. Journal of Climate 12(10): 2996-3003.

Allison, S.D., and Treseder, K.K. 2008. Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. Global Change Biology 14(12): 2898-2909.

Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R., Simpson, L.G., and Vinson, T.S. 1993. Boreal forests and tundra. Water, Air, and Soil Pollution 70(1-4): 39-53.

Attiwill, P.M., and Adams, M.A. 1993. Nutrient cycling in forests. New Phytologist 124(4): 561-582.

Beniston, M. 1997. Variations of snow depth and duration in the Swiss Alps over the last 50 years: Links to changes in large-scale climatic forcings. Climatic Change 36(3-4): 281-300.

Bergner, B., Johnstone, J., and Treseder, K.K. 2004. Experimental warming and burn severity alter soil CO2 flux and soil functional groups in a recently burned boreal forest. Global Change Biology 10(12): 1996-2004.

Bernier, P., and Schoene, D. 2009. Adapting forests and their management to climate change: an overview. Unasylva 60(231/232): 5-11.

Bonan, G.B., and Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. Annual review of ecology and systematics. Vol. 20: 1-28.

Bonan, G.B., Shugart, H.H., and Urban, D.L. 1990. The sensitivity of some high-latitude boreal forests to climatic parameters. Climatic Change 16(1): 9-29.

Bond-Lamberty, B., Peckham, S.D., Ahl, D.E., and Gower, S.T. 2007. Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature 450(7166): 89-92.

Bond-Lamberty, B., Peckham, S.D., Gower, S.T., and Ewers, B.E. 2009. Effects of fire on regional evapotranspiration in the central Canadian boreal forest. Global Change Biology 15(5): 1242-1254.

Bradshaw, C.J.A., Warkentin, I.G., and Sodhi, N.S. 2009. Urgent preservation of boreal carbon stocks and biodiversity. Trends in Ecology and Evolution 24(10): 541-548.

Bronson, D.R., Gower, S.T., Tanner, M., Linder, S., and Van Herk, I. 2008. Response of soil surface CO2 flux in a boreal forest to ecosystem warming. Global Change Biology 14(4): 856-867.

Bronson, D.R., Gower, S.T., Tanner, M. and Van Herk, I., 2009. Effect of ecosystem warming on boreal black spruce bud burst and shoot growth. Global Change Biology, 15(6): 1534-1543.

Certini, G. 2005. Effects of fire on properties of forest soils: A review. Oecologia 143(1): 1-10.

Chapin III, F.S., Callaghan, T.V., Bergeron, Y., Fukuda, M., Johnstone, J.F., Juday, G., and Zimov, S.A. 2004. Global change and the boreal forest: Thresholds, shifting states or gradual change? Ambio 33(6): 361-365.

Chapin III, F.S., McGuire, A.D., Randerson, J., Pielke Sr, R., Baldocchi, D., Hobbie, S.E., Roulet, N., Eugster, W., Kasischke, E., Rastetter, E.B., Zimov, S.A., and Running, S.W. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. Global Change Biology 6(SUPPLEMENT 1): 211-223.

Clemmensen, K.E., Michelsen, A., Jonasson, S., and Shaver, G.R. 2006. Increased ectomycorrhizal fungal abundance after long-term fertilization and warming of two arctic tundra ecosystems. New Phytologist 171(2): 391-404.

Conen, F., Leifeld, J., Seth, B., and Alewell, C. 2006a. Warming mobilises young and old soil carbon equally. Biogeosciences Discussions 3(4): 1355-1366.

Côté, L., Brown, S., Paré, D., Fyles, J., and Bauhus, J. 2000. Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. Soil Biology and Biochemistry 32(8-9): 1079-1090.

Crawford, R.M.M., Jeffree, C.E., and Rees, W.G. 2003. Paludification and forest retreat in northern oceanic environments. Annals of Botany 91(SPEC. ISS. JAN.): 213-226.

Czimczik, C.I., Schmidt, M.W.I., and Schulze, E.D. 2005. Effects of increasing fire frequency on black carbon and organic matter in Podzols of Siberian Scots pine forests. European Journal of Soil Science 56(3): 417-428.

Dabros, A. 2008. Effects of simulated climate change on post-disturbance «Populus tremuloides - Picea mariana» ecosystems in northwestern Quebec. In Department of Natural Resource Sciences. McGill, Montreal, Quebec, Canada

Dabros, A., and Fyles, J.W. 2009. Effects of open-top chambers and substrate type on biogeochemical processes at disturbed boreal forest sites in northwestern Quebec. Plant and Soil: 1-15.

Davidson, E.A., and Janssens, I.A. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440(7081): 165-173.

Davidson, E.A., Belk, E., and Boone, R.D. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biology 4(2): 217-227.

Davidson, E.A., Janssens, I.A., and Lou, Y. 2006. On the variability of respiration in terrestrial ecosystems: Moving beyond Q10. Global Change Biology 12(2): 154-164.

Decker, K.L.M., Wang, D., Waite, C., and Scherbatskoy, T. 2003. Snow removal and ambient air temperature effects on forest soil temperatures in Northern Vermont. Soil Science Society of America Journal 67(4): 1234-1242.

Domisch, T., Finér, L., Laine, J., and Laiho, R. 2006. Decomposition and nitrogen dynamics of litter in peat soils from two climatic regions under different temperature regimes. European Journal of Soil Biology 42(2): 74-81.

Dorrepaal, E., Cornelissen, J.H.C., Aerts, R., Wallén, B., and Van Logtestijn, R.S.P. 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? Journal of Ecology 93(4): 817-828.

Dunn, A.L., Barford, C.C., Wofsy, S.C., Goulden, M.L., and Daube, B.C. 2007. A long-term record of carbon exchange in a boreal black spruce forest: means, responses to interannual variability, and decadal trends. Global Change Biology 13(3): 577-590.

Dunn, A.L., Wofsy, S.C., and Bright, A.V.H. 2009. Landscape heterogeneity, soil climate, and carbon exchange in a boreal black spruce forest. Ecological Applications 19(2): 495-504.

Eliasson, P.E., McMurtrie, R.E., Pepper, D.A., Strömgren, M., Linder, S., and Agren, G.I. 2005. The response of heterotrophic CO2 flux to soil warming. Global Change Biology 11(1): 167-181.

Fan, Z., Neff, J.C., Harden, J.W., and Wickland, K.P. 2008. Boreal soil carbon dynamics under a changing climate: A model inversion approach. Journal of Geophysical Research G: Biogeosciences 113(4).

Fenton, N., Lecomte, N., Légaré, S., and Bergeron, Y. 2005. Paludification in black spruce (Picea mariana) forests of eastern Canada: Potential factors and management implications. Forest Ecology and Management 213(1-3): 151-159.

Fenton, N.J., and Bergeron, Y. 2007. Sphagnum community change after partial harvest in black spruce boreal forests. Forest Ecology and Management 242(1): 24-33.

Fierer, N., Colman, B.P., Schimel, J.P., and Jackson, R.B. 2006. Predicting the temperature dependence of microbial respiration in soil: A continental-scale analysis. Global Biogeochemical Cycles 20(3).

Fisher, R.F., Binkley, D. 2000. Ecology and management of forest soils. JohnWiley and Sons, New York. 512 pp.

Fisk, M.C., Schmidt, S.K., and Seastedt, T.R. 1998. Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. Ecology 79(7): 2253-2266.

Flannigan, M.D., Bergeron, Y., Engelmark, O., and Wotton, B.M. 1998. Future wildfire in circumboreal forests in relation to global warming. Journal of Vegetation Science 9(4): 469-476.

Flannigan, M., Campbell, I., Wotton, M., Carcaillet, C., Richard, P., and Bergeron, Y. 2001. Future fire in Canada's boreal forest: Paleoecology results and general circulation model - Regional climate model simulations. Canadian Journal of Forest Research 31(5): 854-864.

Flannigan, M.D., Logan, K.A., Amiro, B.D., Skinner, W.R., and Stocks, B.J. 2005. Future area burned in Canada. Climatic Change 72(1-2): 1-16.

Flannigan, M.D., Amiro, B.D., Logan, K.A., Stocks, B.J., and Wotton, B.M. 2006. Forest fires and climate change in the 21ST century. Mitigation and Adaptation Strategies for Global Change 11(4): 847-859.

Flannigan, M.D., Krawchuk, M.A., De Groot, W.J., Wotton, B.M., and Gowman, L.M. 2009. Implications of changing climate for global wildland fire. International Journal of Wildland Fire 18(5): 483-507.

Gamache, I., and Payette, S. 2005. Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. Journal of Biogeography 32(5): 849-862.

Giardina, C.P., and Ryan, M.G. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404(6780): 858-861.

Gibbard, S., Caldeira, K., Bala, G., Phillips, T.J., and Wickett, M. 2005. Climate effects of global land cover change. Geophysical Research Letters 32(23): 1-4.

Gillett, N.P., Weaver, A.J., Zwiers, F.W., and Flannigan, M.D. 2004. Detecting the effect of climate change on Canadian forest fires. Geophysical Research Letters 31(18): L18211 1-4.

Glooschenko, W.A., Roulet, N.T., Barrie, L.A., Schiff, H.I., and McAdie, H.G. 1994. The northern wetlands study (NOWES): an overview. Journal of Geophysical Research 99(D1): 1423-1428.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecological Applications 1(2): 182-195.

Goulden, M.L., Wofsy, S.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.M., Sutton, D.J., Bazzaz, A., and Munger, J.W. 1998. Sensitivity of boreal forest carbon balance to soil thaw. Science 279(5348): 214-217.

Grant, R.F., Barr, A.G., Black, T.A., Margolis, H.A., Dunn, A.L., Metsaranta, J., Wang, S., McCaughey, J.H., and Bourque, C.A. 2009. Interannual variation in net ecosystem productivity of Canadian forests as affected by regional weather patterns - A Fluxnet-Canada synthesis. Agricultural and Forest Meteorology 149(11): 2022-2039.

Groffman, P.M., Driscoll, C.T., Fahey, T.J., Hardy, J.P., Fitzhugh, R.D., and Tierney, G.L. 2001b. Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry 56(2): 135-150.

Gulledge, J., and Schimel, J.P. 2000. Controls on soil carbon dioxide and methane fluxes in a variety of taiga forest stands in interior Alaska. Ecosystems 3(3): 269-282.

Hamann, A., and Wang, T. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87(11): 2773-2786.

Harden, J.W., Manies, K.L., Turetsky, M.R., and Neff, J.C. 2006. Effects of wildfire and permafrost on soil organic matter and soil climate in interior Alaska. Global Change Biology 12(12): 2391-2403.

Harding, R., Kuhry, P., Christensen, T.R., Sykes, M.T., Dankers, R., and Van der Linden, S. 2002. Climate feedbacks at the tundra-taiga interface. Ambio 31(SPEC. ISS. 12): 47-55.

Hardy, J.P., Groffman, P.M., Fitzhugh, R.D., Henry, K.S., Welman, A.T., Demers, J.D., Fahey, T.J., Driscoll, C.T., Tierney, G.L., and Nolan, S. 2001. Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. Biogeochemistry 56(2): 151-174.

Hart, S.C., DeLuca, T.H., Newman, G.S., MacKenzie, M.D., and Boyle, S.I. 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. Forest Ecology and Management 220(1-3): 166-184.

Hawkins, B.A. 2004. Summer vegetation, deglaciation and the anomalous bird diversity gradient in eastern North America. Global Ecology and Biogeography 13(4): 321-325.

Högberg, M.N., Högberg, P., and Myrold, D.D. 2007. Is microbial community composition in boreal forest soils determined by pH, C-to-N ratio, the trees, or all three? Oecologia 150(4): 590-601.

Houghton, J.T., Ding, Y., Griggs, D.J. et al. (2001) Climate Change 2001: the Scientific Basis. Third IPCC Report. Cambridge University Press, Cambridge.

Houghton, J. 2005. Global warming. Reports on Progress in Physics 68(6): 1343-1403.

IPCC. 2007. Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Edited by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller. Cambridge University Press, Cambridge, UK and New York.

Johnson, D.W., and Curtis, P.S. 2001. Effects of forest management on soil C and N storage: Meta analysis. Forest Ecology and Management 140(2-3): 227-238.

Johnstone, J.F., and Kasischke, E.S. 2005. Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. Canadian Journal of Forest Research 35(9): 2151-2163.

Jump, A.S., and Penuelas, J. 2005. Running to stand still: Adaptation and the response of plants to rapid climate change. Ecology Letters 8(9): 1010-1020.

Kaplan, J.O., Bigelow, N.H., Prentice, I.C., Harrison, S.P., Bartlein, P.J., Christensen, T.R., Cramer, W., Matveyeva, N.V., McGuire, A.D., Murray, D.F., Razzhivin, V.Y., Smith, B., Walker, D.A., Anderson, P.M., Andreev, A.A., Brubaker, L.B., Edwards, M.E., and Lozhkin, A.V. 2003. Climate change and Arctic ecosystems: 2. Modeling, paleodata-model comparisons, and future projections. Journal of Geophysical Research D: Atmospheres 108(19): ALT 12-1 - 12-17.

Kasischke, E.S., and Johnstone, J.F. 2005. Variation in postfire organic layer thickness in a black spruce forest complex in interior Alaska and its effects on soil temperature and moisture. Canadian Journal of Forest Research 35(9): 2164-2177.

Kellomaki, S., and Kolstrom, M. 1992. Simulation of tree species composition and organic matter accumulation in Finnish boreal forests under changing climatic conditions. Vegetatio 102(1): 47-68.

Keyser, A.R., Kimball, J.S., Nemani, R.R., and Running, S.W. 2000. Simulating the effects of climate change on the carbon balance of North American high-latitude forests. Global Change Biology 6(SUPPLEMENT 1): 185-195.

Kirschbaum, M.U. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biology and Biochemistry 27(6): 753-760.

Kirschbaum, M.U.F. 2000a. Will changes in soil organic carbon act as a positive or negative feedback on global warming? Biogeochemistry 48(1): 21-51.

Kirschbaum, M.U.F. 2000b. Forest growth and species distribution in a changing climate. Tree physiology 20(5-6): 309-322.

Kirschbaum, M.U.F. 2004. Soil respiration under prolonged soil warming: Are rate reductions caused by acclimation or substrate loss? Global Change Biology 10(11): 1870-1877.

Kirschbaum, M.U.F. 2006. The temperature dependence of organic-matter decomposition - Still a topic of debate. Soil Biology and Biochemistry 38(9): 2510-2518.

Knorr, W., Prentice, I.C., House, J.I., and Holland, E.A. 2005. Long-term sensitivity of soil carbon turnover to warming. Nature 433(7023): 298-301.

Kreutzweiser, D.P., Hazlett, P.W., and Gunn, J.M. 2008. Logging impacts on the biogeochemistry of boreal forest soils and nutrient export to aquatic systems: A review. Environmental Reviews 16: 157-179.

Lavoie, M., Paré, D., Fenton, N., Groot, A., and Taylor, K. 2005a. Paludification and management of forested peatlands in Canada: A literature review. Environmental Reviews 13(2): 21-50.

Lavoie, M., Paré, D., and Bergeron, Y. 2005b. Impact of global change and forest management on carbon sequestration in northern forested peatlands. Environmental Reviews 13(4): 199-240.

Liski, J., Nissinen, A., Erhard, M., and Taskinen, O. 2003. Climatic effects on litter decomposition from arctic tundra to tropical rainforest. Global Change Biology 9(4): 575-584.

Lloyd, J., and Taylor, J.A. 1994. On the temperature dependence of soil respiration. Functional Ecology 8(3): 315-323.

Lükewille, A., and Wright, R.F. 1997. Experimentally increased soil temperature causes release of nitrogen at a boreal forest catchment in southern Norway. Global Change Biology 3(1): 13-21.

Lundström, U.S., Van Breemen, N., and Bain, D. 2000. The podzolization process. A review. Geoderma 94(2-4): 91-107.

Luo, Y., Wan, S., Hui, D., and Wallace, L.L. 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413(6856): 622-625.

Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H., Lévesque, E., Molau, U., MÃ¸lgaard, P., Parsons, A.N., Svoboda, J., and Virginia, R.A. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biology 3(SUPPL. 1): 20-32.

McGuire, A.D., Sitch, S., Clein, J.S., Dargaville, R., Esser, G., Foley, J., Heimann, M., Joos, F., Kaplan, J., Kicklighter, D.W., Meier, R.A., Melillo, J.M., Moore Iii, B., Prentice, I.C., Ramankutty, N., Reichenau, T., Schloss, A., Tian, H., Williams, L.J., and Wittenberg, U. 2001. Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO2, climate and land use effects with four process-based ecosytem models. Global Biogeochemical Cycles 15(1): 183-206.

MacIver, D.C and Isaac, J.L. 1989. Profils bioclimatiques pour le Canada, 1951- 1980. Environnement Canada, Service de l'environnement atmosphérique.

McHale, P.J., and Mitchell, M.J. 1996. Disturbance effects on soil solution chemistry due to heating cable installation. Biology and Fertility of Soils 22(1-2): 40-44.

Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., and Morrisseau, S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. Science 298(5601): 2173-2176.

Mellander, P.E., Laudon, H., and Bishop, K. 2005. Modelling variability of snow depths and soil temperatures in Scots pine stands. Agricultural and Forest Meteorology 133(1-4): 109-118.

Moore, T.R. 1978. Soil oil Formation in Northeastern Canada Edited by Annals of the Association of American Geographers. Taylor & Francis, Ltd. on behalf of the Association of American Geographers. pp. 518-534

Neff, J.C., and Hooper, D.U. 2002. Vegetation and climate controls on potential CO2, DOC and DON production in northern latitude soils. Global Change Biology 8(9): 872-884.

Neff, J.C., Harden, J.W., and Gleixner, G. 2005. Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. Canadian Journal of Forest Research 35(9): 2178-2187.

Niinistö, S.M., Silvola, J., and Kellomäki, S. 2004. Soil CO2 efflux in a boreal pine forest under atmospheric CO2 enrichment and air warming. Global Change Biology 10(8): 1363-1376.

O'Connell, K.E.B., Gower, S.T., and Norman, J.M. 2003. Comparison of net primary production and light-use dynamics of two boreal black spruce forest communities. Ecosystems 6(3): 236-247.

Oechel WC, and Van Cleve K. 1986. The role of bryophytes in nutrient cycling in the taiga. In: K Van Cleve, FS Chapin III, PW Flanagan, LA Viereck, and CT Dyrness (eds.), Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function, Springer-Verlag, New York. pp. 121-137.Oechel, W.C., Vourlitis, G.L., Hastings, S.J., Ault Jr, R.P., and Bryant, P. 1998. The effects of water table manipulation and elevated temperature on the net CO2 flux of wet sedge tundra ecosystems. Global Change Biology 4(1): 77-90.

Oechel, W.C., Vourlitis, G.L., Hastings, S.J., Ault Jr, R.P., and Bryant, P. 1998. The effects of water table manipulation and elevated temperature on the net CO2 flux of wet sedge tundra ecosystems. Global Change Biology 4(1): 77-90.

O'Donnell, J.A., Turetsky, M.R., Harden, J.W., Manies, K.L., Pruett, L.E., Shetler, G., and Neff, J.C. 2009. Interactive effects of fire, soil climate, and moss on CO2 fluxes in black spruce ecosystems of interior Alaska. Ecosystems 12(1): 57-72.

O'Neill, K.P., Kasischke, E.S., and Richter, D.D. 2002. Environmental controls on soil CO2 flux following fire in black spruce, white spruce, and aspen stands of interior Alaska. Canadian Journal of Forest Research 32(9): 1525-1541.

O'Neill, K.P., Kasischke, E.S., and Richter, D.D. 2003. Seasonal and decadal patterns of soil carbon uptake and emission along an age sequence of burned black spruce stands in interior Alaska. Journal of Geophysical Research D: Atmospheres 108(1): FFR 11-1 FFR 11-15.

Osterkamp, T.E., and Romanovsky, V.E. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. Permafrost and Periglacial Processes 10(1): 17-37.

Pajari, B. 1995. Soil respiration in a poor upland site of Scots pine stand subjected to elevated temperatures and atmospheric carbon concentration. Plant and Soil 168-169(1): 563-570.

Paré, D., Boutin, R., Larocque, G.R., and Raulier, F. 2006. Effect of temperature on soil organic matter decomposition in three forest biomes of eastern Canada. Canadian Journal of Soil Science 86(2): 247-256.

Peterjohn, W.T., Melillo, J.M., Bowles, F.P., and Steudler, P.A. 1993. Soil warming and trace gas fluxes: experimental design and preliminary flux results. Oecologia 93(1): 18-24.

Peterjohn, W.T., Melillo, J.M., Steudler, P.A., Newkirk, K.M., Bowles, F.P., and Aber, J.D. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. Ecological Applications 4(3): 617-625.

Ping, C.L., Michaelson, G.J., Packee, E.C., Stiles, C.A., Swanson, D.K., and Yoshikawa, K. 2005. Soil catena sequences and fire ecology in the boreal forest of Alaska. Soil Science Society of America Journal 69(6): 1761-1772.

Read, D.J., Leake, J.R., and Perez-Moreno, J. 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Canadian Journal of Botany 82(8): 1243-1263.

Reichsten, M. 2007. Impact of climate change on forest soils carbon:principles, factors, models, uncertainties. Forestry and climate change: 125-135.

Rivers, A.R., and Lynch, A.H. 2004. On the influence of land cover on early Holocene climate in northern latitudes. Journal of Geophysical Research D: Atmospheres 109(21): D21114 1-19.

Robinson, C.H., Wookey, P.A., Parsons, A.N., Potter, J.A., Callaghan, T.V., Lee, J.A., Press, M.C., and Welker, J.M. 1995. Responses of plant litter decomposition and nitrogen mineralisation to simulated environmental change in a high arctic polar semi-desert and a subarctic dwarf shrub heath. Oikos 74(3): 503-512.

Robinson, C.H., Michelsen, A., Lee, J.A., Whitehead, S.J., Callaghan, T.V., Press, M.C., and Jonasson, S. 1997. Elevated atmospheric CO2 affects decomposition of Festuca vivipara (L.) Sm. litter and roots in experiments simulating environmental change in two contrasting arctic ecosystems. Global Change Biology 3(1): 37-49.

Robinson, C.H., Saunders, P.W., Madan, N.J., Pryce-Miller, E.J., and Pentecost, A. 2004. Does nitrogen deposition affect soil microfungal diversity and soil N and P dynamics in a high Arctic ecosystem? Global Change Biology 10(7): 1065-1079.

Roy, V., Bernier, P.Y., Plamondon, A.P., and Ruel, J.C. 1999. Effect of drainage and microtopography in forested wetlands on the microenvironment and growth of planted black spruce seedlings. Canadian Journal of Forest Research 29(5): 563-574.

Rustad, L.E., and Fernandez, I.J. 1998. Soil warming: Consequences for foliar litter decay in a spruce-fir forest in Maine, USA. Soil Science Society of America Journal 62(4): 1072-1080.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, J., Alward, R., Beier, C., Burke, I., Canadell, J., Callaghan, T., Christensen, T.R., Fahnestock, J., Fernandez, I., Harte, J., Hollister, R., John, H., Ineson, P., Johnson, M.G., Jonasson, S., John, L., Linder, S., Lukewille, A., Masters, G., Melillo, J., Mickelsen, A., Neill, C., Olszyk, D.M., Press, M., Pregitzer, K., Robinson, C., Rygiewiez, P.T., Sala, O., Schmidt, I.K., Shaver, G., Thompson, K., Tingey, D.T., Verburg, P., Wall, D., Welker, J., and Wright, R. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126(4): 543-562.

Saxe, H., Cannell, M.G.R., Johnsen, Ã., Ryan, M.G., and Vourlitis, G. 2001. Tree and forest functioning in response to global warming. New Phytologist 149(3): 369-400.

Sauer, D., Sponagel, H., Sommer, M., Giani, L., Jahn, R., and Stahr, K. 2007. Podzol: Soil of the year 2007. A review on its genesis, occurrence, and functions. Journal of Plant Nutrition and Soil Science 170(5): 581-597.

Sazonova, T.S., Romanovsky, V.E., Walsh, J.E., and Sergueev, D.O. 2004. Permafrost dynamics in the 20th and 21st centuries along the East Siberian transect. Journal of Geophysical Research D: Atmospheres 109(1): D01108 1-20.

Seibert, J., Stendahl, J., and Sørensen, R. 2007. Topographical influences on soil properties in boreal forests. Geoderma 141(1-2): 139-148.

Serreze, M.C., Walsh, J.E., Chapin Iii, F.S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W.C., Morison, J., Zhang, T., and Barry, R.G. 2000. Observational evidence of recent change in the northern high-latitude environment. Climatic Change 46(1-2): 159-207.

Shaw, M.R., and Harte, J. 2001. Control of litter decomposition in a subalpine meadow-sagebrush steppe ecotone under climate change. Ecological Applications 11(4): 1206-1223.

Skre, O., Baxter, R., Crawford, R.M.M., Callaghan, T.V., and Fedorkov, A. 2002. How will the tundra-taiga interface respond to climate change? Ambio 31(SPEC. ISS. 12): 37-46.

Smith, P., Fang, C., Dawson, J.J.C., and Moncrieff, J.B. 2008. Impact of Global Warming on Soil Organic Carbon. In Advances in Agronomy. pp. 1-43.

Spittlehouse, D.L. and R.B. Stewart. 2003. Adapting to climate change in forest management. BC Journal of Ecosystems and Management 4(1): 7–17.

Spittlehouse, D.L. 2005. Integrating climate change adaptation into forest management. Forestry Chronicle 81(5): 691-695.

Stone, R.S., Dutton, E.G., Harris, J.M., and Longenecker, D. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change. Journal of Geophysical Research D: Atmospheres 107(9-10): 10-1.

Strömgren, M., and Linder, S. 2002. Effects of nutrition and soil warming on stemwood production in a boreal Norway spruce stand. Global Change Biology 8(12): 1195-1204.

Stützer, A. 1999. Podzolisation as a soil forming process in the alpine belt of Rondane, Norway. Geoderma 91(3-4): 237-248.

Trainor, S.F., Calef, M., Natcher, D., Chapin Iii, F.S., McGuire, A.D., Huntington, O., Duffy, P., Rupp, T.S., Dewilde, L., Kwart, M., Fresco, N., and Lovecraft, A.L. 2009. Vulnerability and adaptation to climate-related fire impacts in rural and urban interior Alaska. Polar Research 28(1): 100-118.

Trumbore, S.E., Chadwick, O.A., and Amundson, R. 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science 272(5260): 393-396.

Van Cleve, K., Oechel, W.C., and Hom, J.L. 1990. Response of black spruce (Picea mariana) ecosystems to soil temperature modification in interior Alaska. Canadian Journal of Forest Research 20(9): 1530-1535.

Van Cleve, K., and Powers, R.F. 1995. Soil carbon, soil formation, and ecosystem development. Carbon forms and functions in forest soils: 155-200.

Verburg, P.S.J., Van Loon, W.K.P., and Lukewille, A. 1999. The CLIMEX soil-heating experiment: Soil response after 2 years of treatment. Biology and Fertility of Soils 28(3): 271-276.

Veillette, J.J. 1994. Evolution and paleohydrology of glacial Lakes Barlow and Ojibway. Quaternary Science Reviews 13(9-10): 945-971.

Viereck, L.A., Dyrness, C.T., Van Cleve, K., and Foote, M.J. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Canadian Journal of Forest Research 13(5): 703-720.

Vogel, J.G., Valentine, D.W., and Ruess, R.W. 2005. Soil and root respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates. Canadian Journal of Forest Research 35(1): 161-174.

Vygodskaya, N.N., Groisman, P.Y., Tchebakova, N.M., Kurbatova, J.A., Panfyorov, O., Parfenova, E.I., and Sogachev, A.F. 2007. Ecosystems and climate interactions in the boreal zone of northern Eurasia. Environmental Research Letters 2(4).

Waldrop, M.P., and Harden, J.W. 2008. Interactive effects of wildfire and permafrost on microbial communities and soil processes in an Alaskan black spruce forest. Global Change Biology 14(11): 2591-2602.

Wickland, K.P., and Neff, J.C. 2008. Decomposition of soil organic matter from boreal black spruce forest: Environmental and chemical controls. Biogeochemistry 87(1): 29-47.

Wurzburger, N., Hartshorn, A.S., and Hendrick, R.L. 2004. Ectomycorrhizal fungal community structure across a bog-forest ecotone in southeastern Alaska. Mycorrhiza 14(6): 383-389.

Yoshikawa, K., Bolton, W.R., Romanovsky, V.E., Fukuda, M., and Hinzman, L.D. 2003. Impacts of wildfire on the permafrost in the boreal forests of interior Alaska. Journal of Geophysical Research D: Atmospheres 108(1): FFR 4-1 FFR 4-14.

Zhang, T., Frauenfeld, O.W., Serreze, M.C., Etringer, A., Oelke, C., McCreight, J., Barry, R.G., Gilichinsky, D., Yang, D., Ye, H., Ling, F., and Chudinova, S. 2005. Spatial and temporal variability in active layer thickness over the Russian Arctic drainage basin. Journal of Geophysical Research D: Atmospheres 110(16): 1-14.

Zhang, D., Hui, D., Luo, Y., and Zhou, G. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. Journal of Plant Ecology 1(2): 85–93.