Effects of simulated climate change on post-disturbance *Populus tremuloides* - *Picea mariana* ecosystems in northwestern Quebec

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CONTRIBUTIONS OF THE AUTHORS TO THE THESIS

The six chapters of this thesis were written in the form of manuscripts, which will be submitted shortly to ecological and forestry scientific journals. The candidate and first author, Anna Dabros, and the supervisor, Dr. James W. Fyles, were in charge of main research design and data analysis for the project. Additional advice was given by the project committee members Dr. Benoît Côté and Dr. Timothy Moore. Anna Dabros was in charge of experimental design, setup, and field data collection for Chapters 1 and 3-6. Data analysis, interpretation, and manuscript writing of these chapters were performed by Anna Dabros under the supervision of Dr. James W. Fyles. Anna Dabros, Dr. James W. Fyles, Dr. Ian Strachan, and Dr. Benoît Côté contributed to experimental design and setup, data collection, analysis and interpretation, and writing of the manuscript for Chapter 2, which has been submitted to Agricultural and Forest Meteorology journal.

ABSTRACT

In the mixedwood-boreal transitional forest of northwestern Quebec, the establishment of trembling aspen (*Populus tremuloides* Michx.) has been observed at the extremes of their regional distribution, in areas previously dominated by black spruce (*Picea mariana* (Miller) BSP). Our main objective was to explore how climate change could affect the growth and performance of aspen and black spruce. Climate change simulation was provided by the installation of twenty open-top chambers (OTCs) and twenty control plots in the summer of 2005 at three disturbed sites (post-fire, logging road and logging). Each plot enclosed a pair of aspen and spruce seedlings. In comparison to control plots, the conditions in the OTCs were marked by higher air temperatures (2-3°C), drier soil (up to 10% volumetric moisture content) and cooler soil (up to 2.6°C), lower supply rates of Ca and Mg, and slower decomposition of aspen litter. Warm weather and high rainfall were likely responsible for increased height growth and advanced spring bud burst of aspen growing in the OTCs during the 2006 growing season, but not during the cooler and drier season of 2007. Leaf calcium concentration was higher, and beetle leaf herbivory was lower for OTC aspen in comparison to control plot aspen. Spruce was not affected by OTC treatment in terms of height growth, but its final dry biomass was higher, and spring bud burst was advanced by 2-3 days in the OTCs compared to control plots. Both species showed trends of higher root tip number and lower % ectomycorrhizae (ECM) colonization in the OTCs, and vice versa in the control plots. Aspen appeared to be more dependent on ECM colonization; therefore, potential effects of climatic changes on ECM would have a larger impact on aspen than spruce. Overall, aspen may be more responsive (positively and negatively) than spruce to erratic inter-seasonal weather conditions often associated with climate change. A less sensitive, more stable response to weather variations may give spruce an advantage over aspen in the long term, as the years in which the conditions are less favourable towards the physiological requirements of aspen may be detrimental to their regional populations.

RÉSUMÉ

L'établissement de peupliers faux-trembles (*Populus tremuloides* Michx.) fut observé au nord de sa distribution, dans la forêt boréale mixte, en des endroits auparavant dominés par l'épinette noire (*Picea mariana* (Miller) BSP). Nous avons réalisé une simulation de réchauffement climatique, dans le but d'explorer comment les changements climatiques pourraient influencer la croissance du peuplier faux-tremble et de l'épinette noire. Le traitement de réchauffement fut fourni par l'installation, à l'été 2005, de vingt chambres sans toit (CST) et de vingt parcelles témoins et ce, sur trois sites distincts (post-incendie, route forestière et site de coupe). Chaque parcelle comprenait un jeune peuplier faux-tremble et une jeune épinette noire. Comparativement aux parcelles témoins, les conditions dans les CST furent marquées par des températures supérieures (2-3°C), un sol plus sec (jusqu'à 10% du contenu volumétrique) et plus frais (jusqu'à 2,6°C), une disponibilité plus faible du Ca et du Mg, ainsi que par une décomposition plus lente de la litière de peuplier faux-tremble. Les conditions plus chaudes et les précipitations plus intenses de la saison 2006 furent probablement responsables pour la croissance supérieure et l'éclosion plus hâtive des bourgeons, mais pas durant la saison fraîche et pluvieuse de 2007. Les dommages dus aux coléoptères furent moins importants dans les CST, ce qui peut être explicable par la concentration foliaire de calcium supérieure qu'on y observa. La croissance de l'épinette noire ne fut pas affectée en terme de hauteur par les CST, mais sa biomasse finale y était supérieure et l'éclosion des bourgeons s'y faisait 2-3 jours plus tôt que dans les parcelles témoins. Les deux espèces développèrent davantage de radicelles et furent moins colonisées par les ectomycorhizes (ECM) dans les CST que dans les parcelles témoins. Le peuplier faux-tremble sembla plus dépendant de la colonisation par le ECM, donc des effets potentiels des changements climatique sur les ECM se répercuteraient davantage sur cette espèce que sur l'épinette noire. En somme, le peuplier faux-tremble semble répondre davantage (à la fois positivement et négativement) aux variations climatiques erratiques associées aux changements climatiques. La réponse moins drastique de l'épinette noire aux variations météorologiques pourrait à long terme lui donner un avantage par rapport au peuplier faux-tremble, puisque les années pendant lesquelles les conditions sont défavorables à ses besoins physiologiques pourraient affecter négativement sa population régionale.

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LITERATURE REVIEW

…"At this stage it is not possible to say with any degree of certainty what will happen. In all likelihood what will happen is that different species will respond individually to a changing climate, migrating in different directions and at different rates. New combinations of species will arise and old ones will disappear as occurred in the past (Davis 1984). Thus, any prediction of how the boreal forest will respond to a changing climate requires recognition of the different functional roles of the current species and the heterogeneity of soils and disturbance regimes in the landscape".

(Pastor and Mladenoff 1992)

Boreal forests in the changing climate

The boreal forest ecosystem occupies 12 x 10^6 km^2, or 17% of the land surface in the world (Melillo et al. 1996). Found within the high latitudes of the Northern Hemisphere, boreal forests are of critical importance not only from the socio-economic perspective in terms of resource utilization, but also because they affect the biogeochemical, climatic and ecological processes, both at the global and regional scale (Bonan et al. 1992; Melillo et al. 1996). Boreal forests play an important role in global carbon storage and cycling (an estimated 50-250 Tg carbon/year) (Melillo et al.1996; Moore 1996), which leads to continuous interactions and reciprocal effects between boreal forests and the global climate (Bonan et al. 1992).

As predicted by General Climate Models (GCMs), a notable rise in concentration of greenhouse gases (CO_2, NO_x, CH_4, O_3) may result in a global change of climatic patterns, with especially pronounced effects noticeable at high latitudes (ACIA 2004; IPCC 2007). Since pre-industrial times, the concentrations of global atmospheric CO_2 and

NO_x have risen by 30% and 36% respectively (Barnola et al. 1995; Stott et al. 2000; IPCC 2007). The most recent IPCC report states that the global mean CO_2 concentration was at 379 ppm in the year 2005, in comparison to an estimated 280 ± 20 ppm in the mid-18th century (IPCC 2007).While changes in climate have accompanied the Earth since pre-historic times, the underlying premise of the increasing rate of presently observed climate change is the unquestionable role of anthropogenic causes, including fossil fuel combustion, deforestation, fertilization, and agricultural waste management (Keeling et al. 1995; Karnosky et al. 2001).

Higher concentrations of greenhouse gases result in increased trapping of long wave radiation, leading to an unprecedented and continuing rise of the global surface mean temperature, which increased by $0.74^{o}C \pm 0.18$ between 1906 and 2005, the majority of which occurred within last the 50 years (IPCC 2007). This global warming is already having noticeable effects on numerous interdependent environmental factors, from precipitation regimes, through soil moisture and temperature, thereby influencing decomposition and mineralization processes, to pronounced alterations in fire regimes (Weber and Flannigan 1997). Since these processes consist of an interplay of complex interactions between the living organisms and environmental factors, including the biochemistry of their ecosystems, climatic changes are expected to have a dramatic effect on the biogeochemical processes occurring in the boreal forest community. It is expected that changes in these interactions will be reflected in changes to the vegetational composition and current boundaries of boreal forest (Weber and Flannigan 1997).

Plant and ecosystem responses to global change: multilevel perspective

The interaction of elevated greenhouse gases and global temperatures on plant growth are complex at numerous levels (Johnson et al. 2001). Apart from directly playing a key role in internal physiological and metabolic plant processes, including photosynthesis and respiration (Körner 2006), temperature has an indirect effect on plant growth and performance by affecting the length of the growing season (Jarvis and Linder 2000), and nutrient availability due to its role in biogeochemical processes such as litter decomposition (Meentemeyer 1978; Hobbie 1996; Melillo et al.1996; Rustad and

Fernandez 1998; Melillo et al. 2002), microbial respiration (MacDonald et al. 1995; Rustad et al. 2001), nutrient cycling, (Van Cleve et al. 1983; MacDonald et al.1995; Melillo et al. 2002; Strömgren and Linder 2002), and nutrient uptake (Bassirirad et al. 2000).

Jarvis and Linder (2000) argued that annual growth of boreal trees is determined predominantly by the timing of spring thaw and autumn freeze, by the capture of CO_2 in the spring, and by nutrient capture in the summer - all of which are directly or indirectly linked to soil and air temperature conditions. Increasing levels of greenhouse gases lead to global increases in temperature, thus affecting all of the above-mentioned temperature-related effects on plant growth and performance. However, elevated greenhouse gas concentrations alone, also have a direct impact on plants. Depending on their nature and properties, various greenhouse gases have different effects on plants and their ecosystems. For example, while increased levels of CO_2 and the higher availability of nitrogen originating from atmospheric deposition are generally associated with a positive response on plant growth and ecosystem functioning, the effects of O_3 are largely negative (Karnosky et al. 2001, 2003). Secondly, high concentrations of some greenhouse gases may ultimately contribute to growth acceleration to the point where the plant will have no time for physiological adaptation to the rapidly changing environmental conditions (Karnosky et al. 2001). For instance, in the northern coniferous forests, luxurious nitrogen deposition may induce growth of new shoots too late in the season for them to survive through the winter, or it may cause an increase in root mortality and decrease in root-mycorrhizal associations (Aber et al. 1989; Karnosky et al. 2001). Thirdly, responses to elevated greenhouse gases and associated climatic changes differ between individual plant species, and even between different genotypes within the same species (Karnosky et al. 2003). Finally, the effects of climate change differ across different ecosystems and habitats, affecting in a unique manner grasslands and forests, and on a smaller scale, temperate and boreal forests (Breymeyer et al. 1996). Even within the same region, different types of forests (e.g. mixed or coniferous) are expected to show varying responses to climate change and the factors associated with and influenced by it, such as the fire regimes (Bergeron and Flannigan 1995).

Climate change, nutrient cycling and decomposition rates

One of the major limiting factors affecting the growth, performance and composition of forest vegetation is nutrient availability (Chapin et al. 1986; Mahendrappa et al. 1986; Jarvis and Linder 2000). Physiological plant processes (growth rate, photosynthesis, respiration, nutrient uptake) and soil processes (microbial activity, decomposition rates) are associated with nutrient cycling and are highly dependent on temperature and moisture regimes. Consequently, the cycling of nutrients such as carbon, nitrogen and phosphorus is especially susceptible to modifications under the changing climatic conditions (Weber and Flannigan 1997).

Elevated CO_2 concentrations often lead to a short-term increase in plant biomass (Kimball 1983), which may have a positive effect on nutrient uptake and plant performance. Increases, for example, in root biomass may facilitate water uptake and allow for more extensive soil exploration and access to new nutrient pools (Johnson et al. 2001). However, in the long run, plant performance will ultimately depend on the balance between nutrient uptake and nutrient loss, which in turn are influenced by microbial activity and decomposition rates that regulate the availability of nutrients (Arp et al. 1997).

Increased plant growth as a result of CO_2 fertilization and higher temperatures may also be constrained by water shortage, due to increased evapotranspiration (Saxe et al. 2001). For example, in a study of response of Arctic plants to treatments of experimental summer warming and increased winter snow depth, Welker et al. (2005) found that in comparison to dry tundra, plants growing in moist tundra were overall much more responsive to climatic change simulation treatments, with up to 25% increases in foliar N concentrations. Drier soil conditions may also inhibit decomposition process, and, thus, nutrient availability (Aerts 2006). For example, Robinson et al. (1995) observed a significant decomposition increase only upon experimental water addition, but not under experimentally elevated temperatures alone.

It has been suggested that in a positive feedback loop, warmer soils may accelerate decomposition process and release of CO_2 into the atmosphere, which may, in turn, lead to further temperature increases (Kirschbaum 2000; ACIA 2004; Knorr et al.

2005; Powlson 2005; IPCC 2007). Experimentally elevated CO_2 levels have caused significant increases in numerous factors known to be crucial in soil respiration (e.g. King et al. 2001; Emmett et al. 2004), microbial biomass and microbial enzymes (e.g. Larson et al. 2002; Phillips et al. 2002), microbial respiration (e.g. Phillips et al. 2002) and soil moisture (e.g. Karnosky et al. 2003). Coupled with soil warming caused by the heat-trapping effect of greenhouse gases, this suggests that elevated CO_2 would lead to higher rates of microbial activity and thus, higher decomposition rates.

Both CO_2 and temperature increases may also, nonetheless, induce negative feedbacks constraining further warming: accelerated nutrient cycling due to increased decomposition rates, continuous 'CO_2 fertilization' and warmer temperatures are expected to promote plant growth and thus provide more plant biomass available for storage of excess carbon, thus reducing the CO_2 levels which contributed to higher temperatures in the first place (Myneni et al. 1997; Ciais et al. 2000). A large part of the apparently sequestered carbon, however, is stored in short-lived plant tissues such as foliage, which decompose rapidly during the initial breakdown of labile carbon; meanwhile the accumulation of carbon in the recalcitrant litter pool characterized by extremely slow turnover is rather limited (Schlesinger and Lichter 2001). Ultimately, carbon storage within soil and plant tissues may be curtailed by limited carbon accumulation within the long-lasting, slowly decomposing C pools, and by the limitations of water and nutrients (especially nitrogen) on plant growth and production of biomass available to C sequestration (Oren et al. 2001; Melillo et al. 2002; Aerts 2006).

Higher temperatures and CO_2 levels may increase plant biomass production per unit uptake of N (Zak et al. 1993), widening the C:N ratio, and/or potentially increasing the lignin and cellulose content in plants (Johnson et al. 2001). For example, increased foliar C:N ratio has been reported under experimentally elevated CO_2 conditions for trembling aspen (*Populus tremuloides* Michx.) (Lindroth et al. 2001). Such changes in plant chemical composition result in plant litter with slower decomposition rates (Arp et al. 1997). This has been shown, for example, in the study conducted on the effects of elevated CO_2 on birch (*Betula pendula* Roth.) and sitka spruce (*Picea sitchensis* (Bong.) Carr.), where Cotrufo and Ineson (1995) reported an increase in C:N ratio, and observed decreased decomposition rates. Laboratory studies on tulip poplar (*Liriodendron* *tulipifera* L.) in CO_2-enriched environment also resulted in slower decomposition rates of the produced plant litter (Boerner and Rebbeck 1993). Meanwhile, Johnson et al. (2000) found no effects of elevated CO_2 on decomposition and nitrogen mineralization of litterfall in ponderosa pine (*Pinus ponderosa* Lawson.).With all the conflicting evidence, the final verdict on the potential effects of CO_2 increases on litter quality and decomposition rates remains inconclusive (Johnson et al. 2001).

Finally, the rates of decomposition and the magnitude of the response to changing climatic conditions will depend on inherent traits of plant type. In a study on decomposition of foliar litter in different forest types of British Columbia, Prescott et al. (2004) concluded that the broadleaf litter decomposed more rapidly than the needle litter within the first year of decomposition. Under the confounding and retroactive effects of changing climatic conditions and system responses to them (Bonan et al. 1992), many habitats may become more suitable for growth of species with previously limited abundances at what were once inhospitable limits of their distributional ranges. This may lead to shifts in current abundances of species within communities, as well as migrations and range expansions of species into new habitats. Thus, superimposed on the changes in decomposition rates caused by climate change-related modifications in the plant tissue chemical structure of the current community plant members, shifts in composition and dominance of different species within communities may lead to further changes in decomposition rates due to inherent interspecific differences in the chemical makeup. With respect to global change, the significance of such community composition shifts lies within the previously discussed impact of decomposition rates on positive feedback to climatic warming, and associated with it, carbon sequestration capacity of different forest community types.

Species migrations and changes in abundance within communities as responses to climate change

Rapid climate warming and its impact on decomposition, nutrient cycling and soil moisture regimes could lead to pronounced shifts in species community composition within biomes (Weber and Flannigan 1997; Saxe et al. 2001; Walther 2003; Parmesan

2006; Walker et al. 2006). Potential alterations in species distribution and vegetation dynamics are expected to be especially prominent within the transition zones of the southern and northern limits of the boreal forest (Weber and Flannigan 1997; Walker et al. 2006). At a smaller scale, this might include shifts in dominance and abundance of already existing plant species and/or plant forms within a community. Such shifts have been reported in climate change simulation studies. For example, after 5-7 years of experimental warming using open-top chambers (OTCs), Hollister et al. (2005) reported decreases between 1.4 - 4.6% in moss species, with simultaneous increases in standing dead plant mass and graminoids. Meanwhile, Jónsdóttir et al. (2005) found that after 5 years of experimental warming in dwarf shrub communities of Iceland, evergreen and deciduous dwarf shrubs increased in abundance by 50%, while bryophytes decreased by 18%. Likewise, meta-analysis of 11open-top chamber experiments forming a part of International Tundra Experiment (ITEX) revealed that responses of tundra plant communities to a 1-3°C temperature increase were observed within two growing seasons, and that the OTC treatment increased the height and cover of deciduous shrubs and graminoids (Walker et al. 2006). Evidence of increases in shrub abundance at high latitudes comes also from Alaska, where the air temperatures have increased ~ 6°C over the past 30 years (Sturm et al. 2001, 2005). Overall, the responses to climate change or the experimental simulations thereof indicate the most pronounced abundance increases of shrubs and graminoids and decreases of bryophytes and lichens.

At a larger scale, massive species migrations and encroaching of southern species into northern habitats have been predicted (Huntley 1991; Prentice 1992; Weber and Flannigan 1997; Karnosky et al. 2001; Hinzman et al. 2005; Parmesan 2006). Encroachments of such kind have already been reported e.g. by Landhäusser and Wein (1993), who observed that in the post-fire tundra of the western Arctic, coniferous stands have been replaced by deciduous species typical of temperate and southern boreal forests, including poplar and birch. Also, the climate change simulation runs made for Canada by the Goddard Institute of Space Studies (GISS) suggest an overall increase of temperate, grassland, transitional grassland and semidesert ecosystems at the expense of subarctic and boreal ecosystems (Rizzo and Wiken 1992).

At the physiological level, intrinsic differences between species may lead to shifts in competitive balance within the ecological community experiencing climatic changes and changing species composition. For instance, encroachment of southern broadleaf deciduous species into northern coniferous boreal habitats (e.g. Landhäusser and Wein 1993) may have a detrimental effect on moss and lichen species, which constitute a prominent ground cover within northern habitats. A specific example of this could be presented with the case of trembling aspen and its negative impact on *Sphagnum* moss through chemical interference and physical effects associated with a broadleaf structure of the litter that can lead to smothering (Fenton et al. 2005).

It has been suggested that in some cases the climatic changes may be progressing too rapidly to stay in equilibrium with the rates of species migration (Huntley 1991). Successful migration of species requires a completion of the full live cycle, from germination through seedling establishment to subsequent reproduction, for many individuals of a given species (Weber and Flannigan 1997). Those species that are not able to adapt quickly enough to climatically induced changes are likely to become extinct (Huntley 1991; Weber and Flannigan 1997; IPCC 2007). The extinction events may represent responses to both, stresses from changing abiotic factors for which the species is not physiologically ready, and from changing biotic factors, such as competitive pressure of more successful species, which may eventually replace the maladapted species (Weber and Flannigan 1997; IPCC 2007).

Paleoclimatic and paleoecological research of Lavoie and Payette (1996) suggests that the boundaries of the boreal forest in subarctic Quebec remained stable during the last 2000-3000 years. Yet, they go on to claim that global temperature changes in the order of several degrees Celsius, (current projections for the global warming) could induce noticeable movement of these boundaries. The potential of sudden disturbance of the stability, which has been maintained over the last 2000-3000 years, demonstrates the severity of the unprecedented rate of climate change.

Ultimately, the adaptation potential and/or successful migration of an individual species in the face of projected climatic changes will determine the species' survival and persistence. However, it should be stressed that predictions for the species' migratory patterns in response to global warming are difficult to make, not only because of the overall uncertainty of the impacts of global change, but also because migrations are expected to vary across different regions, even within the same ecosystem, such as the boreal forest (Bergeron and Flannigan 1995).

Climate change and phenology

In a recent global meta-analysis on the climate change impact on natural systems, Parmesan and Yohe (2003) reported that 62% of the 677 assessed plant and animal species have shown trends of advanced phenology in the spring, with the mean forward shift of 2.3 days in timing of spring life events. For plant species, advancement of over two days in spring growth initiation could have a profound impact on the species' overall performance over the season, especially in climates characterized by seasonality such as the northern regions, where the length of the growing season is often relatively short.

The timing of the spring thaw, autumn freeze and snowfall define the length of the growing season in northern regions (Jarvis and Linder 2000). Consequently, changes in the amount of snow precipitation and the timing of the winter freeze and snowmelt may lead to shifts in the timing of bud burst, leaf development, and flower blooming in the spring, as well as leaf and flower senescence in the late summer and fall. The issue of winter precipitation and snowmelt under changing climate remain largely unresolved (Qin et al. 2006; Edwards et al. 2007). Some researchers (e.g. Galen and Stanton 1993) claim that the temperature increase will reduce snow accumulation by advancing the snowmelt and prolonging the growing season. However, "colder soils in a warmer climate" (Groffman et al. 2001), resulting from an earlier snowmelt and the exposure of the soil to frequent freezing episodes of early spring may compromise plant growth and performance, ultimately diminishing potential benefits of the longer growing season. Nonetheless, extensive phenological surveys and studies of boreal and northern regions indicate that the growing season indeed became longer over the past few decades, and spring phenological events are occurring earlier in the season (e.g. Arft et al. 1999; Menzel and Fabian 1999; Ahas et al. 2002; Walker et al. 2006). For example, in Europe the timing of leaf development advanced on average by six days over the last 30 years (Menzel and Fabian 1999).

Experimental simulations of climatic changes likewise support the evidence that warmer climate will prolong the growing season of northern plants. For example, Slaney et al. (2007) observed that bud development and shoot extension of Norway spruce (*Picea abies* (L.) Karst.) were advanced by two to three weeks under a simulated climate warming of 3°C in the summer and 5°C in the winter, using whole-tree chambers. Also, in meta-analysis of 13 northern latitude sites of the International Tundra Experiment (ITEX), one to four years of passive warming treatment using open-top chambers lead to earlier leaf bud burst and flowering (Arft et al. 1999).

Following the required chilling period over the fall and winter seasons, the occurrence of mild temperatures in spring allows for accumulation of sufficient heat sums for the initiation of phenological spring events such as bud burst (Slaney et al. 2007). Therefore, a warmer and earlier spring should result in earlier accumulation of heat sums and advanced spring phenology. However, Strömgren and Linder (2002) found that even with six years of soil warming using electrical cables, the bud break of Norway spruce always commenced during the first week of June and that within about five days of this commencement almost all shoots had flushed; the warming treatment had no effect on the timing of bud development. This happened despite the fact that warmer soil treatment lead to an earlier snowmelt and prolonged growing season. Warmer growing conditions also did not advance the spring phenology in a study by Bailey and Harrington (2006), who monitored bud burst of Douglas fir (*Pseudotsuga menziensii* (Mirb.) Franco) at cooler and warmer microsites. They observed that in two out of three sampling seasons, saplings at the cooler microsites broke bud two to four days earlier than those at the warmer microsites. This suggests that factors other than spring air and soil temperatures, for example, day length and accumulated duration of light, are among other cues, which may play a fundamental role in the timing of spring phenological events of northern plant species (Slaney et al. 2007). While the day length and associated photoperiod can vary seasonally at northern latitudes, unlike soil and air temperatures, they will not be affected by the current climatic changes as far as we are concerned at the moment.

Climate change, forest fires and successional patterns

As major factors characterizing forest fires, including fire intensity, frequency, size, type (crown, surface, ground) and severity (depth of burn) are highly dependent on climate, global climate changes may lead to dramatic alterations of forest fire regimes (Weber and Flannigan 1997). More precisely, warmer post-fire soils may enhance microbial activity, thus accelerating decomposition and nutrient mineralization rates, promoting plant growth and subsequent litter (fuel) production - all of which create conditions conductive to fires (Anderson 1991; Weber and Flannigan 1997). Indeed, fire events have increased substantially in Canada since 1970s (Kurz et al. 1995). However, it should be noted that these increases are largely confined to drier regions of western Canada, while in eastern Canada fire frequency has actually decreased (Bergeron et al. 2004). These observations are consistent with simulation models of Bergeron and Flannigan (1995), and Flannigan et al. (2001) who predicted a dramatic increase of fire events over western Canada, with a simultaneous decrease in fire frequency for eastern Canada.

Inherent climatic differences between western and eastern regions may be responsible for differences in potential modifications to fire regimes under the global climate change. On a smaller scale, within a particular region, fundamental differences in the structure and function of a particular forest type are expected to result in different responses to fire regimes. For example, increased soil temperature and pH after the fire, may enhance mineralization, which, along with the contribution of mineral ashes, may restore the habitat to potentially higher nutrient levels than in the pre-fire conditions (Dyrness and Norum 1983). Such post-fire conditions are favourable to the colonization of early successional deciduous species such as trembling aspen, which is associated with a high mineral nutrient demand, and as such, should perform optimally in the nutrient-rich habitats with the forest floor of shallow organic matter and easy accessible mineral layer (Alban et al. 1978; Van Cleve et al. 1983; Brais et al. 1995).

Species composition, and the time since last fire are among the factors influencing the composition and properties of the forest floor (Paré et al. 1993). In the southern boreal forests of Quebec, trembling aspen along with the white birch (*Betula papyrifera*

Marshall) are among the pioneer hardwood species that first colonize the post-fire sites (Brais et al. 1995). The traditional view was that with time, these burned boreal forest sites follow a natural succession, accumulating slowly decomposing organic matter and creating cool, nutrient-poor conditions, typical of late successional stands of black spruce, which eventually become one of the dominant species in these systems (Bergeron and Dubuc 1989). However, the successional pathway of mixwood-boreal transitional zone in NW Quebec follows a complex multi-cohort process. The apparent transition from "early successional hardwoods" to "late successional conifers" is, in fact, a long, gradual process occurring over several generations, and even 230 years after disturbance remnants of first post-disturbance cohort are present within stands (Bergeron 2000). Eventually, the first cohort of hardwoods such as aspen is followed by a mix of second aspen cohort and coniferous species (Bergeron 2000). This mixedwood stand structure can be maintained in quasi-equilibrium, punctuated by small-scale disturbances (Bergeron 2000). As such, a late successional old-growth conifer dominated forest, considered traditionally as the successional climax, may never be reached; the mixedwoods, dominated by hardwoods such as trembling aspen and conifers such as black spruce *are* the climax. Following a climatic gradient from south to north these mixedwoods will eventually give way to black-spruce dominated boreal stands.

The unprecedented changes of climate, combined with, and influenced by anthropogenic disturbances, such as logging, may contribute to serious alterations of fire regimes, leading to apparent anomalies of natural successional patterns occurring in the forests. The transitional zones where one habitat type gradually turns into another, may be especially sensitive to sudden environmental changes, and be susceptible to serious imbalances in the usual successive progression of species composition in these respective forest zones (Weber and Flannigan 1997). Severe imbalances may affect the resistance and resilience of these systems to the point where they will be taken to another stability level, and turned into new systems with different species composition, different productivity levels and different successional pathways (Davis 1984; Pastor and Mladenoff 1992).

Examples of climate change impact on biological plant interactions

Aboveground interactions: insect herbivory

Predicted increases of herbivore insect outbreaks associated with changing climate conditions (Bhatti et al. 2003) may result from simultaneous effects of climatic changes on the life cycle and survival of insects, as well as on the growth and chemical composition of host plants. For example, in terms of climate change effects on insect life cycle, recent outbreaks of spruce beetles (*Dendroctonus rufipennis* Kirby) in Yukon are believed to result from a series of warmer than usual winters, which may have led to an increased survival rate of the spruce beetle, and warmer summers, which may have allowed the completion of the beetle's life cycle within one year as opposed to the usual two (ACIA 2004). Both these events can contribute to substantial increases of spruce beetle populations (ACIA 2004).

With respect to plants, changes in herbivory may result from alterations of tissue nutrient concentrations, and thus the quality of herbivore food. Climatic changes marked by the elevations of CO_2 and temperature can lead to increased plant biomass production per unit uptake of nitrogen (N) (Zak et al. 2000). Hence, the concentrations of nutrients could become lower in the faster growing plants. Lower nutritional quality of foliage may lead to an increase or decrease of leaf herbivory alike. Lincoln et al. (1993) stated that the plants grown in CO_2 enriched environments tend to be of lower nutritional quality from the herbivore perspective, as foliar N dilution and ratio of carbon-based defences to nitrogen increases. Consequently, herbivore leaf consumption could increase, as insects consume more plant biomass to meet their nutritional demands. Conversely, a decrease in herbivory could result if an insect chooses to search for higher quality foliage, abandoning the low nutrient quality host plant.

Higher growth and better performance of plants in warmer and more CO_2-rich climates may lead to allocation of resources into growth at the expense of allocating them into chemical defence. For example, Glynn et al. (2003) reported that under high nutrient treatment, the relative growth rate, total biomass and total leaf area of black poplar (*Populus nigra* L.) increased, but herbivore concentrations of defence compounds, such as foliar phenolics, were reduced. Similarly, Holopainen et al. (1995) found that in N-rich habitats, the concentrations of amino acids in shoots increased, but total phenolics and resins were reduced in Scots pine (*Pinus silverstrus* L.), making the species more susceptible to insect attacks.

Due to inherent physiological differences among plant and insect species, alterations of herbivory patterns under the changing climate will not affect all plants equally, and will further depend on the species of the herbivore. For example, leaf consumption by gypsy moth (*Lymantria dispar* L.) has increased dramatically under elevated CO_2 conditions for trembling aspen but not for red oak (*Quercus rubra* L.) or sugar maple (*Acer sacchrum* Marshall.), while consumption by forest tent caterpillar *(Malacosoma disstria* Hubner) increased for all three tree species under high CO_2 levels (Lindroth et al. 1993). Also, the effects of herbivory on plant growth may be indirect and cyclic, in that changes in magnitude and patterns of herbivory resulting from climate change may reciprocally affect the microclimatic and soil nutrient conditions, which in turn affect plant growth. For example, Classen et al. (2005) found that in semiarid coniferous forest, herbivory-induced changes in tree architecture lead to increased soil moisture and temperature by 35% and 26%, respectively - shifts of magnitude similar to predicted global change scenarios. Likewise, beetle folivory has been reported to significantly increase light penetration and soil moisture in monocultures of goldenrod (Brown 1994), which lead to an increase in net N mineralization rates.

Belowground interactions: mycorrhizal associations

Mutually beneficial symbiotic associations of mycorrhizal fungi with the roots occur in the vast majority of vascular plants ranging from ferns, through grasses, forbs to trees, but with a noticeable exception for most genera in mustard (*Brassicae*), sedge (*Cyperaceae*) and beet (*Chenopodiaceae*) families (Johnson et al. 1999). Most herbaceous and angiosperm deciduous woody species are associated with at least one of the ~ 200 endomycorrhizae (EDM) which penetrates the cortex root cells. Other angiosperm deciduous and most gymnosperm trees form associations with one or more of ~ 5 000 species of ectomycorrhizae (ECM) which cover the root surface with hyphal mantle (Johnson et al. 1999) and penetrate the roots by developing extensive Hartig nets surrounding the cortical cells, without actually penetrating them (Johnson et al. 1999).

In the northern forest systems, ectomycorrhizae are prevalent in major families of tree species, including *Pinaceae* for conifers, and *Fagaceae, Betulaceae*, and *Salicaceae* for deciduous species. The Hartig net of ECM greatly extends the surface area for nutrient and water uptake, while the mycelial strands extending from the hyphal mantle provide extensions of the root systems, which may help in soil nutrient exploration and form connections with other plant species (Johnson et al. 1999). While the host plant provides the mycorrhizal fungus with physical support and carbohydrates, the fungus increases the ability of the host plant to capture essential nutrients. Recently, mycorrhizae have also been recognized for their role in breaking down complex organic matter polymers into simpler components (monomers), thus making them more available for the host plants (Dighton 1991; Schimel and Bennett 2004).

Modifying the architecture of roots and the structure of soil, while acting as a storage and potential sink of carbon, the belowground fungal communities, including mycorrhizae, are anticipated to have a profound effect on belowground processes under the present climatic changes (Hetrick 1991; Fitter et al. 2000; Treseder and Allen 2000; Kubiske and Godbold 2001; Söderström 2002; Staddon et al. 2002; Fitter et al. 2004; Pendall et al. 2004; Treseder 2004). In meta-analysis of mycorrhizal responses to nitrogen, phosphorus and CO_2 fertilization, Treseder (2004) found that mycorrhizal abundance decreased by 15% and 32% under N and P fertilization, respectively, but increased by 47% under elevated CO_2 conditions. As such, Treseder (2004) concluded that mycorrhizae stocks are predicted to increase under enriched CO_2 conditions. The ubiquity of mycorrhizae, the potential future increase of it, and the fact that up to ~ 30% of plant-assimilated carbon have been reported to be consumed by the mycorrhizal symbiotic partner (Söderström 2002) underlines the potentially vital importance of mycorrhizae systems in the wake of continuously increasing atmospheric CO_2 levels. Further research towards a deeper understanding of the mycorrhizae-plant relations under increasing CO_2 levels and the changing climatic conditions has been recognized as essential (Treseder and Allen 2000; Söderström 2002).

Despite their significant role in soil ecosystems, mycorrhizal associations are often overlooked in ecological studies of forest communities (Kubiske and Godbold 2001; Staddon et al. 2002). The complexity of the issue is multileveled, as the potential effects associated with climatic change have a varying and often contrasting impact on colonization and functions of mycorrhizae, depending on mycorrhizae type and species, host plant species, as well as the age of the host plant species (Kubiske and Godbold 2001). For example, elevated CO_2 concentrations resulted in increased ECM colonization in a wide range of temperate forest tree species, but this increase was greater in deciduous trees species in comparison to conifers (Kubiske and Godbold 2001). The effects of EDM have been more variable, reporting both increases and decreases in the degree of infection (Kubiske and Godbold 2001). For example, elevated CO_2 levels had no effect on degree the of EDM colonization of *Populus tremuloides* (Klironomos et al. 1997), but increased under hemlock (*Tsuga canadensis* (L.) Carrière). Likewise, in terms of the function of mycorrhizae, potential environmental factors associated with climate change appear to have different effects depending on both the species of the mycorrhizal fungus (e.g. Bending and Read 1995) and the host plant species (e.g. Landhäusser et al. 2002).

In conclusion, the responses of mycorrhizal fungal communities to climatic changes may be strongly dependent on and connected to the climate change effects on plant communities and all the community level biotic interactions (Staddon et al. 2002).

Ground surface interactions: Sphagnum mosses

Sphagnum moss constitutes an important component of boreal habitats, where it is believed to play a major role in maintaining cool and moist substrate conditions (Van Cleve et al. 1983). With respect to global warming, it has been shown that several species of *Sphagnum* moss exhibited increased growth in height under experimental increases in air temperatures (e.g. by 5°C, Robroek et al. 2007). As such, *Sphagnum* substrates may have a negative effect on growth of tree seedlings, not only due to inherently low nutrient availability associated with cool habitats, but also because of competitive interactions of mosses overgrowing slow growing vascular species (Ohlson and Zackrisson 1992; Groot and Adams, 1994; Fleming and Mossa 1994; Dorrepaal et al. 2006). The generally slower growing trees like black spruce could be more negatively affected by increased growth of *Sphagnum*, than faster growing species like trembling aspen; on the other hand potential increases in accumulation and abundance of inherently cool, low-nutrient *Sphagnum* habitats may have a long term negative effects on regeneration and persistence of aspen, which in comparison to black spruce has a higher nutrient requirement (Alban et al. 1978).

However, the drying effects associated with climate change could also become detrimental to *Sphagnum,* since mosses in general are highly depended on high moisture levels (Turetsky et al. 2003). *Sphagnum* species in particular have been reported to be negatively affected in terms of growth and/or abundance under open-top chamber climate simulation treatment (Dorrepaal et al. 2004; Hollister 2005; Walker et al. 2006). Drying effects have been predicted to result in potential decreases of peat accumulation and abundance (Peregon et al. 2007). Ultimately, the responses of *Sphagnum* in terms of growth and abundance to climatic changes will depend of relative prevalence of generally positive growth effects associated with higher temperatures and generally negative effects of potentially lower moisture conditions, and these may vary further depending on particular species of *Sphagnum* (Robroek et al. 2007).

GENERAL INTRODUCTION

Mixedwood-boreal transitional forest zone in northwestern Quebec

The long term goal of the present research is to explore the potential impact of climatic changes on the model system of the mixedwood-boreal black spruce transitional forest zone in southern James Bay-northern Abitibi region, northwestern Quebec. The study area (49°37’ N; 79°00’ W) constitutes part of the Clay Belt physiographic region spanning northwestern Quebec and northeastern Ontario. The region has developed on fine-textured lacustrine and glacio-lacustrine deposits, which are the remnants of glacial lakes Barlow and Ojibway formed after the initiation of melting of the Laurentide Ice Sheet ~ 9000 years ago (Bergeron and Dubuc 1989; Paré et al. 2001; Lefort 2003). The Clay Belt covers approximately 125 000 km^2 of poorly drained clay soils, with nearly level topography (Lefort 2003).

The early successional mixedwood-boreal part of the region is dominated by jack pine (*Pinus banksiana* Lamb.) on well-drained sites, while white birch (*Betula paperifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) dominate the mesic sites (Bergeron and Dubuc 1989; Lefort 2003). Later successional pathways lead to dominance of balsam fir (*Abies balsamea* L.*)*, white spruce (*Picea glauca* (Moench) Voss), cedar (*Thuja occidentalis* L.), and black spruce (*Picea mariana* (Miller) BSP), with the last species progressively attaining overall dominance with increasing latitude, as the system changes from mixedwood to black spruce boreal forest (Lefort 2003). Presently, the forests of this region constitute one of the major sites of forestry operations in Quebec, with regional Tembec and Abitibi-Consolidated being among the largest and most active forestry companies in North America (Lee et al. 2004).

Past, current and future climatic trends of northwestern Quebec

The regional climate of northwestern Quebec is described as subpolar, subhumid continental, with cold dry winters and moist warm summers (Lefort 2003; Bergeron et al.

2004). Trends of rising temperatures have been observed recently in the region, and are linked to the northern migration of the polar front, with the simultaneous penetration of warm, moist southerly air farther north into the boreal forest (Lefort 2003).The bioclimate profiles showing past, current and future climate trends developed by the Ontario Ministry of Natural Resources (MacIver 1986) and Environment Canada (MacIver and Isaac 1989; MacIver and Whitewood 1992) for the Amos region, northwestern Abitibi (48°3' N; 78°70' W), give evidence of regional warming. The summary which follows, in conjunction with Table 0.1, describes these climatic trends for Amos, based on the bioclimate profiles developed using Canadian General Climate Models (CGCM M1 GA1 (SRES)) from the sources and by the authors cited above.

The bioclimate profiles for Amos show steadily increasing average annual temperatures from 0.9°C for the period of 1951-1980, to 1.2°C for 1971-2000 (Table 0.1). Further model prognoses anticipate that these trends will continue at a much steeper rate, with the average annual temperature of 5.6°C predicted for 2070-2099 (Table 0.1). This means that between 1951 and 2099, the average annual temperature is expected to increase by ~ 4.7°C in northwestern Quebec. In that, the most significant temperature rise is projected to occur over late winter and early spring, with ~6.7°C increase predicted to occur between 1951 and 2099 for the months of January to March, followed by ~ 4.1°C increase for April to October, and ~ 3.6°C for November and December (Table 0.1). Maximum temperature extremes in July are also predicted to increase from ~ 37°C for the period of 1951-1980 to ~ 40°C for 2070-2099. By comparison, based on the B2 emission scenario of IPCC 2001 general climate models, the annual average temperatures across the land area of the Arctic (i.e. the regions anticipated to experience the most pronounced climatic changes globally) are projected to increase between 1990 and 2090 by ~ 3-5°C (4-7°C in winter time only) (ACIA 2004).

With respect to precipitation, the CGCM GA1 projections indicate increasing current and future precipitation regimes for Amos (Table 0.1). Bioclimate profiles for Amos show precipitation totals of 875 mm for 1951-1980, through 926 mm for 1971-2000, to 1000 mm for 2070-2099 (Table 0.1). Annual days with rain precipitation are expected to rise from ~ 96 to ~ 116, while annual days with snow precipitation are expected to fall from ~ 57 to ~ 36 between 1951 and 2099 for Amos according to bioclimate profiles. These trends indicate that while the total annual precipitation is predicted to increase over the region within the next century, there will be a shift of increasing rain but decreasing snowfall – a prediction which bears a great deal of significance with respect to the previously discussed prolongation of the growing season for the regional vegetation. Indeed, the projections of decreased annual snowfall, in conjunction with the high temperature rise predicted for the early springtime (Table 0.1) support the conditions for an advancement of spring phenological events.

While the total annual precipitation is expected to increase over the next decades in the Amos region, so is the actual and potential evapotranspiration. According to CGCM GA1 calculations, the maximum annual evapotranspiration values around July reached ~ 95 mm and ~ 120 mm for the actual and potential evapotranspiration respectively, for the period of 1951-1980. These values are predicted to rise to ~ 105 mm and 135 mm for the actual and potential evapotranspiration, respectively, for the period of 2070-2099.

The CGCM GA1 projections of increasing total annual precipitation in the Abitibi region are consistent with the global trends given by the latest IPCC report (2007), stating that precipitation has generally increased over land north of 30°N between 1900 and 2005. However, it should be noted that northwestern Quebec was not included in these projections as it was identified, along with numerous other regions globally, to have insufficient data at the moment to provide reliable and accurate precipitation trends (IPCC 2007).

Table

Table 0. 1 Summary of bioclimate profiles (MacIver and Isaac 1989)[1] for climate station in Amos, NW Quebec, showing past and future projected average temperatures and annual total precipitation for six 30-year periods: 1951-1980, 1961-1990, 1971-2000, 2010-2039, 2040-2069, 2070-2099. The bioclimate profiles were developed by FORTRAN program (Vincent et al. 2008)[2] and are provided by Environment Canada. The future projected profiles are based on Canadian Global Climate Models and emission scenarios (CGCM1 GA1).

Year	Months	Temperature average (^{o}C)	Precipitation totals (mm)
1951-1980	January - March	-13.8	140
	April - October	10	603
	November - December	-8.8	124
	Annual	**0.9**	**875**
1961-1990	January - March	-13.6	139
	April - October	10.1	653
	November - December	-8.8	129
	Annual	**1.0**	**918**
1971-2000	January - March	-13.6	144
	April - October	10.3	650
	November - December	-8.6	131
	Annual	**1.2**	**926**
2010-2039	January - March	-11.2	148
	April - October	11	683
	November - December	-7.5	117
	Annual	**2.4**	**945**
2040-2069	January - March	-9.5	175
	April - October	12.2	692
	November - December	-6.4	129
	Annual	**3.7**	**993**
2070-2099	January - March	-7.1	166
	April - October	14.1	695
	November - December	-5.2	142
	Annual	**5.6**	**1000**

[1] MacIver, D.C. and Isaac, J.L. 1989. *Bioclimate Profiles for Canada 1951- 1980*. Environment Canada, Atmospheric Environment Service

[2] Vincent, L. Louie, P, and Sajecki P. 2008. Canadian Climate Impact Scenarios.

http://www.cics.uvic.ca/scenarios/

Implications of climate change for the mixedwood-boreal transitional forest zone in northwestern Quebec

While fire remains a major natural disturbance factor shaping the dynamics of the NW Quebec transitional forest zone, logging operations initiated in 1912 constitute an increasingly influential anthropogenic disturbance within the Clay Belt forest region (Lefort 2003). Hypothetically, continued anthropogenic disturbance, along with the changing climate could result in the creation of more habitats suitable for regeneration and growth of trembling aspen. Logging activities create open habitats, often with exposed mineral soil, which provide suitable conditions for aspen establishment (Carleton and MacLellan 1994). Global warming resulting in higher soil temperatures could stimulate microbial activity, with subsequent increases in nutrient availability, thus promoting the establishment and growth of nutrient demanding aspen.

Indeed, the current presence of aspen in the black spruce dominated stands suggests that aspen may have the potential for further migration, and possible replacement of black spruce. Despite the fact that aspen in traditionally considered an early successional species, its presence at the northern extremes of its regional distribution in NW Quebec may actually indicate successional climax, perpetuated by cycling re-sprouting of suckers after disturbance. This would be the case especially if there are no other "late successional" species (such as black spruce or balsam fir (*Abies balsamea* (L.) Miller)), growing in the understory, or present in close vicinity to take over and continue what is perceived as the traditional successional pathway.

Whether the presence of aspen is an invasive range expansion of the species, or in-filling of the newly disturbed habitats that are not optimally suitable for colonization of black spruce at the present successional stage, is a matter of further investigation and depends on three major factors: 1) the trends and the rate of climatic changes affecting the regions of northwestern Quebec; 2) the responses of the ecosystem's abiotic and biogeochemical properties to the changing climate; and 3) the responses of aspen and black spruce to these changing environmental factors. Comparison of the responses of aspen and black spruce to potential future climatic changes may provide some indications as to which of the two species may benefit more and become more prominent under modified environmental conditions.

Inherent in the uncertainty about what may actually occur in terms of climate change are two issues of crucial importance. The first issue, although highly significant, is nonetheless very unpredictable with respect the changing climate: the decisions and actions of humans regarding further exploitation of non-renewable and renewable resources. An example of such uncertainty may be exemplified by the recently adopted logging techniques on peatland black spruce sites, such as Harvest with Regeneration Protection (HARP) in Ontario, or Cutting with Protection of Regeneration and Soil (CPRS) in Quebec. The premise of these innovative logging approaches is based on using the least habitat destructive machinery, and preserving certain aspects of the pre-logging forest in order to maintain natural species diversity and ensure healthy site regeneration (Lefort 2003; Groot 2005). However, the long term results from application of these techniques still remain uncertain with respect to the future forest regeneration and its influence on regional climate dynamics over the coming decades (Lefort 2003; Groot 2005).

The second issue is that the amplification of responses caused by the changing climate could trigger sudden thresholds. A recent example of this is the temperature threshold exhibited by white spruce in central Alaska and western Canada. An average temperature above 16°C during summer triggers a sharply negative decrease in the growth rate of white spruce (ACIA 2004). Though before 1950s such high summer mean temperatures were hardly ever reached, in more recent times it is becoming a frequent phenomenon. It is predicted that this could ultimately lead to the decline and elimination of white spruce at the treeline (ACIA 2004).

In light of the uncertainty of human actions, combined with feedbacks and thresholds prompted by these actions, the projections of global warming patterns and effects on the composition of the mixedwood-boreal forest in northwestern Quebec beg thorough investigation. To complicate the matter, despite the theoretical promotion of aspen growth under increased temperatures and fire frequency, recent dieback and reduced growth of aspen in western Canadian boreal forests has been reported (Frey et al. 2004; Hogg and Wein 2005). It is possible that the changes in the interdependent factors associated directly (greenhouse gas levels, temperatures) and indirectly (fire, diseases, pests, droughts) with the global climate change are progressing too fast for the physiological adaptations of western Canadian aspen. Interactions of defoliation by forest tent caterpillar (*Malacosoma disstria* Hubner), drought history, and poor soil structure, among other factors, have been reported to contribute to an extensive decline of aspen in northeastern Ontario as well (Candau et al. 2002). Although climate and soils are different in eastern Canada, it is possible that modification of ceratin combination of environmental factors will likewise affect eastern Canadian aspen stands and make them prone to declines. Sudden climatic changes may be one of the interacting factors contributing to these negative responses.

In NW Quebec, the reconstruction of fire history based on aerial photographs, archives, and dendroecological data taken in the transition mixedwood-coniferous forests suggests that fire frequency has decreased dramatically in these regions over the past ~150 years (Bergeron et al. 2004). Moreover, Bergeron and Flannigan (1995) and Flannigan et al. (2001) used Canadian general climate models to predict that under double the current CO_2 levels, fire frequency will continue to decrease. If fire frequency continues to decrease in northwestern Quebec, increased logging of the coniferous forests will result in a reduction of organic matter and easier accessibility to mineral soil, which may lead to the creation of habitats suitable for colonization of aspen and other mixedwood species (birch, balsam fir, white spruce), potentially causing expansion of their distribution boundaries into the north (Bergeron et al. 2004). However, these habitats may likewise become suitable for the establishment of black spruce, especially since this slow growing species may have the physiological ability to adapt to complex and interacting factors of the rapidly changing environmental conditions, and other, fast growing species may not, as suggested by the current aspen decline in western and parts of eastern Canada.

New open post disturbance sites may become equally available for both trembling aspen and black spruce/peat moss colonization, leading to a potential migration of both these species into habitats, which they previously may not have occupied. Shifts and changes in species composition along the gradient of the transitional zone of the southern James Bay-northern Abitibi region in these circumstances are conceivable. Invading suddenly available habitats created by logging, aspen may not have the time to develop resistance to insects, which also may be profiting from the increasing temperatures and changing climate (e.g. Fleming and Volney 1995; Bhatti et al. 2003).

Inherent differences in adaptations and physiological tolerance levels of different species are expected to lead to species-unique responses to climate change and secondary impacts associated with it, such as shifts within disturbance regimes and nutrient cycling. Depending on the magnitude and direction of responses to climatic changes, different species may either be greatly benefited by the modified growing conditions, or they may be weaken physiologically to the point where they become more prone to secondary negative effects such as insect outbreaks, diseases or fire (Bhatti et al. 2003). Slow responding, slow growing and stress resistant species (Grime 1977) such as black spruce may be less affected by sudden environmental changes, whether these changes are positive or negative with respect to physiological adaptation and tolerance levels of the species.

In conclusion, the effects of climate change on growth and performance of trembling aspen and black spruce, as well as the indirect effects of climate change and human action with respect to creation of habitats suitable for regeneration of the two species under the changing environmental conditions in NW Quebec need to be explored. It is possible that both aspen and black spruce may benefit from the projected climatic changes, or perhaps that one of the species would be less prone and less affected by its negative effects. With the overall objective of addressing these issues, we explored and compared the suitability of post-fire and post-logging habitats on growth and performance of trembling aspen and black spruce seedlings under a variety of microclimatic conditions, including conditions subjected to a treatment of simulated climatic changes.

Summary of research approach

Ecosystem responses to climate change involve interactions between plant species' autoecology and biogeochemical ecosystem processes. Climate related changes of the physical and biological properties and biogeochemical processes of the habitat, and species' responses to these changes, may culminate in alteration of species community composition in the transitional zones of the boreal forests by means of colonization of the newly accessible post-disturbance habitats.

Assessment of trembling aspen and black spruce responses under simulated climate change conditions at post-disturbance fire and logging sites may help in formulating predictions about which species would be more fit to colonize these habitats under conditions of interacting factors of climate change and human actions associated with forest timber. Depending on when and where fire or logging occurs, species colonization of the suddenly accessible open sites may advance its migration into regions beyond the species' previously defined regional distribution boundaries. The occurrence of such 'advance' populations in habitats found beyond the regional distribution boundaries of the species, may serve as a nucleus for further species expansion and migration (Prentice 1992).

The general objective of this study was to investigate the impact of potential climatic changes on growth and performance of trembling aspen and black spruce seedlings at post-disturbance sites in NW Quebec. By performing an experimental simulation of climate change, we explored how the suitability of these post-disturbance habitats could change under the changing climatic regime. The climate change treatment under the field conditions was provided by the installation of the open-top chambers (OTCs) (Heagle et al. 1973; Marion and Pidgeon 1992; Henry and Molau 1997; Marion et al.1997).

Meta-analysis of a variety of experimental climate change simulation techniques across 32 research sites spanning in treatment length from two to nine years, indicated an overall 20% increase in soil respiration response, 46% increase in net nitrogen mineralization, and 19% increase in the aboveground plant growth (Rustad et al. 2001). In recognizing the drawbacks that may have led to discrepancies in the results of climate change simulation treatments, Rustad et al. (2001) stated that the foremost limitation was that the majority of studies focused on either the aboveground plant or belowground soil responses of the system. As such, comprehensive functioning of the response processes to the climate change simulation treatment was limited. The goal of this study was to assess the effects of the climate change simulation treatment on both aboveground and belowground properties of the ecosystem.

The post-logging study sites consisted of the CPRS sites (Cutting with Protection of Regeneration and Soil), where the cutting of trees is performed by using the least habitat destructive machinery techniques (Lefort 2003). The CPRS method usually leaves a series of heavily disturbed transect paths in the places where the logging machinery has passed; however, the moss substrate of the intervals between the paths (where the trees had been removed), remains largely intact (Ministère des Ressources naturelles et de la Faune du Québec 2004). The thick *Sphagnum* layer on the transect machinery paths is usually killed during the operation. Likewise, in burned sites, depending on fire severity, the *Sphagnum* layer may also be eliminated. As *Sphagnum* moss constitutes an important component of black spruce habitats, and it is believed to play a major role in maintaining cool and moist substrate conditions of these habitats (Van Cleve et al. 1983), we assessed the effects of OTC treatment with and without the *Sphagnum* substrate layer.

Summary of general objectives

The general objectives of this research were to assess, at the microhabitat scale, the effects of the simulated climate change using the open-top chambers on:

1) abiotic factors including air temperature and relative humidity, air CO_2 levels, soil temperature, and soil moisture at the post-fire and post-logging sites;
2) biogeochemical processes including soil pH, nutrient supply rates, decomposition rates and chemical changes of the decomposing litter, at the post-fire and post-logging sites;
3) biological factors by testing and comparing the effects of OTC treatment on the height growth, biomass accumulation, foliar and root nutrient concentrations, phenology, foliar herbivory and mycorrhizal colonization of aspen and black spruce seedlings growing on the *Sphagnum* substrates and non-*Sphagnum* substrates of the post-fire and post-logging sites.

Study site selection, description and experimental design of OTC treatment

By using the regional maps provided by the Ministère des Ressources naturelles et de la Faune du Québec in La Sarre, Quebec, and by exploration of the region, we identified three study sites spanning 20 km along the Selbaie road (from 49°38' N; 78°59' W to 49 °45' N; 79°02' W). The road was constructed between 1977 and 1980 to allow access to the Selbaie copper mine located at km 92 of the road (S. Galarneau, personal communication, Ministère des Ressources naturelles et de la Faune du Québec*,* La Sarre, Quebec). We refer to the Selbaie gravel road as a primary forestry road, while the smaller roads laid out perpendicular to it, as secondary forestry roads, or logging roads. Our three study sites consisted of a salvage logged post-fire site, secondary winter forestry road, or the logging road, created to facilitate timber harvest, and the actual post-logging site, where the timber harvest took place. At all sites the disturbance occurred in years 1996-1997.

The post-fire site chosen has been regenerating since a 1997 fire, which covered a total of ~ 15 000 ha. Pre-fire vegetation consisted primarily of black spruce dominated forests and post-fire treatments of the site included some salvage logging (S. Galarneau, personal communication, Ministère des Ressources naturelles et de la Faune du Québec*,* La Sarre, Quebec). Currently, the site consists of burnt spruce snags both standing and fallen, still at relatively early stages of decomposition.

The site was relatively well drained, with a water table found as shallow as 45 cm, though in some places it was deeper than 85 cm. The site was characterized by patches of live moss up to 25 cm high. Humus layer was found at depth 0-15 cm, followed by silty loam at depth 15-30 cm and silty loam and clay at depth > 30 cm. The ground surface was often covered by early successional bryophytes including *Caretodon*, as well as patches of regenerating *Polytrichum* mosses. Wet hollows of *Sphagnum* mosses were also common. Species of *Sphagnum* also constituted a dominant ground cover at the edge boundaries of the fire, and close to road edges. Presence of late successional *Sphagnum* moss patches leads to speculation that at these inherently wetter spots the severity of the fire was diminished, and the *Sphagnum* moss survived the fire.

The post-logging sites chosen included the logging road and the actual logging interval, where the timber was harvested. The logging road site was a winter logging road, created after the 1997 fire in order to salvage log and harvest the remaining timber, as well as to access the forest sites, which were not affected by the fire. As the name suggests, winter roads, also called 'chemins d'hiver' or 'chemin flatté,' are constructed in winter, by means of removing all vegetation while the ground is frozen, thus allowing the operation of heavy machinery (M. McEvoy, personal communication). Though much less expensive to construct than the 'mise-en-forme' roads, which are constructed by removing the vegetation and piling mineral material on top, winter roads are not usually possible to use in the summer time due to soft, boggy ground surface. Passage of heavy machinery would not only be difficult in these conditions, but also extremely destructive by causing soil compaction and rutting (M. McEvoy, personal communication; Arnup 2000).

The winter road used in this particular study presented a highly heterogeneous ground cover including pure or mixed patches of live *Sphagnum* and *Polytrichum* species mosses, as well as humus often covered with *Ceratodon* moss. The site was poorly drained, with the water table as shallow as 10 cm at some places. Live moss layer was up to 25 cm high, and humus layer was found at depth 0 to a maximum of 45 cm. At some places, organic matter layer was not present at all, and the top layer was characterized by silty loam and/or sandy loam texture, followed by clay loam and clay at depth of about 30 cm; these locations were well drained.

The logging interval site resulted from a 1996 CPRS logging event. The site was well drained, with water table at depth of about 70 cm. Live moss layer was up to 20 cm high, followed by humus layer (0-15 cm deep), silty loam (at depth 15-40 cm), sandy loam (at depth 40-50 cm) and sandy clay loam and clay (at depth > 50 cm). This site likewise presented highly heterogeneous patches of pure or mixed *Sphagnum* and *Polytrichum* species mosses (often on a scale as small as 0.25 m^2), as well as feathermosses mosses such *Pleurozium scheberii* (Brid.) Mitt.

All sites were abundant in creeping ericaceous species including *Gaultheria hispidula* (L.) Mulhl. and *Vaccinium oxicoccos* L., and low to medium height ericaceous shrubs including *Andromeda glaucophylla* Link, *Chamaedaphne calyculata* (L.) Moench, *Kalmia polifolia* Wangenh., *Kalmia angustifolia* L., *Ledum groenlandicum* Oeder, and *Vaccinium anugustifolium* Aiton. Numerous species of low to high shrubs of *Salix* species, *Rubus chmaemorus* L. and *R. idaeus* L. were also common at all sites. *Rosa acicularis* Lindley was infrequently encountered at the post-logging road, whereas *Ribes gladulosum* Grauer has been found on several occasions at the post-fire site. Low herbaceous species included an abundance of *Smilacina trifoliata* (L.) Desfontaines in wetter places, and *Cornus canadesis* L. in drier places. Numerous sedges, including *Carex* species (dominant ones being *C. canescens* L., *C. pauciflora* Lightf., *C. magellanica* Lam., *C. trisperma* Dewey, and *C. vaginata* Tausch,), *Scriptus* species, *Eriophorum* species, and *Trichophorum* species, as well as *Typha* species dominated in wetter places, mostly at the post-logging road, usually in the presence of *Sphagnum*. Other common herbaceous vegetation included *Equisetum arvense* L. in wet places, and early successional herbs such as *Epilobium angustifolium* L., *Hieracium ceaspitosum* Dumort. and *Hieracium aurantiacum* L. in drier, highly disturbed places. Among regenerating trees, the most common at all sites were the seedlings and saplings of black spruce and aspen, but *Larix laricina* (Du Roi) K. Koch., *Abies balsamea* (L.) Miller, and *Picea glauca* (Moench) Voss were also frequent at both post-logging sites, and *Populus balsamifera* L. was present at the logging road site only.

In total, we established 40 experimental plots: 20 open-top chambers and 20 control plots. At the fire site there were eight OTCs and eight control plots; at the logging road site there were also eight OTCs and eight control plots; and, at the logging interval site there were four OTCs and four control plots. At each site, every OTC was paired with a control plot established in close proximity.

Synopsis of the chapters

In **Chapter 1,** we describe and compare the distribution of root systems for trembling aspen and black spruce at different types of post-disturbance sites, and on different rooting substrates. This study was performed in addition to and separately from our main experiment involving the open-top chambers (Chapters 2-6). Our objective is to gather background information on root distribution of aspen and spruce seedlings in our study area in order to confirm that the soil temperature, moisture, nutrient supply rates and acidity measurements will be taken at optimal depths in open-top chambers and control plots, with respect to where the roots of the seedlings are found.

In **Chapter 2,** we assess the effects of OTCs on air temperature and relative humidity, air CO_2 concentrations, soil temperature and soil moisture. We also address the potential effects of open-top chambers on the timing of snowmelt and rainfall interception and assess these issues in connection to soil temperature and moisture. Our main objective is to explore the effects of OTCs on microclimate and physical properties of soil, and thus evaluate the effectiveness of OTCs as climate change simulation devices.

In **Chapter 3,** we assess the effects of OTCs on soil acidity, soil nutrient supply rates and decomposition rates, as well as chemical change of different litter types (aspen, *Sphagnum*, and spruce). Our main interest lies in determining which microclimatic or chemical and physical soil properties affect the decomposition process the most, and whether different factors played a major role in the decomposition process for each litter type between the open-top chambers versus ambient conditions. The effects of open-top chambers (as simulators of the potential climatic change) on soil acidity, nutrient supply rates and decomposition process, are discussed in the context of our broader investigation of potential shifts in community composition along transitional mixedwood-boreal forests in northwestern Quebec.

In **Chapter 4,** we assess the responses in height growth and aboveground biomass accumulation of trembling aspen and black spruce seedlings to the simulated climatic changes provided by the open-top chambers. We expect that the microenvironmental modification caused by the OTC treatment may have a direct effect on the growth patterns of the two species, as well as an indirect effect on their performance by affecting growth and abundance of coexisting vascular and bryophyte vegetation present in our plots. As such, we monitor the growth of our experimental aspen and spruce trees, as well as changes in the cover abundance of all other plant species coexisting within our experimental plots.

In **Chapter 5,** we explore the potential factors which resulted in growth and biomass responses of aspen and spruce seedlings to OTC treatment. Firstly, we compare the timing of spring phenological events inside and out of open-top chambers. Secondly, we explore the effects of OTCs on foliar and root nutrient concentrations of aspen and spruce. Thirdly, we investigate the effects of the chambers on insect herbivory of aspen leaves, suspecting that the change in the quality of aspen leaves in OTCs could alter the magnitude of insect herbivory.

In **Chapter 6,** we address the effects of open-top chambers on root tip numbers and percent colonization of ectomycorrhizae (ECM) for trembling aspen and black spruce. To explore both the above and belowground responses of the investigated ecosystem, we compare the relationship of root tip numbers and % ECM colonization with growth responses and root and foliar nutrient concentrations of aspen and spruce, as well as soil acidity, temperature, moisture, and nutrient supply rates in the open-top chambers and the control plots.

Specific predictions

Effects of simulated climate change on abiotic factors, biogeochemical processes and biological factors

1) The OTC treatment will increase the air temperature, which will warm the soil inside the open-top chambers (OTCs), and increase microbial activity, decomposition rates and available nutrient supply rates. Increased microbial respiration, as well as reduced air mixing and exchange, may elevate CO_2 levels in the chambers. **Alternatively,** increased temperature of the air inside the OTCs may also lead to drier soil conditions, reduced heat conductivity in the soil, slower microbial activity and decomposition rates, and lower nutrient supply rates.

2) The OTC treatment may lead to an earlier snowmelt inside the chambers due to warmer air temperatures. This may lead to earlier exposure of ground to frequent freezing episodes of early spring, and thus result in lower soil temperatures in the spring. **Alternatively,** reduced wind conditions inside OTCs may lead to a delayed snowmelt, with the insulating snowpack protecting the soils from the freezing episodes of early spring.

3) Decreased mixing of air may lead to higher concentrations of CO_2 inside the chambers compared to the control plots. However, during the growing season, warmer ambient temperatures inside the OTCs may cause increased growth rate of vegetation. The increased growth may cause an increased CO_2 uptake, leading to net decrease of ambient CO_2 concentrations inside the chambers.

4) Soil temperature will be lower and soil moisture will be higher in *Sphagnum* substrate plots versus non-*Sphagnum* substrate plots. The effects of OTC treatment may be intensified or reversed by the presence or absence of *Sphagnum* substrate.

Effects of simulated climate change on plant performance and mycorrhizae symbiosis

1) Both trembling aspen and black spruce seedlings will experience accelerated growth inside the OTCs, due to increased air and soil temperature and nutrient availability. However, the OTC treatment will stimulate the height growth and biomass accumulation of aspen (a fast growing species) more than that of black spruce (a slow growing species.). Also, overall aspen will be more responsive in terms of advanced spring phenology and higher tissue nutrient concentrations under the OTC treatment. **Potential negative feedbacks:** larger biomass of plants in the OTCs may provide more shade to the soil, and result in lower surface soil temperatures. The warming treatment may also contribute to drier soil conditions inside the OTCs due to increased evapotranspiration, leading to slower nutrient uptake and slower growth rates of the plants.

2) Trembling aspen and black spruce will experience highest growth rates and plant tissue nutrient concentrations under different combination of OTC/substrate type conditions. For example, aspen may grow the most under OTC treatment with a non-*Sphagnum* substrate and black spruce may grow the most under OTC treatment with the *Sphagnum* substrate.

3) The open-top chamber treatment will promote the growth of *Sphagnum* and intensify the competition of peat moss with the seedlings, potentially reducing their growth. **Alternatively,** the drying effects of OTC treatment may have a negative effect on *Sphagnum*, which would reduce the competition of peat moss with seedlings, and improve their growth and performance.

4) Elevated air temperature and earlier snowmelt may advance spring bud burst and leaf development of the seedlings growing in the OTCs, effectively prolonging their growing season and thus contributing to increased growth.

5) Higher growth rates and increased nutrient concentrations may reduce the foliar herbivory of the seedlings growing in the chambers, as insects would have to consume less leaf biomass in order to meet their nutritional requirements. **Alternatively,** nutrient dilution due to increased growth rates may lead to a lower nutritional quality of the leaves, and thus a reduced foliar herbivory, as insects would search for higher quality food, **or** an increased foliar herbivory, as insects would need to consume **more** leaf biomass to meet their nutritional requirements.

6) The effects of the OTC treatment on percent ectomycorrhizae (% ECM) colonization will vary, having a positive or a negative effect, depending both on plant host species and ECM species.

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Part II: Background study

CHAPTER 1: Root differentiation as a factor in coexistence of trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* Miller (BSP)) seedlings at post-disturbance sites in northwestern Quebec

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Abstract

At post-fire and logging disturbance sites in the transitional mixedwood-boreal zone of northwestern Quebec, frequent co-occurrence of young trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* Miller (BSP) is prominent, with the seedlings of the two species often growing less than a meter apart. We hypothesize that the coexistence of aspen and black spruce seedlings at disturbed sites within the northern portion of the transitional zone may result from root partitioning facilitating the coexistence of the two species. We excavated the root systems of 54 aspen and 54 spruce seedlings across six replicates of each, fire, logging road, and logging sites to: i) compare root depth and length for spatially proximate aspen and spruce seedlings; ii) determine the effects of disturbance type and rooting substrate (organic matter versus mineral soil) on root distribution of the two species, and; iii) explore the relationship of seedling rooting patterns with their age and height. We found that, on average, aspen seedlings root deeper and extend their roots farther horizontally than spruce seedlings. Root depth was generally not related to age and height of the seedlings, but root length was; this suggests that at least in terms of depth, root partitioning between the two species may have already been established, and is likely to persist into maturity of the two species, leading to establishment of mixedwood forests in NW Quebec.

Introduction

In the mixedwood-boreal transitional forest zone of northern Abitibi-southern James Bay region in Quebec, trembling aspen *Populus tremuloides* (Michx.) and black spruce (*Picea mariana* (Miller) BSP) frequently co-occur at post-fire and post-logging disturbance sites, with the seedlings of the two species growing less than a meter apart. Since seedbed moisture and nutrient conditions are crucial for seed germination and establishment (Zasada et al. 1992; Greene et al. 1999; Nguyen-Xuan et al. 2000), on a microhabitat scale, high environmental variability of substrates at disturbance sites probably results in small patches of different microenvironmental conditions, which accommodate the requirements for successful germination and establishment of both black spruce and aspen seedlings in close proximity.

With regard to species' persistence and performance, environmental heterogeneity may reduce aboveground and belowground interspecific competition, thus increasing the potential for species' coexistence (Holt 2001). The aboveground competition, e.g. for light, presumably plays a minor role at the open habitat early successional stages, and thus may have insignificant influence on co-occurrence of juvenile trembling aspen and black spruce at disturbance sites. However, in terms of belowground competition, the partitioning of the underground water and nutrient resources, resulting from differentiation in root distribution, may be of crucial importance for the interspecific coexistence of close plant neighbours (Parrish and Bazzaz 1976; Goldberg and Barton 1992). Predicting root partitioning as a potentially important contributing factor to the co-occurrence of aspen and spruce seedlings, we explored the underground growth patterns of young trees by means of interspecific comparison of the relationship between the rooting substrate properties and vertical and horizontal root distribution at post-fire and post-logging sites, in the transitional mixedwood-boreal forest zone of northeastern Quebec. Intrinsic differences between natural and anthropogenic disturbance sites may have different effect on aspen and black spruce seedling root distribution, persistence and growth and thus, coexistence potential (Brumelis and Carleton 1988; Carleton and MacLellan 1994).

Distribution of rooting patterns and underground resource partitioning of plants are widely recognized and have been explored for numerous plant species and across various ecosystems, including desert, semi-desert and grass-shrub ecosystems (Cable 1969; Davis and Mooney 1985; Manning and Barbour 1988; D'Antonio and Mahall 1991; Oscar et al. 1996), maritime cedar-hemlock forests (Bennett et al. 2002), and boreal forests (Persson 1983; Strong and La Roi 1983; Gale and Grigal 1987). In the meta-analysis of 19 studies on vertical root distributions for northern tree species with an average stand age of 40, Gale and Grigal (1987) hypothesized that root depth is determined genetically, with shade intolerant species rooting deeper, and thus having a larger exploratory potential than tolerant species. Based on the frequent observation of aspen seedlings and black spruce seedlings co-occurring within disturbed sites, we hypothesized that both vertical and horizontal root differentiation exists. By using the age of the young trees as a covariate, we planned to determine if the patterns of root differentiation between the two species change in the early years of growth of the seedlings. If root differentiation remains constant or increases over time, the two species have a higher chance of coexisting into maturity. However, if root differentiation (and thus resource partitioning) decrease with time, interspecific competitive pressure may lead to more frequent cases of one species outcompeting the other.

We expected that in the case of early successional stages at the disturbance sites in the transitional mixedwood-boreal zone, root partitioning may inhibit competitive exclusion during early succession, thus allowing aspen seedlings to develop clonal structures, which could increase their chance of persisting into later phases of succession through various patterns of opportunistic spatial spread of remets. Ultimately, coexistence of aspen and black spruce seedlings during early succession should facilitate progress towards the mixedwood succession stage.

Specific objectives of our study were: i) to compare vertical and horizontal root distribution of spatially proximate aspen and black spruce seedlings at disturbance sites; ii) to determine the effects of the disturbance type (post-fire versus post-logging), and rooting substrate type (organic matter versus mineral soil) on root distribution of aspen and black spruce seedlings; and iii) to explore the relationship between seedling rooting patterns and their age and height.

Methods

Study site description

The study site was situated in the southern part of the James Bay area (49°37' N; 79°00' W), and constitutes a part of the Clay Belt physiographic region spanning northwestern Quebec and northeastern Ontario. The region has developed on fine textured lacustrine and glacio-lacustrine deposits, which are the remnants of glacial lakes Barlow and Ojibway, formed after the initiation of melting of the Laurentide Ice Sheet ~ 9000 years ago (Bergeron and Dubuc 1989; Paré et al. 2001). The Clay Belt covers approximately 125 000 km^2 of poorly drained soils, and has a nearly level topography (Lefort 2003).

While fire continues to be a major natural disturbance factor shaping the dynamics of the transitional forest zone in the Clay Belt region, logging operations initiated in 1912 constitute an increasingly influential anthropogenic disturbance (Lefort 2003; Bergeron et al. 2004). Presently, the forests of these regions constitute one of the major sites of forestry operations in Quebec and Ontario, with Tembec and Abitibi-Consolidated being among the largest and most active forestry companies in North America (Lee et al. 2004). Black spruce is considered among the most economically valuable tree species (Lefort 2003).

The three disturbance types chosen in our research consisted of post-fire sites, logging roads, and logging sites. By using the regional maps provided by the Ministère des Ressources naturelles et de la Faune du Québec in La Sarre, Quebec, and through exploration of the region, we identified three locations for each disturbance type, for a total of nine locations spanning 20 km of Selbaie road, which was constructed between 1977 and 1980 to allow access to Selbaie copper mine located at km 92 of the road (S. Galarneau, personal communication, Ministère des Ressources naturelles et de la Faune du Québec, La Sarre, Quebec). The fire and logging events at the locations chosen occurred in the years 1996-1997, thus the sites have been regenerating for over 10 years. Pre-disturbance vegetation consisted primarily of black spruce dominated forests, about 120 years old and a regeneration time of 75-100 years, growing at a density of 1 000 to 1 200 trees per hectare (S. Galarneau, personal communication; Toribio Fajardo 2005).

The fire disturbance locations originate from fire episodes in the summer of 1997, which covered a total of ~ 15 000 ha (S. Galarneau, personal communication). Post-fire treatments of the site included salvage logging and aerial re-seeding of black spruce at some locations (S. Galarneau, personal communication). Currently, the sites consist of burnt tree snags both standing and fallen, still at relatively early stages of decomposition.

The water table at the fire locations were our study took place, was as shallow as 45 cm, although at some places it was located deeper than 85 cm. Patches of live moss were up to 25 cm high, humus layer up to 15 cm deep, silty loam up to 30 cm deep, while clay loam and clay were usually found deeper than 30 cm. The ground cover substrates consist mainly of patches of mineral soil or humus, bare or covered with sparse *Ceratodon* and regenerating *Polytrichum* mosses, as well as wetter hollows and hummocks dominated by *Sphagnum* and brown moss species. The presence of late successional *Sphagnum* moss patches suggests that lower fire severity at the inherently wetter locations allowed the *Sphagnum* moss to survive the fire.

The logging locations in our study consisted of the logging roads and the actual logging intervals, where the timber was harvested. The logging roads were constructed perpendicular to the Selbaie road to allow access to the logging intervals. The water table at the logging sites ranged from depths of 10-30 cm at the poorly drained locations, to deeper than 50 cm at the well drained locations. Moss hummocks were sometimes up to 40 cm high, although bare humus or mineral soils were often common. Silty loam layer was often found at depths 0-30 cm and clay and clay loam layer at depths > 30 cm. The sites often present highly heterogeneous (sometimes on a scale as small as 1 m^2) patches of mineral soil and humus, either bare or covered with varying degrees of pure or mixed *Sphagnum* and *Polytrichum* mosses, as well as species of *Ceratodon* mosses, feathermosses, and brown mosses.

Sampling design and data collection

In early June 2006, at each of the nine locations, we selected and marked between 20 and 60 young individuals each of trembling aspen and black spruce. The selection was based on meeting the following criteria: 1) as we wanted to test the presence of aspen seedlings, we deliberately looked for young aspen individuals found in the absence of potential parent trees; 2) based on the assumptions that small trees are young, and still in their seedling stage, the individuals had to be less than 150 cm in height; 3) since we wanted to compare root patterns of the two species coexisting in close proximity, we selected aspen individuals that were found within at least 5 (preferably less) meters of radial distance from spruce individuals, and vice versa; 4) the seedling had to grow on organic matter (OM, including humus, *Sphagnum* moss, or decomposing wood) or on mineral soil (MS, including bare mineral soil, or mineral soil with sparse *Polytrichum* or *Ceratodon* moss cover).

From the previously marked individuals, at each location we randomly chose three seedlings of each species growing on organic matter substrate, and three seedlings of each species growing on mineral soil substrate, for a total of six seedlings per species per location. In cases where we found a connection of the aspen root system to another aspen individual, the individual was not used as one of our experimental samples, and another individual was chosen instead.

In summary, our experimental design consisted of three disturbance types, each one replicated at three locations, together resulting in a total of nine locations. At each location, there was a factorial "treatment" of two species and two substrate types, resulting in four potential combinations of species and substrate types. Every combination was replicated three times at each of the nine locations, resulting in twelve plots per location. Overall, we had 54 individuals of each species and a total of 108 sample units.

For each individual tree, we collected information on the distance (cm) from the surface ground level down to the root crown; we chose this point as a boundary of the root system and the trunk. This assumption allowed us to be consistent with regard to measuring root depth, root length and seedling height, since the transition between the trunk and the root system was often not obvious, especially for the seedlings growing on thick *Sphagnum* hummocks. Root depth (cm) was measured from the root crown vertically to the deepest point reached by any part of the root system. Root length (cm) involved measuring the furthest point reached horizontally by any part of the root system, starting at the root crown. We then measured the distance (cm) from the ground level up to the terminal tip of the stem. Addition of this distance to the distance between the ground level and the root crown gave us the height (cm) of the tree. Each tree was then cut at the root crown to determine its age based on the number of tree rings.

Statistical analysis

Exploratory analyses were performed by determining the mean, standard deviation, and range for the distance from the surface ground level to the root crown, root depth and length, as well as seedling height and age, separately for trembling aspen and black spruce. For each species, the statistics were obtained for all 54 samples, and also separately for each of the three disturbance types, (fire, logging road, logging interval), as well as for the samples growing on OM and MS substrates.

To account for the fact that with age, the seedlings become bigger and their root systems increase in terms of both vertical and horizontal root extension, we included seedlings' age as a covariate in the analysis of the effects of disturbance type, species, and substrate type on root patterns. To determine whether the differences between the species remain constant as the trees get older, we tested the interactions of age with species; significant interaction could indicate that as the seedlings get older, the differences in root partitioning between the two species become larger (increased competition) or smaller (decreased competition).

Using procedure MIXED (SAS system 2007), we tested the effects of the exploratory variables, including disturbance type, species, and substrate type, on responding variables, including the distance to root crown, maximum depth of the root system, and the length of the roots, through analysis of covariance (ANCOVA), with seedling age as a covariate in the model. An analysis of variance (ANOVA) was used if the age covariate was not significant. The disturbance type (n = 3; fire, logging interval, or logging road), species (n = 2; trembling aspen or black spruce), and the substrates type (n = 2; organic matter or mineral soil), as well as all the possible interactions between these three factors, were treated as fixed factors. The location (three replicates for every disturbance type) nested in the disturbance type, as well as the two-way and three-way interactions of the location with the species and the substrate type, nested in the disturbance type, were included in the model as random factors. We performed separate analysis for each of the three responding variables including the distance to root crown, maximum depth of the root system, and the length of the roots. Least-squares (LS) means were used to determine specific differences among the levels, or combination of levels, of the exploratory variables. To meet the assumptions of normality, it was necessary to square root transform all three responding variables prior to analysis. To explore the relationship of seedlings' age and height with their root distribution parameters, as well as the relationship among the root distribution parameters themselves, we performed Pearson's correlations (procedure CORR in SAS; SAS system 2007).

Results

Descriptive statistics indicated that the distance from the ground level to the root crown was ~ 2-3 cm longer for aspen than for spruce seedlings (Table 1.1), ranging from 0.5 to 30 cm for aspen and 1 to 20 cm for spruce. Also, the distance to root crown on organic matter (OM) substrates ranged from 0.5 to 30 cm, and on mineral soil (MS) substrates from 0 to 16 cm. The distance to root crown was significantly longer for aspen seedlings in comparison to spruce seedlings ($p = 0.0001$), and it was significantly longer on OM substrates than on MS substrates ($p < 0.0001$) (Table 1.2). The main effect of disturbance type was not significant on distance to the root crown; however, there was a significant three-way interaction between disturbance type, species, and substrate type ($p = 0.032$) (Table 1.2). Least-squares means revealed that for the seedlings rooting on organic matter substrates, the distance to root crown was larger for aspen than for spruce at all three disturbance sites; however, for seedlings rooting on mineral soil, root crown was deeper for aspen than spruce at the fire and logging interval sites, but shallower at the logging road sites.

Age was included as a significant covariate in the analysis of the effects of disturbance type, species, and the substrate type on the distance to the root crown (Table 1.2). There was also a significant interaction between the age covariate and the species. Exploratory plots (not shown) comparing the slopes for the age covariate plotted against the distance to the root crown revealed that the slope for aspen is slightly steeper than that for spruce, indicating that the distance to the root crown increases faster with age for the aspen seedlings than for the spruce seedlings. The distance from the surface ground level to root crown was significantly correlated with root length for aspen, and root depth for spruce (Table 1.3). Also, there was a significant positive correlation between the distance to root crown and age and height for both species (Table 1.3).

On average, aspen seedlings rooted ~ 4 cm deeper than black spruce seedlings (Table 1.1). Rooting depth for aspen and spruce ranged from 2 to 50 cm and 3 to 40 cm respectively, across all disturbance locations and all substrate types. Seedlings age covariate was not significant in the analysis of the effects on root depth variable, therefore to test the effects of disturbance type, species and substrate type on root depth, we fitted an ANOVA model. There were no significant interactions among the fixed factors, and the main effects of disturbance type and rooting substrate type were not significant on rooting depth (Table 1.2). The main effects of the species were significant ($p = 0.031$), with the LS means indicating that aspen seedlings rooted significantly deeper than spruce seedlings (Table 1.2). There was no correlation of root depth with any measured parameters for aspen, but there was a significant positive correlation of root depth with distance to root crown and age for spruce (Table 1.3).

The roots of aspen seedlings were on average ~ 40 cm longer that the roots of spruce seedlings (Table 1.1). Aspen roots ranged from 10 to 460 cm in length, while spruce roots ranged from 8 to 249 cm. Just like in the case of root depth, there were no significant main effects of disturbance and rooting substrate types on root length, but there was a significant difference in root length between the two species ($p = 0.016$), with the LS means indicating that aspen seedlings had significantly longer roots than spruce seedlings (Table 1.2). Age was included as a highly significant covariate in the analysis of the disturbance type, species and substrate type on root length (Table 1.2). Interactions of age covariate with any of the explanatory variables were not significant, and there were no significant interactions for any combination of explanatory variables. Root length was significantly correlated with distance to root crown, seedling height, and seedling age for aspen; and with height and age for spruce (Table 1.3).

Discussion

Root partitioning of neighbouring trembling aspen and black spruce seedling at disturbance sites of the mixedwood-boreal transitional zone

Holt (2001) defines species coexistence as “the state of two or more species being found in the same place at the same time”. Historical approaches to explaining the coexistence of species within a community include the theory of limiting similarity (MacArthur and Levins 1967) and niche divergence (Pianka 1983). Stimulated by Hutchinson’s definition of niche (1978), the theory of limiting similarity states that there is a quantifiable limit to the degree of niche overlap and similarity of resource use in sympatric species, which allows different species to coexist. At disturbed sites of the transitional mixedwood-boreal forest zone in northwestern Quebec, vertical and horizontal root partitioning may play an important role in proximal coexistence of trembling aspen and black spruce seedlings.

Distance to root crown was significantly deeper for aspen seedlings than for black spruce (Tables 1.1 and 1.2), which suggests that spruce is able to establish and develop a root system within the top layer of organic matter such as live *Sphagnum* moss (Strong and La Roi 1983; Brumelis and Carleton 1988; Greene et al. 2004). It is possible that aspen seedlings were less successful than spruce seedlings in germinating at microsites with thick moss substrate, and germinated instead at surfaces with thin layers of moss, which eventually developed and thickened, and then covered the aspen roots already established in its lower layers. Meanwhile some spruce seedlings were successful at germinating and establishing on the already thick moss substrates, and developing root systems within the top portion of these thick moss mats. Indeed, Greene et al. (2004) observed that at post-fire sites, apart from mineral soil, *Sphagnum* patches were the best seedbeds for the germination of black spruce.

Significant age covariate with regard to distance to root crown, as well as significant positive correlation of age with the distance to root crown for both species, suggests that as the seedlings age, their root crown get deeper. Jayen et al. (2006) concluded that after the fire, seedlings of black spruce, aspen and jack pine establish and persist most successfully at the substrates where the thickness of the residual organic matter is the lowest. Presumably, the moss seedbeds grow thicker in the years following germination and establishment of the seedlings (in our case the maximum time would be six years, as that was the maximum age of the seedlings we studied), thus increasing the distance from the surface ground level of the moss to root crown. Indeed, the root crowns were significantly deeper for both species when rooted on the organic matter substrates, which often included thick *Sphagnum* hummocks, than on the mineral soil substrates (Table 1.1).

In accordance with the findings of a meta-analysis conducted by Gale and Grigal (1987), the results of our study indicate that in terms of the vertical root distribution, the deepest point reached by any part of the rooting system was significantly greater for trembling aspen seedlings than for black spruce seedlings (Tables 1.1 and 1.2). Gale and Grigal (1987) attributed these differences to genetically controlled inherent morphological root differences of early and late successional species. Early successional species should be better adapted to nutrient deficient soil conditions by having the morphological potential for deep-soil exploration, whereas the shallow-rooted late successional species should be able to exploit the nutrients concentrated near the ground surface (Gale and Grigal 1987). The vertical root differentiation we observed may have already reached a stable state, at least for trembling aspen, since root depth was not correlated with age or height of aspen seedlings (Table 1.3 a). Also, age was not a significant covariate in testing the effects of disturbance type, species and substrate type on root depth (Table 1.2). As the maximum rooting depths of boreal trees are usually attained at a young age (Strong and La Roi 1983; Gale and Grigal 1987), vertical root partitioning in the early successional stages, which we hypothesize to be an important factor for proximal coexistence of young aspen and black spruce seedlings, should presumably extend into maturity and facilitate the coexistence of these species at the mature mixedwood stand stage (even after accounting for interspecific and intraspecific thinning episodes occurring over the succession).

Differences in soil exploration between aspen and spruce seedlings occur not only vertically but also horizontally: root length for aspen seedlings was significantly higher than for black spruce seedlings (Tables 1.1 and 1.2). The length of the roots was positively correlated with the age and height of both species (Table 1.3) and age was a highly significant covariate in the analysis of the effects of the disturbance type, species and the substrate type on root length (Table 1.2). Therefore, unlike root depth, which appears to be established within the early years of seedlings life, the exploratory potential in terms of horizontal distribution has not yet been reached by either of the species.

Gale and Grigal (1987) hypothesized that the rooting morphology of early successional species (such as aspen) should allow them to better exploit the available soil resources in terms of vertical root distribution. Our results show that the coexistence of trembling aspen and black spruce seedlings may be facilitated by both vertical and horizontal root distribution. Additionally, although not measured directly in this study, root density is likely another crucial factor allowing for the optimal partitioning of the belowground resources between the two species. Strong and La Roi (1985) found that in nine boreal-mixedwood stands in Alberta, the highest root density of dominating tree species, including trembling aspen, was found in the lower portion of forest floor or immediately below it, and thus they concluded that the top 25 cm of the soil profile was of primary importance in terms of underground resource acquirement. Meanwhile, Bhatti et al. (1998) reported that more than 80% of the fine roots of black spruce were found in the live moss layers and top 10 cm of peat. Since both the root crown and the deepest point reached by the roots were significantly shallower for spruce than for aspen, we suspect that spruce's maximum root densities were also reached at a shallower point than those of aspen.

On a larger spatial scale, there were no differences in rooting patterns across different disturbance types, and no interactions of disturbance types with species in terms of root crown depth and overall root depth (Table 1.2), which supports the theory that root distribution is, to a certain degree, determined genetically (Gale and Grigal 1987). Nonetheless, the role of large-scale environmental conditions, such as disturbance type, with regard to rooting patterns and coexistence of species at different post-disturbance sites, should not be underestimated. Complex interactions of disturbance regime properties, such as size, intensity, severity, and type of fire at post-fire sites, or harvesting strategies at post-logging sites, lead to highly variable modifications of the surface layer. Modified surface layers often differ profoundly in terms of chemical, physical and mechanical properties, (e.g. nutrient availability and acidity resulting from removal of organic matter through burning, versus physical organic matter removal during site preparation for harvesting (Brais et al. 2000; Goodale et al. 2000)). Ground surface layer modifications through different types of disturbances generally have a strong impact on vegetation regeneration regimes and subsequent species composition – a topic that has been widely explored across North American forest ecosystems, at logged sites (e.g. Harvey and Bergeron 1989; Harvey et al. 1995, 2002; Brais et al. 2004), post-fire sites (e.g. Greene and Johnson 1999; Greene et al. 1999), post-fire sites that have been salvage harvested (Purdon et al. 2004; Macdonald 2007) and both post-logged and post-fire sites in terms of comparison (e.g. Nguyen-Xuan et al. 2000; Reich et al. 2001; Wang and Su 2002).

The significant interaction between the disturbance type, the substrate, and the species with regard to the distance between the ground surface level and the root crown suggests that, while the root crown was generally found deeper for aspen than spruce, this trend was reversed at the logging road site for the seedlings rooting on mineral soil (Table 1.2). Frequent removal of the organic matter layer during construction of secondary forestry roads, often leads to the exposure of mineral soil. It is possible that the germination rate is higher for aspen precisely at these bare mineral soil patches than at the patches with residual organic matter layer at the logging road sites. Meanwhile spruce may be equally likely to germinate at both bare mineral soil and residual and/or compacted organic matter patches found at the logging road sites. Again, this is supported by Greene et al. (2004), who concluded that both mineral soil and *Sphagnum* were equally suitable in providing the best seedbeds for germination of black spruce.

Regardless of disturbance type, high variability of rooting substrate types at a small spatial scale is known to promote plant biodiversity, and thus facilitate spatially-proximate coexistence of species (e.g. Vivian-Smith 1997). Organic matter substrates such as *Sphagnum* hummocks, or mineral substrates such as sand or clay, are likely to affect the rooting patterns of species, as indicated by the highly significant effect of substrate type on root crown depth in our study (Tables 1.1 and 1.2). Microtopography of the substrate may affect root distributions; for example, plants rooting at thick nutrient-poor *Sphagnum* moss hummocks may have to root deeper in search of available nutrient resources than plants rooting straight on nutrient-rich mineral soil. Consequently, we could deduce, that the proximity of *Sphagnum* hummock next to a mineral soil patch, could lead to establishment and coexistence of two seedlings of different species rooting at different depths.

Notwithstanding a certain degree of overlap in root distribution patterns for both species (Table 1.1), our results indicate that at the level of our sample size (108 individuals), there were probably numerous seedlings for which the three rooting parameters we measured did not overlap. This number of seedlings was high enough to create a significant difference between the two species, in all three cases indicating that aspen roots grow deeper overall, and that they are horizontally distributed further than spruce (Tables 1.1 and 1.2). It is precisely that differing fraction of seedlings, which may allow for coexistence of the two species and the progression towards future mixedwood stands, where the two species may not only coexist, but to a certain degree even facilitate each other's persistence and nutritional requirements. For example, Légaré et al. (2004) found that in the mixedwood trembling aspen-black spruce stands of northwestern Quebec, the presence of aspen in proportions lower than 41% of total stand basal area resulted in significantly higher black spruce diameter at breast height (DBH) and overall height. However, dominance of aspen (i.e. over 41%) in the mixed stands led to decreased DHB and overall height of black spruce, which Légaré et al. (2004) explained to be an effect of increased interspecific competition for light, nutrients and water. They suggested that the presence (but not in dominating proportions) of aspen in mixed stands has a positive effect on nutrient cycling, and by offsetting the negative effects of black spruce on nutrient cycling, can ultimately benefit both species. Positive influences of aspen on nutrient cycling in jack pine (*Pinus banksiana* Lambert) dominated southern boreal mixed forests of Quebec have also been reported (Longpré et al. 1994).

The establishment and coexistence of deciduous and coniferous species at transitional mixedwood-boreal zones may be affected by the changing climate, and responses of species to these changes will ultimately determine future species composition within these zones. Further research involving the investigation of species responses in terms of growth, phenology, and plant tissue nutrient concentrations to simulated climatic changes may facilitate prognosis with regard to the future of trembling aspen and black spruce at the boundaries of mixedwood and boreal forests.

Tables

Table 1. 1 Means and standard deviations (SD) for the age (years), height (cm), the distance from the ground level to the root crown, the depth of the roots (cm), and the length of the roots (cm), for the seedlings of a) trembling aspen, and b) black spruce, uprooted from organic matter substrate or mineral soil substrate at fire, logging interval (Log int.) and logging road (Log road) disturbance sites of the transitional mixedwood-boreal forest zone in northwestern Quebec.

a) Trembling aspen

		Organic matter substrate					**Mineral soil substrate**					**All substrates**				
		Age	**Height**	**Root crown**	**Root depth**	**Root length**	**Age**	**Height**	**Root crown**	**Root depth**	**Root length**	**Age**	**Height**	**Root crown**	**Root depth**	**Root length**
Fire	**Mean**	4	55.2	12	20	127	3	43	5	23	75	**3**	**49**	**9**	**22**	**101**
	SD	1.4	11.1	5.0	5.3	65.1	1.1	11.3	2.1	14.1	35.6	**1.3**	**12.5**	**5.2**	**10.5**	**57.5**
Log int.	**Mean**	3	68	11	21	165	2	45	4	19	90	**2**	**56**	**8**	**20**	**128**
	SD	1.7	37.5	6.5	4.4	122.1	0.8	27.6	2.3	8.7	60.7	**1.4**	**34.0**	**5.9**	**6.8**	**101.4**
Log road	**Mean**	3	65	15.5	22	160	2	59	2	18	148	**3**	**62**	**9**	**20**	**154**
	SD	0.9	23.9	6.1	11.6	64.2	1.1	20.5	1.1	8.7	120.4	**1.1**	**21.8**	**8.0**	**10.2**	**93.8**
All sites	**Mean**	**3**	**63**	**13**	**21**	**150**	**2**	**49**	**4**	**20**	**104**	3	56	8	20	127
	SD	**1.4**	**26.0**	**5.9**	**7.5**	**86.4**	**1.1**	**21.4**	**2.2**	**10.6**	**83.7**	1.3	25.0	6.3	9.2	87.5

b) Black spruce

		Organic matter substrate					Mineral soil substrate					All substrates				
		Age	**Height**	**Root crown**	**Root depth**	**Root length**	**Age**	**Height**	**Root crown**	**Root depth**	**Root length**	**Age**	**Height**	**Root crown**	**Root depth**	**Root length**
Fire	**Mean**	3	36	8	19	80	3	35	3	14	117	**3**	**36**	**6**	**16**	**99**
	SD	1.0	14.0	3.9	7.4	43.6	1.6	15.0	2	5.2	78.8	**1.3**	**14.1**	**4.2**	**6.8**	**64.5**
Log int.	**Mean**	3	33	6	15	93	4	35	3	18	95	**3**	**34**	**4**	**16**	**94**
	SD	1.7	11.2	4.3	7.5	60.5	1.4	8.9	2.2	9.1	42.5	**1.6**	**9.9**	**3.6**	**8.3**	**50.7**
Log road	**Mean**	3	35	10	17	76	3	31	4	14	72	**3**	**33**	**6.8**	**16**	**74**
	SD	1.6	10.5	6.2	9.9	48	1.6	13.8	1.1	7.2	52.8	**1.6**	**12**	**5.3**	**8.5**	**49**
All sites	**Mean**	**3**	**35**	**8**	**17**	**83**	**4**	**33**	**3**	**15**	**95**	**3**	**34**	**6**	**16**	**89**
	SD	**1.4**	**11.6**	**5.0**	**8.3**	**49.8**	**1.5**	**12.5**	**1.8**	**7.3**	**60.6**	**1.5**	**11.9**	**4.5**	**7.8**	**55.3**

Table 1. 2 Effects of disturbance type (fire, logging road, logging interval), seedlings species (trembling aspen, black spruce) and rooting substrate type (organic matter, mineral soil) on distance from the ground level to root crown, and on root depth and length. Only significant interactions are included in the final models.

Factor		**Root * crown**	**Root ** depth**	**Root *** length**
Disturbance type	F value	1.53	0.10	0.80
	P value	0.256	0.906	0.471
Species	F value	15.93	6.01	7.49
	P value	**0.001***	**0.031**	**0.016**
Substrate type	F value	96.9	0.74	0.20
	P value	**<0.0001**	0.406	0.668
Disturbance*species*substrate	F value	2.39	-	-
	P value	**0.032**	-	-
Age covariate	F value	15.5	-	69.1
	P value	**0.001**	-	**<0.0001**
Age covariate*species	F value	6.37	-	**-**
	P value	**0.013**	-	**-**

***** Seedlings' age was included as a covariate in the ANCOVA model for distance to root crown, and for root length.

******For root depth, the ANOVA model was fitted, since age covariate was not significant.

*** Significant results are in bold.

Table 1. 3 Pearson's correlation coefficients and associated probabilities (below in parenthesis) of distance from the ground level to root crown,of root depth and length, and of seedlings' age and height, for a) trembling aspen and b) black spruce, uprooted at fire, logging road and logging interval disturbance sites of the transitional mixedwood-boreal forest zone in northwestern Quebec.

	Root crown	**Root depth**	**Root length**	**Height**	**Age**
a) Trembling aspen					
Root crown	-	0.24 (0.085)	0.32 **(0.019)***	0.32 **(0.019)**	0.35 **(0.011)**
Root depth		-	-0.16 (0.249)	0.20 (0.157)	0.12 (0.408)
Root length			-	0.55 **(<0.0001)**	0.56 **(<0.0001)**
Height				-	0.60 **(<0.0001)**
Age					-
b) Black spruce					
Root crown	-	0.33 **(0.015)**	0.26 (0.056)	0.41 **(0.001)**	0.43 **(0.001)**
Root depth		-	0.08 (0.560)	0.23 (0.091)	0.30 (**0.030**)
Root length			-	0.53 **(<0.0001)**	0.59 **(<0.0001)**
Height				-	0.65 **(<0.0001)**
Age					-

*Significant results are in bold.

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Connection of Chapter 1 with Chapter 2 and the thesis in general

In **Chapter 1** we described and compared the distribution of root systems for trembling aspen and black spruce at different types of post-disturbance sites, and on different rooting substrates. We determined that on average, aspen rooted at depth of ~ 20 cm, and that aspen roots extended 127 cm horizontally, while black spruce rooted on average 4 cm shallower and extended its roots horizontally 38 cm less than aspen. Since in **Chapter 2** we want to assess the effects of open-top chambers on soil temperature and moisture, one of our objectives in Chapter 1 was to gather information on root distribution of aspen and spruce seedlings in our study area in order to confirm that the soil temperature and moisture measurements will be taken at the optimal depth with respect to where the roots of the seedlings are found. This will also apply to measuring the soil acidity, nutrient supply rates and decomposition rates in **Chapter 3**. In the context of the whole thesis, we also wanted to verify the presence of aspen seedlings as opposed to aspen suckers at disturbance sites of our study area, in order to find support to our premise that climate change presently may facilitate regeneration of aspen through seed, which is considered to be a less frequent means of regeneration than through asexual means. Also, by addressing the issue of aspen and black spruce seedlings coexistence in close proximity due to root segregation, we wanted to develop predictions with regard to potential coexistence of the two species in the future, as part of mixedwood forests in northwestern Quebec.

Part III: Abiotic and biogeochemical responses to simulated climate change

CHAPTER 2: Effects of open top chambers on physical properties of air and soil at post-disturbance sites of transitional forest zone in northwestern Quebec

Abstract

Predictions of ecosystem's responses to current global climate change can be made by experimental climate simulations. One such simulation method includes open-top chambers (OTCs) used for experimental warming and/or experimental increases of greenhouse gases. Advantages of OTCs include simple and quick construction, low cost and technology, as well as easy transport and accessibility of construction materials, allowing for a high number of replicates, and making OTCs especially attractive for field studies in remote areas. However, the potential effects that OTCs have on environmental factors are complex, and comprehension of numerous interactions among these factors is crucial for the proper use of such chambers. We studied the effects that OTCs constructed on plots with and without *Sphagnum* moss substrate had on microclimatic factors, including ambient temperature and relative humidity, and soil temperature and moisture. Our study involved construction of 20 OTCs (1 m in diameter and 0.75 cm in height; made of clear acrylic plastic) and 20 control plots at post-disturbance sites of the transitional mixedwood-boreal forest in southern part of James Bay region, Quebec. To better comprehend the causes and potential interaction effects indicated by our results, a series of experimental trials were used to test the effects of OTCs on snowmelt, rainfall interception, and CO_2 concentrations. The combination results from our field study at post-disturbance sites in southern James Bay and our experimental trials in both the Montreal region and northern James Bay, suggests that the experimental warming is most evident in terms of increased daytime maximum temperatures (~ 2-3^{o}C), and that cooler (up to ~ 2.4^{o}C) and drier (up to 10% volumetric moisture content) soils may result from earlier snowmelt leading to earlier onset and overall increased evaporation of melt water in the chambers, since advanced ablation of the insulating snow cover and exposure of the soil to low spring temperatures prolongs soil freeze, and inhibits snowmelt water

infiltration. Rain precipitation patterns were affected by the chamber structure primarily in terms of distribution within the chamber but not in terms of the amount of rain entering the chamber. The concentration of CO_2 did not differ more than 1 ppm between the chambers and control plots. Overall, open-top chambers provide effective and simple method of climate change simulation, but it is highly advisable that the complex interactive effects, both desirable and undesirable, are well understood and appreciated before utilizing OTCs for experimental climate simulation.

Introduction

As predicted by General Climate Models (GCM's), a notable rise in the concentration of greenhouse gases is very likely one of the contributing causes of current world-wide changes in climatic patterns (Stott et al. 2000; Houghton et al. 2001; IPCC 2007). Since pre-industrial times, the global atmospheric concentration of the most abundant greenhouse gas, carbon dioxide, has risen by ~ 36% (IPCC 2007). Higher concentrations of greenhouse gases result in increased absorption and emission of long wave radiation, which has lead to an unprecedented and continuing rise of global surface mean temperature, which increased by 0.74°C between 1906 and 2005 (IPCC 2007). The rise in average global temperature is already having noticeable effects on numerous interdependent environmental factors, from precipitation regimes, through soil moisture and temperature which influence decomposition and mineralization processes, to pronounced alterations in fire regimes (Weber and Flannigan 1997).

Temperature has been recognized as a major factor in controlling numerous ecological and biogeochemical processes including litter decomposition (Meentemeyer 1978; Hobbie 1996; Melillo et al. 1996; Rustad and Fernandez 1998; Melillo et al. 2002), microbial respiration (MacDonald et al. 1995; Rustad et al. 2001), nutrient cycling, including N mineralization (Van Cleve et al. 1983; MacDonald et al. 1995; Melillo et al. 2002; Strömgren and Linder 2002), as well as nutrient uptake (Bassirirad 2000) and subsequently, plant performance (Arft et al. 1999). In this study we attempted to experimentally modify the temperature of natural habitats by the use of open-top chambers (OTCs). Specifically, we tested the efficacy of OTCs as passive warming devices, (Marion et al. 1997) aimed at simulating a changed climate at post-disturbance sites of the transitional mixedwood boreal forest in northwestern Quebec. The sites, which experienced fire and logging disturbances in the late 1990s, are currently within the early stages of succession, and their current regeneration process may be affected and shaped by the ongoing climatic changes within that region (Thesis Introduction; Lefort 2003).

The International Tundra Experiment (ITEX) established in 1990 to monitor plant responses to predicted climatic changes at high latitudes, standardized several designs of open-top devices, including ITEX corners, cone chambers, hexagon chambers and plastic tents (Marion and Pidgeon 1992; Henry and Molau 1997; Marion et al. 1997). Their designs attempted to optimize the simulation of predicted climatic changes while minimizing the potential undesired side-effects of the OTC structures.

Recently, Hollister and Webber (2000) provided empirical biotic validation of OTCs as analogues of climatic warming in their study of meadow tundra vegetation in Barrow, Alaska. However, other climate change simulation methods such as electrical heating of the soil (e.g. Bergh and Linder 1999) and the use of infrared heaters (e.g. Bridgham et al. 1999) or free-air CO_2 and/or O_2 enrichment (FACE) systems (Karnosky et al. 2001) eliminate one of the main problems of the chambers, that is, the presence of the enclosure itself. The physical barrier presented by the chamber wall can lead to undesirable side-effects including changes in the distribution and amount of rainfall interception, wind strength, and changes in patterns of insect and mammal herbivory, all of which may compound and complicate accurate assessment of vegetation performance inside the chamber, in comparison to the outside.

Despite these problems, OTCs have numerous advantages that make them very attractive devices for studies in remote areas. OTCs are inexpensive, quick and simple to construct under any conditions, thus making them highly replicable and easily replaceable; the materials required for their construction, such as clear acrylic plastic, are easily accessible and can be purchased in most local hardware stores; and, OTCs are easily transportable and require no electricity or expensive high-technology equipment.

Ultimately, the effects of open-top chambers on microclimatic conditions present an array of interrelated complex processes, which cannot be easily isolated, but rather should be viewed in relation to one another. Although the conditions inside the chambers are complex and dynamic over short and long time scales, certain general patterns can emerge, such that knowing the effects of chamber on even one factor (e.g. soil temperature), or knowing the physical properties of the experimental plot (e.g. soil type) might allow the construction of a series of more specific predictions with respect to microclimatic air and soil conditions in OTCs. This may significantly facilitate experimental design and logistic application of chambers as effective, cost-efficient and easily replicable method of climatic modification in studies dealing with predicting the effects of climate change on natural ecosystems.

We expected that the reduced exchange of air between the chamber and outside would lead to increased air temperatures inside OTCs. This has been observed previously in numerous other studies involving ITEX or modified ITEX open-top chamber designs (e.g. Havström et al. 1993; Wookey et al. 1993; Marion et al. 1997; Hollister 1998; Hollister et al. 2005; Klein et al. 2005; Jónsdóttir et al. 2005; Wahren et al. 2005; Bokhorst et al. 2007). The effects of OTCs on soil temperature and moisture however, are more complex.

Open-top chambers have been found to cause soil drying (Aerts 2006), and the intricate relation between soil moisture and temperature based on the properties of heat transfer may be the source of the mixed effects of OTCs on these two factors. In particular, the alteration of snowmelt patterns (often omitted in the studies by the construction of OTCs after the snowmelt), can have profound effects on the soil thawing process and thus soil temperatures due to ground insulation variability. Consequently, this affects soil moisture, due to evaporation and infiltration of water coming from snowmelt (e.g. Groffman et al. 2001, Hardy et al. 2001, Bayard et al. 2005). Furthermore, the effects of OTCs on soil temperature can vary depending on such factors as soil depth (e.g. Hollister 1998), or the season (e.g. Klein et al. 2005).

Our long term goal was to predict the potential effects of current climatic changes on regeneration and succession patterns of mixedwood-boreal disturbance sites in northwestern Quebec, which could aid in management policy decision making with respect to continuous timber harvest within that region. On a larger scale, the prognosis with respect to regeneration patterns under ongoing climatic changes could provide invaluable information with respect to preservation of the natural integrity of northern Canadian boreal ecosystems. Choosing open-top chambers as the means of experimentally induced warming requires a thorough background research of the properties, effects and efficacy of the open-top chambers as climate change simulation devices.

The effects of the chambers on biogeochemical factors including soil pH, nutrient supply rates, decomposition rates and the chemical compositional change of litter, as well as plant responses in terms of growth, abundance, phenology, insect herbivory, foliar and root nutrient concentrations and root mycorrhizal colonization are addressed in the later chapters of this thesis, and will complete the comprehensive picture of potential effects of climatic changes on regeneration at post-disturbance sites within our study area. In this chapter we focused on the effects that open-top chambers have on microclimatic factors including air temperature and relative humidity, and also on soil temperature and moisture at different depths and substrates (*Sphagnum* versus non-*Sphagnum* dominated).The effects of open-top chambers on snowmelt, rainfall interception, and CO_2 concentrations were also addressed.

Materials and methods

Application of OTCs at post-disturbance sites in James Bay area

The study area (49°37’ N; 79°00’ W) was found in the boreal mixedwood-black spruce transitional forest zone in James Bay area, which constitutes part of the Clay Belt physiographic region spanning northwestern Quebec and northeastern Ontario. The region has developed on fine textured lacustrine and glacio-lacustrine deposits, which are the remnants of glacial lakes Barlow and Ojibway formed after the initiation of melting of the Laurentide Ice Sheet ~ 9000 years ago (Bergeron and Dubuc 1989; Paré et al. 2001; Lefort 2003). The Clay Belt covers approximately 125 000 km^2 of poorly drained clay soils, with nearly level topography (Lefort 2003).

The overall regional climate of the area is described as subpolar, subhumid continental, with cold dry winters and moist warm summers (Lefort 2003; Bergeron et al. 2004). Along the latitudinal gradient, the average annual precipitation ranges from ~ 900 mm to ~ 850 mm from southeast to north respectively, while the average annual temperature changes from ~ 1°C to 0°C, the average winter temperature from –17°C to –20°C, and the average summer temperature from 17°C to 16°C from south to north respectively (Bergeron et al. 2004).

The early successional mixedwood-boreal part of the region is dominated by jack pine (*Pinus banksiana* Lamb.) on well-drained sites, while white birch (*Betula paperifera* Marsh.) and aspen (*Populus tremuloides* Michx.) dominate the mesic sites (Bergeron and

Dubuc 1989; Lefort 2003). Later successional stages lead to dominance of balsam fir (*Abies balsamea* L.*)*, white spruce (*Picea glauca* (Moench) Voss), cedar (*Thuja occidentalis* L.), and black spruce (*Picea mariana* (Miller) BSP), with the last species progressively attaining overall dominance with increasing latitude, as the system changes into northern black spruce boreal forest (Lefort 2003).

We identified three study sites spanning 20 km along the Selbaie road (from 49°37' N; 78°59' W to 49 °45' N; 79°02' W). We refer to the Selbaie gravel road as a primary forestry road, while the smaller roads laid out perpendicular to it, are referred to as secondary forestry roads, or logging roads. Our three study sites consisted of: 1) a salvage logged post-fire site; 2) secondary winter forestry road, or the logging road, created to facilitate timber harvest; 3) and the actual post-logging site, where the timber harvest took place. At all of the sites the disturbance occurred in years 1996-1997. Detailed descriptions of the sites, including soil texture and drainage information, are provided in the general introduction of this thesis.

In total, 40 experimental plots were set up: 20 open-top chambers and 20 control plots. At the fire site there were eight OTCs and eight control plots; at the logging road site there were also eight OTCs and eight control plots; and, at the logging interval site there were four OTCs and four control plots. At each site, every OTC was paired with a control plot established in a close proximity.

In order to test the responses to the OTC treatment in the presence or absence of the live *Sphagnum* moss, at the fire site and the logging road site, for eight pairs of OTC and control plots the dominant substrate consisted of *Sphagnum* moss, while for the other eight pairs the substrate was dominated by sparse *Polytrichum* moss growing on a mixture of humus and mineral soil. Thus the substrate and the warming treatments at the fire and the logging road sites were crossed factorial: four OTCs and four control plots at *Sphagnum*-dominated substrates, and four OTCs and four control plots at non *Sphagnum*-dominated substrates, for a total of sixteen plots per site. At the logging interval site, all of the plots were on live *Sphagnum* moss.

At each of the three sites, for the plots receiving an open-top chamber treatment, we constructed a circular enclosure, 1 m in diameter and 0.75 m in height, built of clear transparent 8 mm thick polymethylmethaacrylate (PMMA, commonly known as acrylic) material. Two flexible PMMA sheets were connected with tie-wraps and supported in two places by plastic stakes inserted in the ground. The walls of the chambers were perpendicular to the ground. A control plot of the same size, not shielded with the acrylic plastic but marked with a nylon thread placed on the ground and secured with metal pegs, was set up close by.

In our trial assessment of open-top chambers, the photosynthetic photon flux density (PPFD) measurements taken continuously at 15 minute intervals inside the chamber were on average only ~ 6% lower in comparison to the control plot over the course of eight days in mid-April of 2005. The MatWeb Material Property Database reported that the transmittance of PMMA material to visible light is between 77-93% (MatWeb 2008). At wavelengths longer than 800 nm pure PMMA material becomes transparent, with no light scattered or absorbed (Zidan and Abu-Elnader 2005). The refractive index of PMMA between wavelength 800 and ~ 1500 nm is between 1.45 and 1.55 (Zidan and Abu-Elnader 2005).

The OTCs and the control plots were installed in late June 2005. In order for the OTC treatment to capture the events of snowmelt and the crucial period in terms of spring phenology and nutrient uptake of plants, the chambers were not removed in the wintertime. Microclimatic conditions including ambient temperature and relative humidity, as well as soil temperature and moisture were measured preliminarily during the summer of 2005. Final decisions on equipment used and the appropriate measurement sampling methods were made throughout this period.

Air temperature inside each of the OTCs and control plots was measured using maximum-minimum thermometers (15-116, Fisher*brand*, Nepean, Ontario and 5458, Taylor, Oak Brook, Illinois). To ensure consistency of the temperature data collection, all thermometers were cross-compared prior to their installation, and were installed 20 cm above the ground, always facing east. White plastic roofs, with vertical shades on three sides were installed over each thermometer in order to reduce direct insolation. Relative humidity (RH) was recorded inside each plot using a digital humidity meter (PTH8708 T/RH Pen, Spectrum Technologies Inc., Plainfield, Illinois). During each measurement event, the meter was placed 10 cm above the ground at the center of each plot for ~ 5 minutes, and the maximum humidity value reached during that time was recorded.

Soil temperatures were measured at depth 12 and 20 cm with soil probe thermometers (DT 130, Thermor, Newmarket, Ontario, and 50266 Tracable, Fisher*brand*, Nepean, Ontario, for 12 and 20 cm thermometer probe length respectively). For each data-gathering event, three temperature measurements, two taken at the opposite sites of the plot, and one taken in the middle were averaged.

The soil moisture in each plot was measured at the same time as the temperature, using a portable time-domain reflectometry (TDR) instrument (Field Scout TDR-100, Spectrum Technologies Inc., Plainfield, Illinois).The moisture was recorded as % volumetric moisture content measured as an average over the length of the 12 and 20 cm long stainless steel rods, with each final measurement represented by an average of six measurements taken randomly over the entire area of the plot.

From May 4 – 18, 2006, we collected spring season microclimatic data on 12 days at four intervals of three consecutive days of measurements. Each of the four 3-day measurement intervals was separated by one day free of measurements. The order of data collection for the three sites was rotated in a fashion so that within each 3-day measurement interval, data was taken once in the morning, once around mid-day and once in the early afternoon at each site. This was done to account for, and average out the potential variability in ambient temperature and soil temperature and moisture as the day progresses. The data for each 3-day interval was then averaged, resulting in four repeated measurements for each plot.

The summer season data was collected on 24 days over July and August 2006. The measurements were always taken three times a week, over eight consecutive weeks. Every week, at each plot, the data was gathered once in the early morning, once around mid-day and once in the afternoon. These three measurements taken in a single week were then averaged to provide one final measurement for that week. In summary, for each plot there were eight repeated measures of air temperature and relative humidity, as well as soil temperature and moisture, with each measurement represented by an average of three measurements taken in the same week at three different times of the day (morning, mid-day and afternoon). The measurements were always taken between 7:00 and 17:00.

In May 2007, we collected another set of spring data following the same procedures as the previous spring, except that the data was collected between May 8 and

23. Summer 2007 data was collected between June 24 and July 4, following the same sampling methods as for the spring data, except that this time three instead of four 3-day measurement intervals were completed.

For each of the four data sets (spring and summer 2006 and 2007), means and standard deviations were calculated for the air temperature (maximum and minimum), relative humidity, soil temperature (depth 12 cm and 20 cm), and soil moisture (probe length 12 and 20 cm), for the OTC treatment (OTC, control), substrate type (*Sphagnum*, non-*Sphagnum*) and disturbance type (fire, logging road, logging interval).

To assess the effects of the OTC treatment and substrate type on each of the microclimatic variables separately, we performed analysis of repeated measures using the procedure MIXED in SAS (version 9.1, SAS Institute 2007). For each analysis of repeated measures, individual plots were the experimental units (subjects). The OTC treatment, the substrate type, and the disturbance type, were the between-subjects fixed factors; the effect of the repeated measurements was the within-subject fixed factor.

The site, or disturbance type, was treated as a block in space and a fixed factor, since the sites were chosen prior to the experiment, and so cannot be considered random. As there are no replicates of the sites, no valid generalizations can be extended with regard to overall effects of these disturbance types on the physical conditions of air and soil we measured; nonetheless, site must be included as a factor in the model to avoid inflation of the error and thus, the possibility of a Type II error.

The plot was a random factor nested within the warming treatment and the substrate type. Interactions between the OTC treatment, the substrate type, the site and the measurement were also tested, and dropped from the final model if not significant. For significant effects, least-squares (LS) means with Scheffé correction for multiple comparisons were used to identify specific differences for treatments with more than two levels (i.e. disturbance type), or, in the case of significant interactions, combinations of treatment levels.

For all of the analyses, the variance-covariance structure for the repeated measurements was selected based on the Schwarz's Bayesian Information Criteria (BIC), with the smallest value indicating the best fit (Littell et al. 1996). All data analyses were checked for normality based on skewness and kurtosis values, as well as for homogeneity of variance (SAS Institute 2007).

Continuous temperature and relative humidity measurements, and snowmelt patterns

Preliminary exploration of microclimatic data collected in 2005 and 2006 prompted us to explore the observed trends at a finer time scale, as well as to address the potential causes of the observed trends. Therefore, in a series of experimental trials exploring the potential effects of chambers on microclimatic conditions, we made continuous measurements of ambient and ground temperature, and relative humidity for two pairs of OTC and control plots. Furthermore, we explored the potential effects of OTC structures on snowmelt and rainfall interception, both of which we suspected to affect soil temperature and moisture regimes.

Two pairs of open-top chambers and control plots were constructed. The first pair, designated OTC1 and C1, were deployed on March 7-21, 2007 at the Macdonald campus of McGill University located in Ste Anne-de-Bellevue (45^{o}24’ N; 73^{o}56’ W). At the time of plot construction, both the chamber and the control plot had about 30 cm of snow cover. As the plots were present over the period of late winter-early spring snowfall-snowmelt episodes, we observed and photographed snowmelt patterns in the chamber and the control plot every day.

As we were interested in the comparison of fine-time scale microclimatic responses to OTC treatment both in the late winter/early spring time and in the summer time, the second pair of OTC and control plots (OTC2 and C2) were deployed in the northern part of the James Bay boreal forest region (52°06’ N; 76°11’ W) in August 26 – September 5, 2007. We expected that the presence of snow and frozen soil in the late winter/early spring versus no snow or frozen soil but live plant cover could lead to different responses to OTC treatment in terms of evapotranspiration and thus relative humidity and air temperatures, as well as soil and plant respiration and thus CO_2 levels (see below). Due to logistic constrains dealing with the availability of equipment, we had to perform the two studies at two different sites.

Continuous ambient temperature and relative humidity were monitored inside all plots using a temperature/relative humidity probe (HMP45A, Vaisala Inc.,Vantaa, Finland) inserted into a radiation shield (10-Plate Gill, R.M. Young, Traverse City, Michigan) mounted 40 cm above the ground. At Macdonald campus site we also measured the ground temperature using an infrared temperature sensor (Raytek MI, Santa Cruz, California) mounted 170 cm above the ground and facing the ground within the chamber. Data was logged continuously at 5 minute intervals by a datalogger (CR23X, Campbell Scientific Inc., Logan, Utah).

Based on the precise time of the sunrise and the sunset at the specific site for each day of data collection, we split the data into daytime and nighttime. Comparison of means, standard deviations and ranges were made between OTCs and control plots for ambient temperature, RH and ground temperature (the last one at Macdonald site only), separately for daytime, nighttime and overall day and night. For visual exploration of daily trends, we compared the differences between OTCs and control plots for the 30 minute interval points collected inside OTCs and control plots for ambient temperature, RH and ground temperature against time (day and hour).

Effects of OTCs on rainfall interception

The fundamental goal of this trial was to explore the potential effects of OTC structure on the quantity and the spatial patterns of rainfall reaching the ground inside the chamber. Since we were interested in the effects of the chamber on rain patterns under a variety of weather conditions (rain intensity, wind) we measured and compared the amount of rain intercepted by a chamber and a control plot on nine different occasions, between April 2 and August 10, 2007, at Macdonald campus site. Collecting the data repeatedly at the same location and within the same plots allowed us to explore if weather conditions including wind direction and rain intensity affect the distribution and/or the amount of rain reaching the ground inside the chamber.

In order to test the effects of the OTC structure on rainfall interception, plastic cups of 150 ml volume were placed inside an OTC and a control plot. The cups were arranged in a cross shape, with six cups spread across the length of the plot for each line of the cross. The two lines ran orthogonally in north-south (NS) and west-east (WE) directions. Each line was extended by three additional cups outside of the plot at each end in order to compare the spatial variation in the amount of water that reached the ground both inside and around the chamber (Fig. 2.1, April 4). The positions were numbered from north to south for NS line and west to east for WE line (Fig. 2.1). After each rain event, the position and the amount of water (in ml) were recorded for the cups in the OTC and the control plot. The amount of rain water collected was recorded promptly after the cup collection, in order to minimize evaporation of water from the cups.

To address the question of whether OTC structure could potentially contribute to decreased soil moisture by reducing rainfall reaching the ground, for each of the nine days of rain collection, we estimated the total amount of rain which entered the plots by extrapolating the amount of rain collected in the cups to the total area of the plots. Since the distribution of the cups inside the plot was not even in terms of the area covered per cup, we divided the plots into three concentric parts: the part closest to the wall or the outer part, the middle part, and the inner part (Fig. 2.1). The outer part included four replicates of cups closest to the chamber wall at positions 4 and 9, the middle part included four replicates of the cups at positions 5 and 7, and the inner part included cups at positions 6 and 7 (Fig. 2.1). We calculated the area of each part, estimated the amount of rainfall intercepted in that part, and then summed up the three parts to obtain the estimated total rain collected for each plot on each rainy day. For consistency, the same procedure was followed for the control plots, although in this case we expected no difference in the amount of rain collected by the outer, middle and inner plot parts.

We explored the patterns of rain water entering the plots, for both the OTC and the control plot, by illustrating the actual amount of rain collected by every cup for every rain day (Fig. 2.1). Based on the patterns of rain quantities collected by the cups inside the chamber plot, we depicted prevailing wind conditions for each day (Fig. 2.1). Our assumptions with regard to wind direction were cross-checked for accuracy and consistency in comparison with data collected at the P.E. Trudeau Airport weather station (situated approximately 15 km away from our study site; Environment Canada: http://climate.weatheroffice.ec.gc.ca), for the time the cups were exposed to the rain.

In order to assess the effects of the chamber wall on the distribution of rain entering the chamber we conducted an ANOVA analysis (procedure MIXED, SAS Institute 2007), with the part of the plot (outer, middle, inner) as an explanatory variable and a fixed factor (n = 3), the four cups inside each plot part as replicates, and the amount of rain collected as a responding variable. Our hypothesis was that if the walls of the chamber have no effect on the distribution of the rain entering the chamber, there should be no differences between the amounts of rain water collected by the cups in the three concentric parts of the plot. We would expect no such differences if the rain was falling straight down, under conditions of no wind. We pulled the data from all nine rain events (n = 9), and treated each rain event as block in time and a random factor. The full model, including the plot part and the rain event, as well as the interaction between these two factors was run first; if the interaction was insignificant it was removed from the analysis, resulting in the final model. Following the same steps, we performed the same analysis for the control plot, expecting no differences among the outer, middle and inner parts of the plot.

Effects of OTCs on CO_2 concentrations

A pair of plots (one open-top chamber and one control plot) was deployed at two locations to compare the concentrations of CO_2 inside and outside of the chambers during spring and summer conditions. The first pair was deployed during snow-covered conditions at the Macdonald campus site on March 22-26, 2007 and the second pair was deployed in the northern part of the James Bay boreal forest region, on August 26 to September 5, 2007. We were interested in the comparison of the late winter/early spring versus summer CO_2 responses to OTC treatment; however, due to logistic constrains dealing with the availability of equipment, we had to perform the two studies at two different sites. We expected that the presence of snow and frozen soil versus live plant cover and unfrozen soil could affect differently the responses to OTC treatment in terms of plant and soil respiration.

Concentrations of CO_2 were measured using an infrared gas analyzer (IRGA; LI-840, LI-COR Inc., Lincoln, Nebraska) and the data were logged continuously at one second intervals by a data logger (CR5000, Campbell Scientific Inc., Logan, Utah). Air samples from the plots were pumped using a micro diaphragm gas pump (UNMP50, KNF Neuberger, Trenton, New Jersey) and a linear-piston vacuum pump (VP0125, Medo, Hanover Park, Illinois) through a multiposition valve (Valco SD, VICI Valco Instruments Co. Inc., Houston, Texas) and into the IRGA. The air flow was maintained at a steady rate by a low-pressure mass-flow controller (EL-FLOW, Bronkhorst High-Tech BV, Ruurlo, Netherlands). The system operated by switching the measurements every three minutes between the OTC and the control plot.

Based on the precise time of sunrise and sunset for every day of the measurement, data collected were separated into 'day' and 'night', and overall mean daytime and nighttime means were compared inside and outside of the chambers at both sites. Half hour intervals were also plotted against time to explore daily trends of [CO_2] in the chambers and control plots.

Results and discussion

Effects of OTCs on air temperature and relative humidity, and soil temperature and moisture

In general, the effects of the passive warming treatment provided by the open-top chambers at post-disturbance sites in the southern part of James Bay region, Quebec, from the end of June 2005 to mid-August 2007 consistently showed higher air temperature and drier, cooler soil conditions. The warmer conditions were especially apparent for daytime maximums, with nighttime minimum temperature differences between the chambers and the control plots being of lesser magnitude in the summer, and statistically negligible in the springtime (Tables 2.1and 2.2).

Descriptive statistics indicate that the mean maximum temperatures were 2°C to 3°C higher inside the OTCs as compared to control plots in the spring and summer 2006 and 2007. The analysis of repeated measures revealed that these differences were highly significant ($p< 0.0001$; Table 2.1 a-c; $p = 0.0006$; Table 2.1 d). However, mean minimum temperatures were significantly higher inside OTCs only in the summer season for both years ($p = 0.0062$, less than 1°C in 2006; and $p = 0.0014$, ~ 1.5°C in 2007; Table 2.1 b, d) while there were no significant differences in the springtime (Table 2.1 a, c). Any significant build-up of heat inside the chambers during the day (leading to maximum daily temperatures) in the springtime was quickly lost during the night, bringing the night temperatures down (to minimum daily temperatures); however, this heat build-up was seen to persist longer into the nights during the summer. This could explain the significant effect of OTC treatment on minimum temperatures in the summertime, but not in the springtime.

The higher, on average, air temperatures inside our OTCs are consistent with the results of other studies, which used similar passive warming treatment devices. In a study of the effectiveness of four open-top designs in simulating climatic warming at high-latitude ecosystems, Marion et al. (1997) reported that mean daily temperatures at four arctic sites were 1.2-1.8°C higher; Hollister (1998) reported an increase in average daily temperatures of up to 2.8°C; and Klein et al. (2005) observed maximum air daily temperatures 2.1-7.3°C higher inside OTCs in comparison with ambient air temperature.

Clearly, the efficacy of open-top chambers as passive warming devices is strongly influenced by the high differences in maximum daytime temperatures (Fig. 2.2; Tables 2.1 and 2.2) resulting probably from the energy trapped in the chamber due to decreased air mixing. By the same token, nighttime inversions could have been stronger inside the chamber than the control plots, as cold dense nighttime air sinks and builds up in the chamber, with reduced, in comparison to the outside, means of mixing and exchanging with the surrounding air (Hollister 1998). Indeed, measured minimum temperatures (which over the 24 hour period were most likely just prior to sunrise) were sometimes lower in chambers than control plots (Table 2.1), suggesting that ground-level nighttime cooling was greater in OTCs. Accordingly, Marion et al. (1997) concluded that most of the heating effect occurred as daytime warming above the ambient temperatures, while night temperatures in the OTCs were occasionally marked by cooling below ambient temperatures, which effectively reduced overall mean daily warming effect of the chambers.

Soil temperatures were consistently significantly lower inside OTCs than Cs at both depths 12 and 20 cm, for both seasons and for both years (Table 2.1). The differences were larger in the spring 2006 than in the spring 2007 ($p < 0.0001$, up to ~2.5°C colder inside OTCs than Cs at depth 20 cm in spring 2006; and $p = 0.003$, ~ 1°C colder inside OTCs than Cs at depth 12 cm in spring 2007; Table 2.1 a, c). Conversely, for the summer season, the differences were larger and significant in summer 2007 ($p = 0.003$, ~ 1.5°C colder inside OTCs than Cs at depth 12 cm; Table 2.1 d), while in summer

2006 the differences between OTCs and Cs were only marginally significant (*p* = 0.041, ~0.5°C colder inside OTCs than Cs at depth 12 cm; Table 2.1 b).

The soil was generally colder, but also drier inside the chambers. In the spring 2007, volumetric soil moisture content was over ~ 10% lower for both TDR probe lengths of 12 and 20 cm – differences which were found to be significant (*p* = 0.017 and *p* = 0.040 for 12 and 20 cm probes respectively; Table 2.1 c). In spring 2006 the soils were ~ 5% and ~ 8% drier for probe lengths of 12 and 20 cm respectively, and the difference was statistically significant only for the 20 cm probe length (*p* = 0.045; Table 2.1 a). Interestingly, differences in soil moisture content between OTCs and control plots decreased to the point of non-significance in the summertime of both years, with a maximum difference of ~ 5% in the summer 2006 for the 20 cm probe length (Table 2.1 b, d).

The observed patterns of abiotic conditions in our study follow a chain of logical explanations: warmer ambient temperature inside the chambers likely induced higher evapotranspiration, which resulted in lower soil temperature and moisture.

An endothermic process, evaporation of water from soils resulting from a conversion of heat energy to latent heat is energetically demanding, with 2257 joules required for every gram of water vaporized, leading to substantially cooler soil conditions. A combination of cooler soil, slightly lower relative humidity and higher air temperatures in the spring time suggest that evapotranspiration was likely higher in the chambers in the springtime after the snowmelt, which probably contributed to drier soil conditions.

To verify this assumption, we calculated potential evapotranspiration using climate data from the station in the city of Val d'Or (48°30' N ; 77°47' W), which was the closest weather station to our study sites in southern James Bay with complete yearly weather record available (Environment Canada, http://climate.weatheroffice.ec.gc.ca. 2008). We used the Thornthwaite method (Thornthwaite and Mather 1955, 1957) with mean weekly temperatures for the whole year (with the exception of days when the mean temperature was below zero) and changing day length to estimate potential evapotranspiration. We then increased all positive mean temperature values by 2.5°C, which is an estimated increase in temperature inside our chambers, in comparison to the control plots. Re-calculation of potential evapotranspiration under higher mean temperatures (all else being equal) revealed that potential evapotranspiration would be about 12.5% higher inside the chambers in both years 2006 and 2007, which could explain the differences of up to 10% lower volumetric moisture content in our chambers as opposed to control plots. These results are in agreement with computer simulations of climatic warming for Finnish boreal forests that have shown that enhanced evapotranspiration would lead to drier soil conditions (Kellomäki and Väisänen 1996).

The fact that the drier soil conditions were more evident in the springtime than summer, prompted us to suppose that the accelerated snowmelt in the chambers (see the following section) led to earlier soil exposure. Therefore, evaporation from snow-free soils in the chambers commenced earlier than in the control plots where the snow cover persisted longer. By the summertime, the evaporative process likely caught up in the control plots, so the soil moisture condition differences between the chambers and control plots decreased.

Spring soil freeze-thaw cycles probably also played an important role in lowering the liquid soil water content in the chambers. Advanced snowmelt in the chambers would result in earlier exposure of soil to frequent spring freezing episodes (i.e. days with temperatures below 0°C), to which the control plot soils would be less exposed due to the presence of insulating snow cover. Consequently, after the final snowmelt, it took longer for the soils in the chambers to thaw completely. Indeed, in the early May we often encountered soil patches, which were still frozen solid at depths ~ 15 cm in the chambers, though we never encountered that in the control plots. As we could not insert the 20 cm TDR probes into these frozen patches, our measurements were taken in the unfrozen parts of the chamber. However, the close proximity of frozen soils around the spots of TDR probe insertion most likely led to lower volumetric moisture content readings, since TDR does not detect water in a frozen state (Kahimba and Ranjan 2006). In summary, increased evapotranspiration of water coming from snowmelt, as well as the more frozen soil patches in the spring likely both contributed to lower liquid water content in OTC soils compared to control plots.

Drier soil conditions inside the chambers may also have induced lower soil temperatures by a reduction of thermal conductivity. As both thermal conductivity and diffusivity are several magnitudes higher for water as opposed to air (Rosenberg et al.

1983), heat passes much faster through water than air. Consequently, as moisture declines and the air content in soils increases, there is a higher resistance to the transfer of heat. Indeed, at the logging road site, where the soil conditions were always the wettest, the average soil temperature was always the highest (Table 2.1). Accordingly, Hollister (1998) found that in comparison to a wet meadow community, soil warming inside OTCs was substantially lower at the inherently drier heath community site, and likewise he attributed this to the higher heat conductivity of wetter soil at the meadow community. Also, Kellner (2001) reported that the ground heat flux in a Swedish mire was almost twice as high in the wet hollows as opposed to the drier ridges, and soil warming was much faster in hollows than at ridges in early summer.

Relative humidity was ~ 1% and ~ 3% lower inside the chambers in the spring of 2006 and 2007, respectively. These differences were marginally significant (Table 2.1 a, c). For the summer season, the differences in relative humidity were not significant in either year. The elevated ambient temperatures in the chambers likely resulted in higher saturation vapour density, leading to lower percent saturation. Marion et al. (1997) likewise reported evidence of decreased relative humidity in their documentation of efficacy of open-top devices, and they attributed this to elevated air temperatures.

Substrate (*Sphagnum* or non-*Sphagnum*) had no effect on ambient and soil temperatures in the spring and summer 2006 and 2007. However, for both seasons and in both years volumetric moisture content was significantly higher at the *Sphagnum* plots. In the springtime, the differences were on average 9-10% and 12% for both years for probes of 12 and 20 cm length respectively. In the summertime, the differences were 9% and 13% for 12 cm probes in 2006 and 2007 respectively, and 10% and 14 % for 20 cm probes for 2006 and 2007 respectively (Table 2.1). In summer 2006 there was also a significant interaction between the substrate type and site, where the soil temperature at depth 12 cm in *Sphagnum* plots at the fire site and the logging interval site was significantly lower than at the *Sphagnum* plots at the logging road site. Substrate had no effect on RH in spring and summer 2006, and in 2007 RH was significantly higher in *Sphagnum* substrate plots in the spring, but not in the summer.

Overall, the presence of the open-top chambers did not seem to intensify, decrease, or reverse the effects of the *Sphagnum* substrate on air temperature or soil temperature and moisture, as there were no significant interactions of the substrate type with the OTC treatment at any of the sites. Accordingly, Weltzin et al. (2001) found that experimental warming treatment had no effect on the productivity of several *Sphagnum*, and one *Polytrichum* species, but their growth was strongly affected by the water table level, with increased production along the gradient of increasing water table heights. They concluded that although an increase in temperature may not have a direct effect on bryophyte production, it might be affected indirectly, through the effects of warming on water table levels. Since our results indicate drier soil conditions under the increased air temperatures, it is expected that, in the long run, the *Sphagnum* substrate may be negatively affected by excessive dryness and this may become reflected in the performance of existing vascular vegetation, e.g. black spruce (Fleming and Mossa 1994).

Comparison of continuous measurements of ambient and ground temperature, relative humidity, and snowmelt patterns in OTCs and control plots

Continuous measurements of ambient temperature, relative humidity and ground surface temperature taken for 14 days in March 2007 (late winter) at Macdonald campus, and for 10 days in August-September 2007 (late summer; no ground surface temperature) in northern James Bay region produced trends which varied not only across the sites but also over the course of the day (Table 2.2; Fig. 2.2).

The average daytime air temperatures were 1-1.7^{o}C higher inside the chambers at both sites, but the average night temperatures were 0.5^{o}C lower in the chambers in the late winter at the Macdonald campus, while there were no differences in the average night temperatures in the late summer at James Bay site (Table 2.2). Overall, the average daily (24-hour) temperatures were ~ 0.5^{o}C higher inside the chambers as compared to control plots at both sites, with the heating effect occurring primarily during the daytime. At its maximum, daytime air temperature was 2^{o}C higher at the Macdonald campus site, and 2.5^{o}C higher at the James Bay site inside the chambers, while at its minimum, the temperature was less than a half degree lower in the chambers at both sites (Table 2.2).

Difference in relative humidity was always most evident at nighttime at the Macdonald site, with an average humidity 4% higher in the chamber than in the control plot. Average daytime differences were slight at about 1% at both sites (Table 2.2).

Overall, daily mean differences were larger at the Macdonald site (~ 1.4 %), and negligible at the James Bay site. The highest difference in maximum relative humidity (over 7% lower in the chamber) and the highest difference in minimum relative humidity (3.5% higher at night in the chamber) were observed at the Macdonald site (Table 2.2).

Ground surface temperature was on average 2°C and 1.6°C higher in the chamber at the Macdonald site in the late winter for daytime and nighttime, respectively (Table 2.2). Overall, daily ground surface temperatures were on average 1.7°C higher inside the chambers than the control plots at the Macdonald site.

Cycles of partial and complete snowmelt followed by snowfall events made the comparison of snowmelt in the chamber and control plot complex, but snowmelt occurring between snowfall events was always visibly accelerated in the chamber (Fig. 2.3). Partial snowmelt (i.e. parts of the plot where the snow melted completely, exposing the ground) was observed for the first time on day 71 (March 12) in the chamber, and on day 74 (March 15) in the control plot. The first complete snowmelt in the entire plot occurred in the chamber on day 73 (March 14) and persisted until day 75 (March 16) when it started snowing again. Over days 73-75, while there was no snow present in the chamber, there was still ~ 10 cm snow cover present over most of the area in the control plot. The first completely snow-free day in the control plot occurred on day 83 (March 24).

The predictions with regard to snow precipitation, snow cover and snowmelt in the wake of the changing climate are far from being unanimous (Qin et al. 2006; Edwards et al. 2007). Due to its high albedo and low thermal conductivity, deep snowpacks may effectively insulate the soil from freezing by way of reducing heat loss through radiation and convection (Bonan 1992; Edwards and Cresser 1992; Groffman et al. 2001; Hardy et al. 2001; Decker et al. 2003; Campbell et al. 2005; Edwards et al. 2007). Delayed snow cover in the fall may lead to early frost penetration, while earlier snowmelt in the spring can cause early spring freeze, which would be reduced with the presence of insulating snow cover. The relation between air and soil temperatures decreases with increasing depth of snowpack and increasing soil depth (Decker et al. 2003; Edwards et al. 2007).

Overall, complex interactions among numerous environmental variables including not only air, ground or snow surface temperatures but also wind exposure, among others, lead to high uncertainty of the effects of OTCs on snowmelt. Indeed, inconsistencies with respect to snowmelt in open-top chambers across different sites have been reported. For example, Marion et al. (1997) observed that while there were no differences in snowmelt dates at two of their sites, at another site snow melted 1-2 weeks earlier inside the chambers. Though we do not have direct evidence of the snowmelt patterns in southern James Bay, we believe that the snow melted earlier inside our chambers, since the soil temperatures were consistently lower inside the chambers in the spring. The forests surrounding our post-disturbance sites presumably shelter them from strong winds, thus making the air temperature a key factor in the process of snow ablation.

Bayard et al. (2005) contrasted two winters, one characterized by heavy snowfall and thick snowpack, and the other by little snow precipitation. They observed that during the first winter, a thick snowpack prevented the formation of soil freeze and resulted in 90-100% of snowmelt water infiltration. During the second winter, reduced snowpack insulation resulted in deep and persistent soil freeze. Our results corroborate these observations, since we observed profoundly reduced soil temperatures (at depths 12 and 20 cm) and more extensive soil freezing in the OTCs in the spring. Furthermore, we observed that decreased soil moisture in open-top chambers was significant in the springtime, indicating that the partially frozen soils prevented melt water infiltration, allowing the water to evaporate instead. In contrast, in the control plots, where the longer presence of snowpack (which melted later in the spring) prevented the soil from freezing extensively, the melt water infiltrated deeper into the soil, thus the soil moisture was higher in control plots than chambers in the springtime.

Jónsdóttir et al. (2005) also reported that the effects of OTCs lead to cooling of the soil at depth 10 cm in Icelandic tundra communities, and upon ruling out plant shading as a factor, they concluded that further research was needed to determine the causes of decreased soil temperatures inside the chambers. As in our case, their OTCs were installed all year round, and the snow inside the chambers melted a few days earlier in springtime (Jónsdóttir, personal communication). On the other hand, Hollister (1998) noted an average increase in soil temperature inside OTCs from 0.1°C at depth 30 cm, through 0.4°C at 10-15 cm , 0.7°C at 5 cm to 1.2°C at 1 cm, but his OTC treatment was applied only between June and August in Barrow, Alaska. We believe that the variability with respect to the effects of OTCs on soil temperature are due in part to snowmelt patterns in the springtime; accelerated snowmelt is likely responsible for the lower soil temperatures due to a lack of insulating snow cover in early spring months, and lower soil moisture due to earlier onset of evaporation of melt water, which cannot infiltrate the frozen soil. On the other hand, delayed snowmelt in the OTCs, or instalment of OTCs after the snowmelt, could lead to no differences in soil temperatures, or to elevated soil temperatures. In addition, the effects of OTCs on soil temperature may also be modified by the complex interactions with soil moisture, which may be connected to the effects of chambers on rainfall interception.

Effects of OTCs on rainfall interception

Comparisons of the estimations of the total amount of rain which entered the chamber versus the control plot on the nine days of data collected, suggested that the chamber received on average ~ 20 % less rainfall (Figs. 2.1 and 2.4). However, the distribution of the rain reaching the soil in the outer parts of the OTC (i.e. closest to the inside chamber wall) was highly dynamic and variable across the rain days, depending on wind direction and rain intensity (Fig. 2.1). Closer inspection of the distributional patterns of the rain entering the chamber suggested that depending on wind direction, the area close to the inside wall of the chamber was receiving less rain water, while there appeared to be little difference in the rain reaching the ground in the inward parts of the chamber, suggesting that the source of variability in terms of rain reaching the soil occurs within a ~ 15 cm ring from the chamber wall (Fig. 2.1). An ANOVA model testing the effects of the three concentric parts within the chamber plot (outward, middle and inward) on the amount of rain collected by the cups indicated that there is a significant difference between the three parts ($p = 0.020$), and least-squares means indicated that the outward part receives significantly less rain than the inward part. The middle part did not differ statistically from either of the two other parts. There was no significant interaction with the date of the rain event, (treated here as block in time and a fixed factor), which indicates that the total amount of rain collected by the cups in the outward part was always smaller than the cups in the inward part of the plot, regardless of the wind direction and the rain intensity. As expected, the final ANOVA model for the control plot did not detect any differences between the outward, middle and the inward parts of the plot (*p* = 0.410), supporting our theory that the walls of the chamber lead to uneven distribution of the rain inside the chamber.

For one plot and date (April 4, Fig. 2.1), we illustrated the expected minimum and maximum in terms of the amount of rain water reaching the ground. We predicted that the actual amount of rain water entering the chamber at the expected maximum of the plot has been underestimated, since depending on wind patterns, a certain amount of rain has encountered the chamber wall, and slid down onto the ground, missing our cups located at the outer positions. With the knowledge of wind speed and direction, as well as some estimation of the size of raindrops, we designed a two-dimensional geometrical model allowing for approximate estimation of the amount of rain, which would encounter the inside wall of the chamber facing the direction of the wind (Figs. 2.5 and 2.6).

The model's assumption is that the speed of the raindrop will remain the same upon entering the chamber, which considering that the diameter of the chamber is only 1 m, is in fact a very close approximation. The stopping distance of a raindrop is a function of its initial velocity and its size (van Mook et al. 1997). Since the wind speed can be assumed to be reduced or even eliminated inside the chamber, the raindrop entering the chamber should be expected to slow down and change its trajectory. However, at a short distance of 1 m, the size of the raindrop would have to be extremely small (<0.1 mm) for that to happen (van Mook et al. 1997). Under wind conditions of approximate speed of 6 m/s and atmospheric conditions of ~ 100 kPa (i.e. average conditions on our example date) we can estimate that the average raindrop size would be 1.8 mm (following Erpul et al. 1998), and the vertical fall speed of the raindrop to be 6.09 m/s (following Gunn and Kinzer 1949). If a raindrop with initial horizontal velocity of ~ 6 m/s and the size of 1.8 mm enters the chamber where the wind is reduced, it would require around 8 m to significantly change trajectory from being nearly linear (van Mook et al. 1997). Therefore, we can assume that if the raindrops entering the chamber are 1.8 mm in diameter, the actual change in their trajectory may be neglected, and a raindrop pushed by the wind will continue to follow the same trajectory upon entering the chamber.

The trajectory of a falling raindrop is a function of its size, which determines its free vertical fall speed (Gunn and Kinzer 1949), and its horizontal velocity is determined by the wind speed. Under conditions of no wind, the fall of a raindrop will approximate its vertical fall speed. Trajectories of five exemplary raindrops of the same size, affected by both vertical (fall speed) and horizontal (wind) velocities are illustrated in Fig. 2.5. The area *V* represents the fraction of the total area within the chamber, which will receive no precipitation under the illustrated wind conditions, while all the raindrops falling beyond boundary *v* in the chamber will either land within area *W*, or will encounter the inside wall of the chamber (Fig. 2.5). Assuming that no rain reached the ground within area *V*, the determination of area *W* within the chamber will allow for an estimation of the fraction of total rainfall, which reached the ground, with the remaining rainfall being the amount, which struck the inside chamber wall. We can calculate area *W* by equating the raindrop shift by the wind to a theoretical shift of the chamber from position OTC to position OTC' by distance *h* (Fig. 2.6) following Equation (1):

$$W = 2r^2\left\{\cos^{-1}\left(\frac{h}{2r}\right) - \frac{1}{2}\sin\left[2\cos^{-1}\left(\frac{h}{2r}\right)\right]\right\} \tag{1}$$

where *r* is the radius of the chamber, and *h* is the raindrop shift by the wind. (A derivation of Equation (1) is provided in Appendix 1). Dividing *W* by the total area of the plot allows the determination of the fraction of rainfall which *directly* reached the ground inside the chamber, with the remaining amount being the rainfall that was intercepted by the inside wall of the chamber and therefore potentially reached the ground *indirectly* by running down the wall. This intercepted rainfall is the cause of the underestimation described earlier (i.e. the rainfall that never reached our cups).

In our example day, both the amount of rain water collected in our cups (Fig. 2.1), as well as the meteorological data collected at the airport weather station indicated that the prevailing wind direction during the time of our rain collection was southeast. The average wind speed over the day was 23.8 km/h (6.6 m/s) and the average atmospheric pressure was 1002 hPa. The total precipitation over a 24 hour period reached 23 mm, which was a record in Montreal that month in terms of rainfall (http://climate.weatheroffice.ec.gc.ca). Under these wind and atmospheric conditions we estimated the average raindrop size to be 1.8 mm (following Erpul et al. 1998), and the vertical fall speed of the raindrop to be 6.09 m/s (following Gunn and Kinzer 1949). We used the dimensions of our chamber (height = 0.75 m, radius = 0.5 m) and Equation (1) to plot a fraction of total rainfall, which would strike the inside chamber wall under wind conditions varying from 0 m/s to 8 m/s (Fig. 2.7).

Our example case illustrates that overall, the effects of the OTC on the amount of rainfall entering the chamber depends strongly on wind conditions and the size of raindrops on a given day. Theoretically, with no wind present, there should be no difference in the amount or the distribution of the rainfall entering and reaching the ground in the OTC or the control plot. However, as wind speed increases, or raindrop size decreases, the area inside the plot receiving rainfall (i.e. area *W* in Figs. 2.5 and 2.6) will decrease, and the fraction of raindrops striking the inside chamber wall facing the wind will increase (arc marked '*bcd'* in Fig. 2.6). Under the average wind conditions of 6.6 m/s during the example rain event, ~ 80% of the rain entering the chamber would strike the inside chamber wall facing the wind, with the remaining 20% reaching the ground directly (Fig. 2.6). Under the conditions of extreme wind, all of the incoming rainfall would strike the inside chamber wall facing the wind, with no rain reaching the ground directly inside the plot. For raindrops of size 1.8 mm in diameter this would occur under the initial horizontal wind velocity of 8 m/s (Fig. 2.7).

The rain water striking the inside wall, will trickle down that wall into the soil, and as the amount of this water increases, it will concentrate by the chamber wall, with the patterns of infiltration remaining largely unpredictable, as they will be influenced by the soil type and surface ground slope, among other factors. In some cases, e.g. in clay dominated soils, the water would infiltrate laterally, toward the drier parts inside the plot, but it may just as likely infiltrate outside of the chamber, since the soil on the other side of the wall will also be much drier (e.g. Fig. 2.1: chamber plot from April 4, cup position 3 in comparison to cup position 4). By the same token, the rainfall striking the outside chamber wall, i.e. windward side of the chamber (represented by raindrop *"A"* in Fig. 2.5) will trickle down the outside chamber wall into the soil, and may just as likely infiltrate into the chamber, where the soil conditions are dry just on the other side of the wall (area *V* in Figs. 2.5 and 2.6).

In summary, the stronger the wind, the more skewed the distribution of rain precipitation will be, with rain water concentrating both, by the inside chamber and the outside chamber wall, facing the wind direction. In that case, it is difficult to conclude that rainfall interception alterations by the chamber structure may ultimately contribute to lower soil moisture inside the chambers over the long term. Nonetheless, we observed lower soil moisture conditions inside the chambers over the two seasons of our study in southern James Bay region, mostly in the spring (Table 2.1).

The fact that the 20 replicates of our chambers were distributed in highly variable sites in southern James Bay, do not allow us to generalize on the effects of chambers on rainfall interception and consequently, on soil moisture. In the years marked by the frequent rain events accompanied by strong winds, highly uneven rain water distribution inside the chambers is more probable to result in rain water infiltrating outside of the chamber, perhaps ultimately contributing to drier soil conditions, though as discussed above, the water infiltrating into the chamber could compensate for that. However, we believe that the reduced soil moisture in the chambers, which we observed primarily in the springtime, is more likely an effect of an earlier snowmelt followed by melt water evapotranspiration due to inhibition of water infiltration into the frozen soil. We base that assumption on several evidence-supporting facts. Firstly, the effects of noticeably reduced soil moisture were generally less noticeable in the summertime when the soils were thawed. Secondly, at least two of the years (2005 and 2007) when our chambers were set up, were marked by low total and rain precipitation. The differences in soil moisture were not significant in the spring (probe length 12 cm) or summer (both probe lengths) of 2006, despite relatively high rainfall, but were significant in the spring of 2007 (Table 2.1), which was marked by a relatively low rainfall. If the open-top chambers were affecting rainfall interception by decreasing the amount of rain entering the chamber, then we would presumably expect to observe reflection of that in soil moisture content in the wetter year, that is, in 2006.

In conclusion, the effects of the chambers on rainfall interception must be considered in the full context of the rain and wind conditions, as well as the physical properties of the site where the chambers are constructed, including the properties of the soil and the physical structures surrounding the chambers, among other factors.

Furthermore, the structure of the open-top chamber alone will have an effect on precipitation interception. The effects of OTC structure on rain entering the chamber will be affected by the shape (e.g. circular versus rectangular, straight walls versus inclined walls), and the size of the chamber (height, diameter). We would expect that the chamber structure with inwardly inclined walls, such as that used e.g. by Hollister (1998), would effectively reduce the amount of rain entering the chamber, even in the total absence of wind. In our case, in the absence of wind we would expect no effects of chamber structure on rain quantity entering the chamber, and rain distribution inside the chamber, since the walls of our chambers were perpendicular to the ground.

Effects of OTCs on CO_2 concentrations

Meta-analysis of 32 studies using warming methods (including passive devices such as OTCs) with the goal of climate change simulation, have shown that experimental warming increases soil respiration rates by about 20% (Rustad et al. 2001). However, our indirect assessment of soil activity by means of comparing carbon dioxide concentrations did not provide strong evidence of different CO_2 levels inside and outside of chambers (Figs. 2.8 and 2.9). Overall, continuous measurements of CO_2 showed that the differences between OTCs and control plots were biologically negligible regardless of the site and the season (Macdonald site in late winter and northern James Bay in late summer) (i.e. ~ 1.5 ppm at the most) (Fig. 2.8).

At the current rate of [CO_2] increase, ambient concentrations may reach 600 ppm by the end of 21st century (Houghton et al. 2001). In the wake of these predictions, numerous studies which intentionally increase CO_2 concentrations to explore, for example, the responses of trees, apply treatments of ambient enrichment of ~ 200 ppm, or even double the present ambient CO_2 levels (e.g. using free air CO_2 enrichment (FACE) systems (Karnosky et al. 2001), or using whole-tree chambers (Kostiainen et al. 2004). In comparison to such treatments, our unintentional increase of ~ 1.5 ppm can hardly be considered a significant CO_2 enrichment; rather, it is a negligible side effect of our open-top chamber design.

Modification of CO_2 levels with our OTC design was not our initial intention; however, we recognized that reduced air mixing and exchange of air with the surrounding ambient air may lead to build up of CO_2 inside the chambers, which along with the changes in soil temperature and moisture could affect soil respiration. With the absence of elevated CO_2 levels in the OTCs, we can rule out the confounding effects of CO_2 fertilization, when assessing the effects of OTC climate change simulation on plant growth.

Conclusion

The general trends in terms of the effects of OTCs on physical properties of air and soil show higher air temperatures, especially in the daytime, lower soil temperatures and soil moisture, especially in the springtime, lower relative humidity in the spring, and no effect on CO_2 concentration. Rain precipitation regimes are altered by the presence of the chamber wall, but generalizations in terms of the effects of chambers on rainfall are difficult as they are highly variable depending on wind direction, rain intensity and chamber structure. Theoretically, the same amount of rainfall should enter the chamber as the control plot, though the distribution of rainfall in the chamber will be affected by the presence of the chamber walls. Ultimately, this may affect soil moisture in the long term, but accelerated snowmelt and increased evapotranspiration appear to play a larger role in contributing to drier and cooler soil conditions inside the chambers.

In the context of applying the chambers as simulations of climatic change, awareness of multiple microclimatic and physical factors is crucial in understanding the functionality of the chambers, as it is based on a system of highly complex and dynamic interactions of these factors. Overall, the chambers present an inexpensive, efficient, durable method of climatic simulation in the field, especially in remote areas. They require no electricity and create little disturbance – traits that make them attractive from the logistic stand point in terms of allowing for high number of replicates, easy replacement, and protection of natural integrity within the research sites. Furthermore, flexibility in terms of design and the timing of OTC application may allow for the desired modification of the climatic conditions. For example, with the intention of reducing rainfall interception, OTC models with inclined walls could be built; warmer soil can be simulated by application of the OTC treatment after the snowmelt and before the snowfall, while a cooler, drier soil conditions are more likely to be achieved by leaving the chambers all year round.

More importantly however, open-top chambers present a plausible scenario of the potential chain of effects of increased air temperatures. A likely induction of earlier snowmelt and evapotranspiration, both of which may effectively contribute to cooler and drier soil conditions, may in fact be an accurate effect of global warming on soils. This paradox of 'colder soils in a warmer world' has been expressed before (Groffman et al. 2001) and has been reported in experimental studies (e.g. Groffman et al. 2001; Hardy et al. 2001). This, along with the logistic attributes of the chambers mentioned above, makes the open-top chambers currently among the most reliable and effective methods of experimental simulation of climate change.

Tables

Table 2. 1 Effects of the warming treatment (open-top chamber [OTC] or control [C]), substrate (*Sphagnum* [S] or non-*Sphagnum* [NS]), and site (fire [F], logging road [LR] or logging interval [LI]) on maximum and minimum temperatures (°C) (MaxT and MinT), soil temperature (°C) at depth 12 and 20 cm (ST12 and ST20), % volumetric moisture content for time domain reflectometry probe length of 12 and 20 cm (%VMC12 and %VMC20) and relative humidity (%RH). Data collected as repeated measurements ('msr') in spring and summer 2006 (a, b respectively), and spring and summer 2007 (c, d respectively). Comparison of means and standard deviations (SD) for the warming treatment, substrate type and disturbance type are also included.

a)				**Spring 2006**						
				Warming treatment: Mean (SD)		Substrate type: Mean (SD)		Disturbance site: Mean (SD)		
Factor	Responding variable	F value	*P*>F	OTC	C	S	NS	F	LR	LI
MaxT	OTC	**69.5***	**<.0001**	**25.2 (4.3)**	**22.5 (4.2)**					
	msr	**555**	**<.0001**							
	substrate	0.53	0.472			24.0 (4.5)	23.5 (4.3)			
	site	**6.77**	**0.004**					**23.1 (4.2)**	**24.1 (4.7)**	**24.6 (4.1)**
	OTC*site	**3.59**	**0.039**							
	OTC*site* msr	**2.95**	**0.001**							
MinT	OTC	0.06	0.815	1.8 (2.5)	1.5 (2.4)					
	msr	**250**	**<.0001**							
	substrate	3.00	0.093			1.5 (2.5)	2.4 (1.8)			
	site	3.10	0.057					2.0 (2.6)	1.3 (2.0)	1.6 (3.0)
	OTC*site* msr	**2.45**	**0.004**							

ST12	OTC	**28.7**	**<.0001**	**4.1 (2.4)**	**6.4 (2.4)**					
	msr	**149**	**<.0001**							
	substrate	0.53	0.473			5.2 (2.7)	5.3 (2.6)			
	site	**4.41**	**0.022**					**4.8 (2.5)**	**5.8 (2.8)**	**5.3 (2.5)**
	OTC*msr	**6.54**	**0.001**							
ST20	OTC	**24.8**	**<.0001**	**3.0 (2.4)**	**5.6 (2.5)**					
	msr	**128**	**<.0001**							
	substrate	0.14	0.708			4.3 (2.7)	4.4 (2.8)			
	site	0.49	0.617					3.7 (2.6)	5.0 (2.9)	4.2 (2.5)
	OTC*msr	**6.11**	**0.001**							
%VMC12	OTC	1.47	0.236	39.0 (15.3)	44.1 (19.2)					
	msr	**8.27**	**<.0001**							
	substrate	**13.0**	**0.001**			**45.4 (20.6)**	**35.7 (8.6)**			
	site	**7.36**	**0.003**					**41.0 (15.3)**	**48.1 (17.2)**	**29.9 (16.2)**
%VMC20	OTC	**4.35**	**0.044**	**49.1 (17.7)**	**57.5 (19.9)**					
	msr	**11.2**	**<.0001**							
	substrate	**22.1**	**<.0001**			**58.2 (21.0)**	**45.8 (13.3)**			
	site	**13.1**	**<.0001**					**55.2 (19.0)**	**58.1 (18.0)**	**40.2 (16.8)**
%RH	OTC	3.52	0.070	55.6 (8.9)	56.9 (9.8)					
	msr	**75.3**	**<.0001**							
	substrate	1.81	0.188			56.1 (9.6)	56.4 (8.9)			
	Site	**35.9**	**<.0001**					**60.9 (7.9)**	**53.1 (9.2)**	**53.0 (8.7)**
	OTC*msr* site	**3.30**	**0.000**							

b)

				Summer 2006						
				Warming treatment: Mean (SD)		Substrate type: Mean (SD)		Disturbance site: Mean (SD)		
Factor	Responding variable	F value	*P*>F	OTC	C	S	NS	F	LR	LI
MaxT	OTC	**26.2**	**<.0001**	**31.6 (2.9)**	**29.6 (2.7)**					
	msr	**128**	**<.0001**							
	substrate	0.49	0.489			30.5 (2.8)	30.6 (3.2)			
	site	0.10	0.903					30.7 (2.5)	30.5 (3.3)	30.5 (3.0)
	OTC*site* msr	**2.60**	**<.0001**							
MinT	OTC	**8.56**	**0.006**	**5.9 (2.3)**	**5.3 (2.3)**					
	msr	**624**	**<.0001**							
	substrate	0.96	0.333			5.7 (2.4)	5.5 (2.3)			
	site	**13.6**	**<.0001**					**5.1 (2.3)**	**5.6 (2.4)**	**6.5 (2.0)**
	OTC*site* msr	**4.71**	**<.0001**							
ST12	OTC	**4.52**	**0.041**	**14.4 (1.2)**	**14.8 (1.4)**					
	msr	**686**	**<.0001**							
	substrate	0.00	0.950			14.5 (1.3)	14.7 (1.4)			
	site	**5.73**	**0.008**					**14.4 (1.4)**	**15.1 (1.2)**	**14.2 (1.1)**
	OTC*msr	**2.76**	**0.009**							
	OTC*msr* site	**3.99**	**<.0001**							
	site*msr	**2.71**	**0.011**							

	site* substrate	**4.49**	**0.042**							
ST20	OTC	3.64	0.066	13.6 (1.1)	14.2 (1.4)					
	msr	**483**	**<.0001**							
	substrate	0.10	0.757			13.8 (1.3)	14.0 (1.2)			
	site	**7.79**	**0.002**					**13.7 (1.3)**	**14.5 (1.1)**	**13.3 (1.1)**
	OTC*msr	**1.92**	**0.010**							
%VMC12	OTC	1.83	0.192	29.0 (13.4)	33.6 (16.5)					
	msr	**32.9**	**<.0001**							
	substrate	**11.2**	**0.003**			**34.9 (17.7)**	**26.0 (7.6)**			
	site	**7.44**	**0.005**					**28.9 (11.3)**	**38.1 (17.2)**	**22.5 (11.2)**
	substrate* msr	**8.28**	**<.0001**							
	OTC*site* msr	**3.42**	**<.0001**							
%VMC20	OTC	1.64	0.209	39.9 (15.9)	45.4 (18.3)					
	msr	**54.0**	**<.0001**							
	substrate	**13.6**	**0.001**			**46.6 (19.6)**	**36.6 (10.8)**			
	site	**8.52**	**0.001**					**41.0 (13.7)**	**49.2 (19.5)**	**32.7 (13.5)**
	substrate* msr	**6.94**	**<.0001**							
	OTC*site* msr	**3.29**	**<.0001**							
%RH	OTC	1.07	0.308	61.2 (9.3)	60.4 (9.4)					
	msr	**108**	**<.0001**							
	substrate	3.61	0.066			61.3 (9.0)	60.0 (9.6)			
	site	**10.9**	**0.001**					**58.8 (8.0)**	**63.4 (10.2)**	**59.6 (8.6)**
	OTC*msr* site	**3.89**	**<.0001**							

c)

				Spring 2007						
				Warming treatment: Mean (SD)		Substrate type: Mean (SD)		Disturbance site: Mean (SD)		
Factor	Responding variable	F value	*P*>F	OTC	C	S	NS	F	LR	LI
MaxT	OTC	**21.8**	**<0.0001**	**26.6** **(2.0)**	**24.8** **(2.0)**					
	msr	**42.1**	**<0.0001**							
	substrate	0.23	0.638			25.7 (2.1)	25.7 (2.3)			
	site	1.30	0.286					25.5 (2.0)	25.7 (2.3)	26.2 (2.3)
	OTC*msr	**4.51**	**0.005**							
	OTC*site*msr	**4.19**	**<0.0001**							
MinT	OTC	1.95	0.172	-1.1 (3.8)	-1.5 (4.0)					
	msr	**1109**	**<0.0001**							
	substrate	0.00	0.951			-1.3 (3.8)	-1.2 (4.1)			
	site	1.71	0.196					-1.0 (4.2)	-1.4 (3.9)	-1.6 (3.5)
	OTC*site*msr	**4.75**	**<0.0001**							
ST12	OTC	**10.1**	**0.003**	**2.3** **(0.7)**	**3.1** **(1.4)**					
	msr	**23.0**	**<0.0001**							
	substrate	0.00	0.973			2.7 (1.3)	2.7 (0.9)			
	site	**3.54**	**0.041**					**2.3** **(0.7)**	**3.1** **(1.4)**	**2.7** **(1.1)**
	OTC*msr	**3.86**	**0.012**							
	OTC*site	**3.78**	**0.033**							
ST20	OTC	**10.5**	**0.004**	**1.4** **(0.6)**	**2.3** **(1.6)**					
	msr	**43.8**	**<0.0001**							

	substrate	1.32	0.261			1.9 (1.4)	1.7 (1.0)			
	site	**6.24**	**0.008**					**1.3** **(0.6)**	**2.4** **(1.5)**	**1.7** **(1.3)**
	OTC*msr	**5.75**	**0.002**							
	OTC*Site*msr	**2.12**	**0.030**							
%VMC12	OTC	**6.30**	**0.017**	**28.4** **(14.5)**	**39.6** **(19.6)**					
	msr	**3.40**	**0.022**							
	substrate	**10.2**	**0.003**			**37.7** **(21.3)**	**28.4** **(9.1)**			
	site	**9.03**	**0.001**					**29.7** **(15.11)**	**43.0** **(17.9)**	**24.6** **(16.1)**
%VMC20	OTC	**4.57**	**0.040**	**34.4** **(15.5)**	**44.5** **(21.5)**					
	msr	**31.2**	**<0.0001**							
	substrate	**13.2**	**0.001**			**44.1** **(22.3)**	**32.5** **(10.5)**			
	site	**8.21**	**0.001**					**36.6** **(18.5)**	**47.5** **(18.7)**	**29** **(16.1)**
%RH	OTC	**3.95**	**0.055**	**36.6** **(8.2)**	**39.7** **(8.3)**					
	msr	**7.91**	**<.0001**							
	substrate	**7.14**	**0.011**			**38.9** **(8.2)**	**36.9** **(8.5)**			
	site	**7.11**	**0.003**					**39.7** **(8.9)**	**38.7** **(8.2)**	**33.7** **(5.6)**

d)

Summer 2007

				Warming treatment: Mean (SD)		Substrate type: Mean (SD)		Disturbance site: Mean (SD)		
Factor	Responding variable	F value	*P*>F	OTC	C	S	NS	F	LR	LI
MaxT	OTC	**15.5**	**0.001**	**29.5 (5.9)**	**27.1 (5.8)**					
	msr	**115.6**	**<0.0001**							
	substrate	0.24	0.627			28.2 (6.0)	28.5 (6.0)			
	site	1.02	0.375					27.8 (5.8)	28.7 (6.1)	28.6 (6.5)
	OTC*site*msr	**2.21**	**0.021**							
MinT	OTC	**12.2**	**0.001**	**5.1 (2.0)**	**3.6 (2.2)**					
	msr	**115.8**	**<0.0001**							
	substrate	0.94	0.339			4.5 (2.1)	4.1 (2.4)			
	site	**4.90**	**0.013**					**4.3 (2.1)**	**3.8 (2.4)**	**5.5 (1.8)**
	OTC*msr	**4.25**	**0.023**							
	OTC*site*msr	**4.12**	**0.001**							
ST12	OTC	10.5	**0.003**	**10.0 (1.9)**	**11.5 (1.2)**					
	msr	**32.2**	**<0.0001**							
	substrate	2.69	0.111			10.9 (1.7)	10.6 (1.9)			
	site	**15.8**	**<0.0001**					**9.5 (1.9)**	**11.8 (8.5)**	**11.0 (0.9)**
	OTC*msr*site	**2.57**	**0.012**							
ST20	OTC	**8.31**	**0.007**	**9.5 (2.1)**	**11.0 (1.4)**					
	msr	2.65	0.083							
	substrate	3.27	0.078			10.4 (1.8)	10.0 (2.1)			

	site	**16.2**	**<0.0001**					8.9 (2.1)	11.5 (1.2)	10.4 (0.9)
	OTC*site*msr	**1.96**	**0.049**							
%VMC12	OTC	0.87	0.358	44.1 (16.7)	46.1 (20.6)					
	msr	**58.9**	**<0.0001**							
	substrate	**16.7**	**0.001**			**50.3 (19.9)**	**37.4 (13.7)**			
	site	2.72	0.080					41.6 (14.0)	51.0 (21.3)	40.5 (19.0)
%VMC20	OTC	0.39	0.538	50.3 (17.2)	53.6 (19.2)					
	msr	**32.5**	**<0.0001**							
	substrate	**15.0**	**0.001**			**57.6 (19.4)**	**43.6 (12.2)**			
	site	**5.78**	**0.007**					**49.1 (13.9)**	**58.3 (20.8)**	**45.2 (17.0)**
	substrate*msr	**3.61**	**0.033**							
	OTC*site*msr	1.67	0.090							
%RH	OTC	3.57	0.067	63.0 (8.5)	65.1 (7.8)					
	msr	**20.5**	**<0.0001**							
	substrate	0.30	0.587			64.5 (7.9)	63.4 (8.6)			
	site	0.46	0.632					64.3 (7.9)	63.2 (8.8)	65.2 (7.7)
	OTC*msr*site	**4.50**	**<0.0001**							

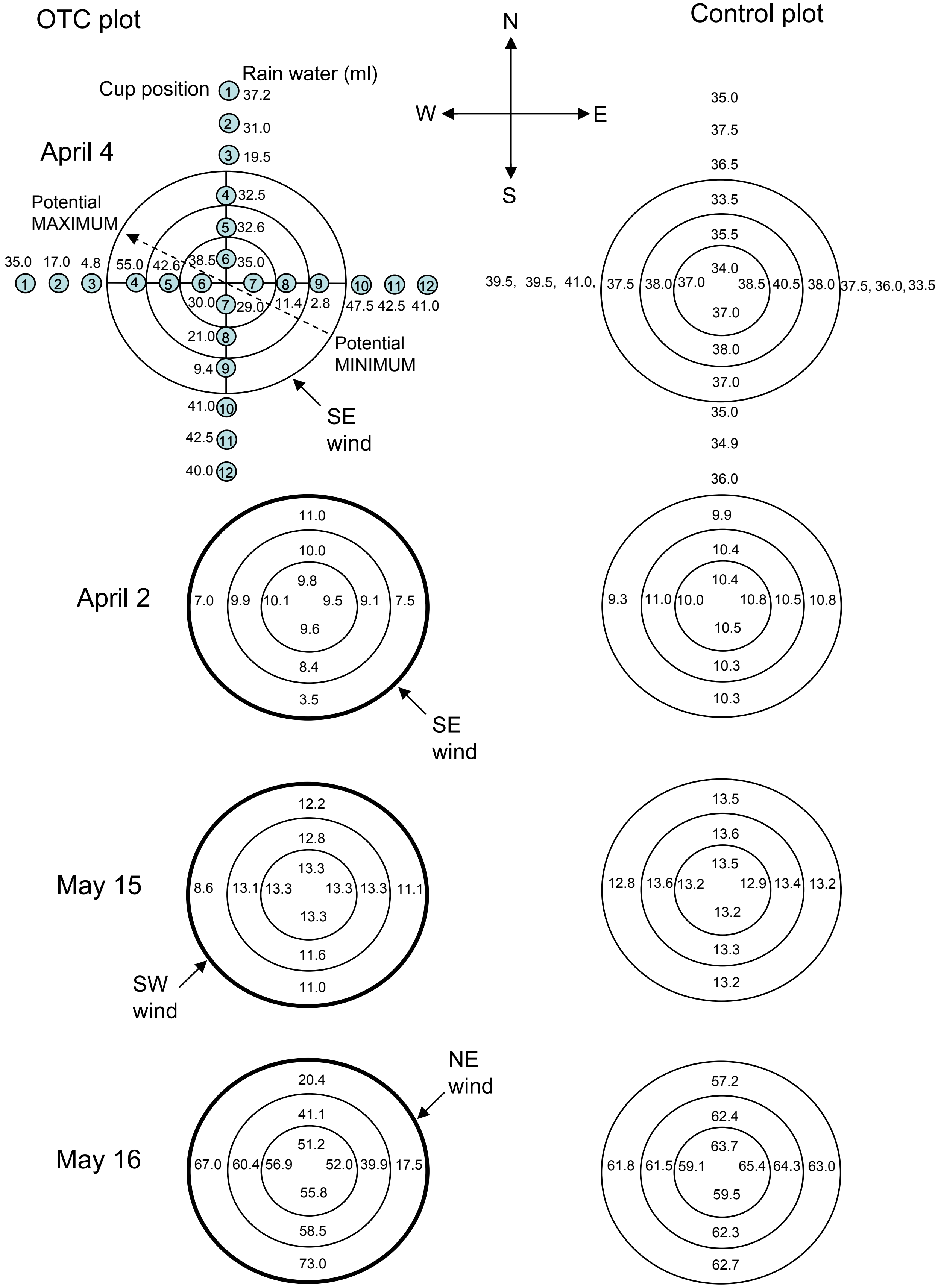
*Significant results are in bold.

Table 2.2 Comparison of means, standard deviations (SD), and ranges [minimum (Min) to maximum (Max)] for continuous measurements of temperature (T; °C), relative humidity (%RH) and ground temperature (GT; °C) taken in March 2007 at Macdonald campus, and in August-September 2007 in northern James Bay, inside open-top chambers (OTC) and control plots (C). Ground temperature was not measured in James Bay.

		March 7-21, 2007						**August 26-September 4, 2007**					
		OTC			**C**			**OTC**			**C**		
		Mean	SD	Min Max	Mean	SD	Min Max	Mean	SD	Min Max	Mean	SD	Min Max
T **(°C)**	Day	**-2.3***	7.4	-22.5 **10.3**	-4.0	7.5	-22.5 8.3	**13.1**	4.3	4.5 **25.4**	12.1	4.0	**4.6** 22.7
	Night	-5.2	8.0	-22.9 8.0	**-4.7**	7.9	**-22.6** **8.1**	**8.1**	3.2	2.4 16.1	8.0	3.2	2.4 16.1
	Daily	**-3.8**	7.8	-22.9 10.3	-4.4	7.7	**-22.6** **8.3**	**11.0**	4.6	2.4 **25.4**	10.3	4.1	2.4 22.7
RH **(%)**	Day	60.0	18.8	25.5 97.9	**61.4**	16.6	**32.6** **99.2**	**80.6**	16.8	**41.9** **98.7**	79.4	16.1	41.5 98.6
	Night	**72.5**	16.3	**37.5** 98.8	68.3	17.9	34.0 **99.9**	**94.3**	5.2	**77.3** **98.3**	93.2	6.2	74.7 98.1
	Daily	66.4	18.6	25.5 98.8	**65.0**	17.6	**32.6** **99.9**	**86.4**	14.8	**41.9** **98.7**	85.3	14.5	41.5 98.6
GT **(°C)**	Day	**-5.3**	6.3	**-24.6** **3.9**	-7.3	7.0	-28.6 0.6	-	-	-	-	-	-
	Night	**-7.3**	7.3	**-24.4** **3.7**	-8.9	8.4	-29.0 1.2	-	-	-	-	-	-
	Daily	**-6.4**	6.9	**-24.6** **3.9**	-8.1	7.8	-29.0 1.2	-	-	-	-	-	-

*In comparing OTC to C, the higher value is presented in bold

Figures


OTC plot
Control plot
N
W
E
S
Cup position
Rain water (ml)
1 37.2
2 31.0
3 19.5
4 32.5
5 32.6
6 35.0
7 29.0
8 21.0
9 9.4
10 41.0
11 42.5
12 40.0
April 4
Potential MAXIMUM
Potential MINIMUM
35.0 17.0 4.8 55.0 42.6 38.5
1 2 3 4 5 6 7 8 9 10 11 12
30.0 11.4 2.8 47.5 42.5 41.0
SE wind
35.0
37.5
36.5
33.5
35.5
34.0
39.5, 39.5, 41.0, 37.5 38.0 37.0 38.5 40.5 38.0 37.5, 36.0, 33.5
37.0
38.0
37.0
35.0
34.9
36.0
April 2
11.0
10.0
9.8
7.0 9.9 10.1 9.5 9.1 7.5
9.6
8.4
3.5
SE wind
9.9
10.4
10.4
9.3 11.0 10.0 10.8 10.5 10.8
10.5
10.3
10.3
May 15
12.2
12.8
13.3
8.6 13.1 13.3 13.3 13.3 11.1
13.3
11.6
11.0
SW wind
13.5
13.6
13.5
12.8 13.6 13.2 12.9 13.4 13.2
13.2
13.3
13.2
May 16
NE wind
20.4
41.1
51.2
67.0 60.4 56.9 52.0 39.9 17.5
55.8
58.5
73.0
57.2
62.4
63.7
61.8 61.5 59.1 65.4 64.3 63.0
59.5
62.3
62.7

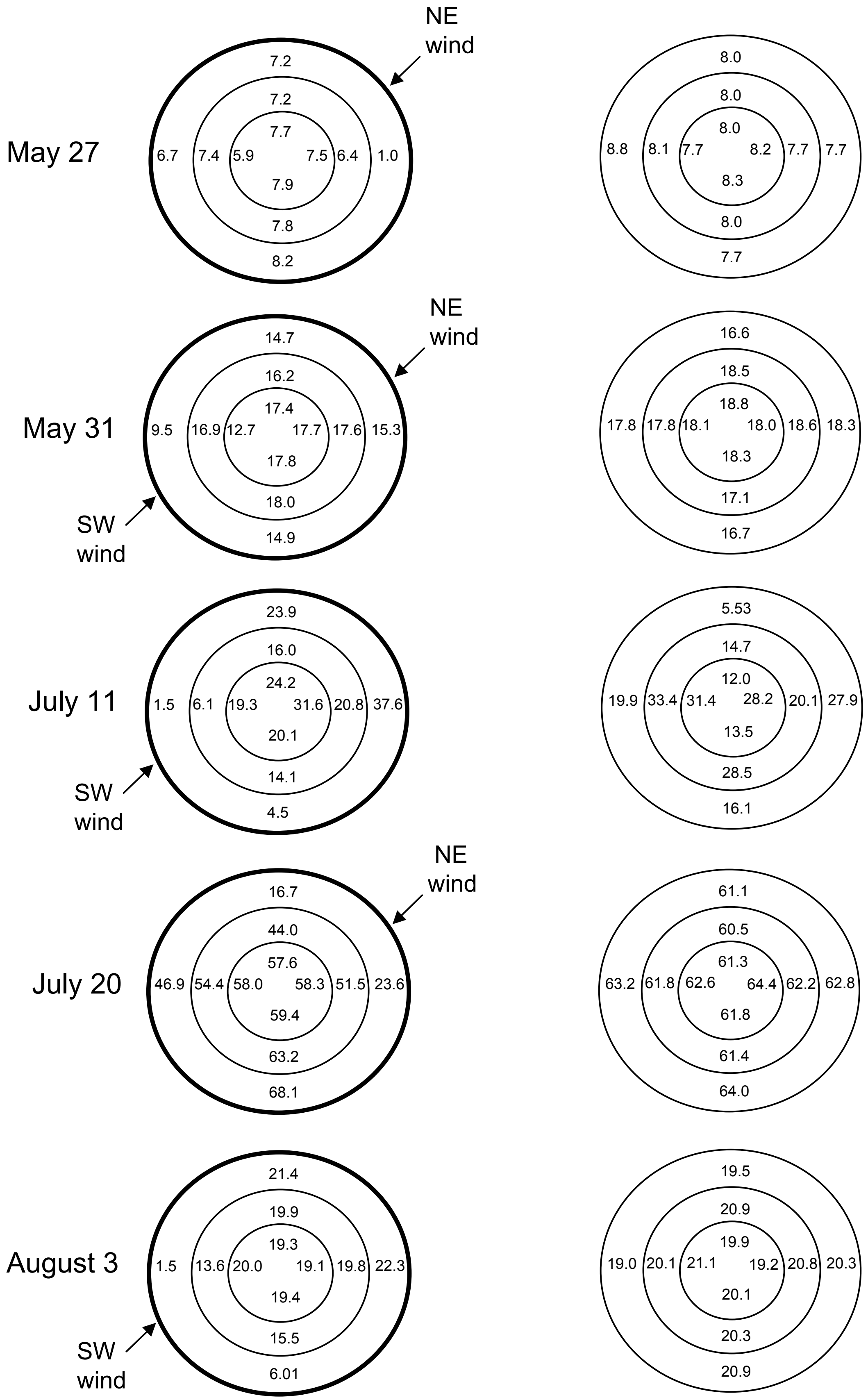
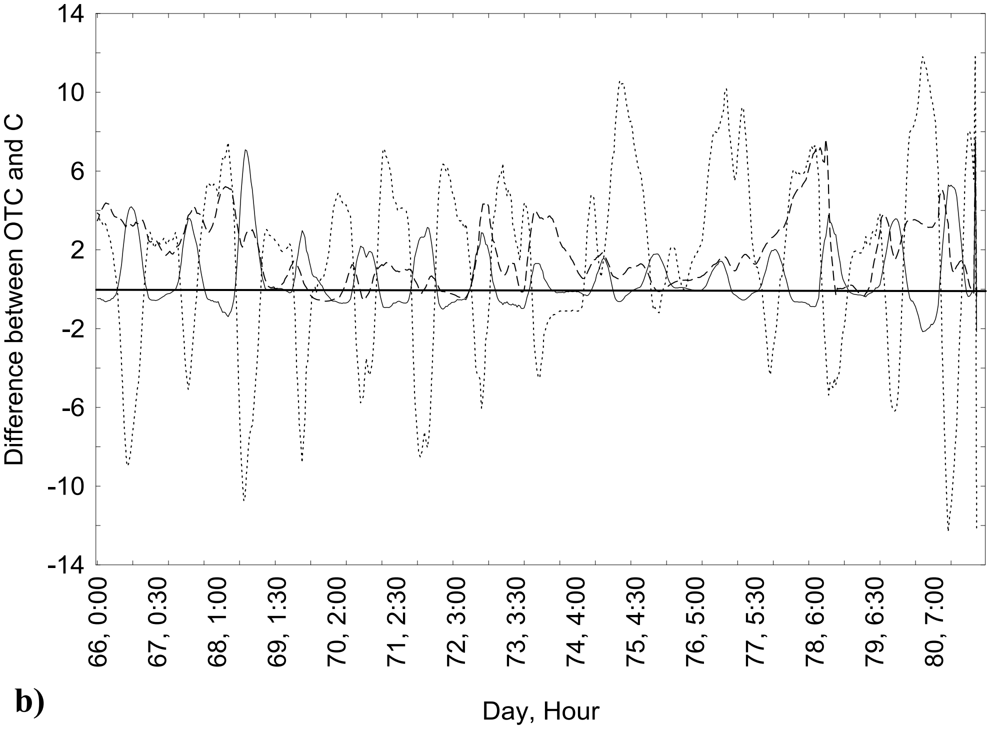

May 27
NE wind
7.2
7.2
7.7
6.7
7.4
5.9
7.5
6.4
1.0
7.9
7.8
8.2
8.0
8.0
8.0
8.8
8.1
7.7
8.2
7.7
7.7
8.3
8.0
7.7
May 31
NE wind
SW wind
14.7
16.2
17.4
9.5
16.9
12.7
17.7
17.6
15.3
17.8
18.0
14.9
16.6
18.5
18.8
17.8
17.8
18.1
18.0
18.6
18.3
18.3
17.1
16.7
July 11
SW wind
23.9
16.0
24.2
1.5
6.1
19.3
31.6
20.8
37.6
20.1
14.1
4.5
5.53
14.7
12.0
19.9
33.4
31.4
28.2
20.1
27.9
13.5
28.5
16.1
July 20
NE wind
16.7
44.0
57.6
46.9
54.4
58.0
58.3
51.5
23.6
59.4
63.2
68.1
61.1
60.5
61.3
63.2
61.8
62.6
64.4
62.2
62.8
61.8
61.4
64.0
August 3
SW wind
21.4
19.9
19.3
1.5
13.6
20.0
19.1
19.8
22.3
19.4
15.5
6.01
19.5
20.9
19.9
19.0
20.1
21.1
19.2
20.8
20.3
20.1
20.3
20.9

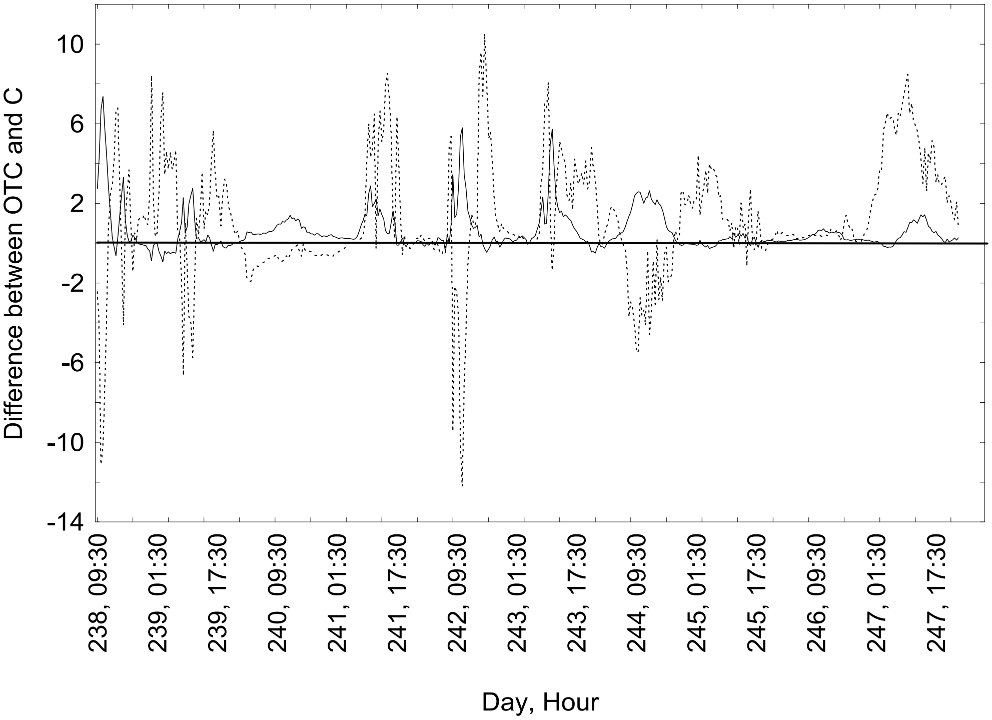
Figure 2. 1 Diagrams representing amounts and distributions of rainfall, as collected inside 150 ml cups arranged along two lines running in north-south (NS) and west-east direction (WE) inside open-top chambers (OTC) and control plots during nine rain events between April and August 2007. Data collected on April 4 illustrates further that the end of each line was extended by three additional cups outside of the plot to also compare the amounts of water that reached the ground around the chamber. Potential maximum and minimum and prevailing wind directions can be deduced from the patterns of rain amount collected on each day. Inner, middle and outer parts are indicated for each plot.

a)



Difference between OTC and C
14
10
6
2
-2
-6
-10
-14
66, 0:00
67, 0:30
68, 1:00
69, 1:30
70, 2:00
71, 2:30
72, 3:00
73, 3:30
74, 4:00
75, 4:30
76, 5:00
77, 5:30
78, 6:00
79, 6:30
80, 7:00
Day, Hour

b)



Difference between OTC and C
10
6
2
-2
-6
-10
-14
238, 09:30
239, 01:30
239, 17:30
240, 09:30
241, 01:30
241, 17:30
242, 09:30
243, 01:30
243, 17:30
244, 09:30
245, 01:30
245, 17:30
246, 09:30
247, 01:30
247, 17:30
Day, Hour

Figure 2. 2 Half-hour intervals of continuous measurements of ambient temperature (°C; continuous line), ground surface temperature (°C; interrupted line) and % relative humidity (dotted line) showing the difference between the open-top chambers and control plots for a) March 2007 (between day 66 and 80) at Macdonald campus in Ste. Anne-de-Bellevue, and b) August-September 2007 (between day 238-247) in northern James Bay region. Ground temperate was not measured in northern James Bay region. The scale for day and hour is shown at every 23:20 interval for Macdonald campus site, and every 24-hour interval for northern James Bay site.

Figure 2. 3 Open-top chamber and a control plot at Macdonald campus, Ste Anne-de-Bellevue, on March 13, 2007, showing accelerated snowmelt in the chamber.

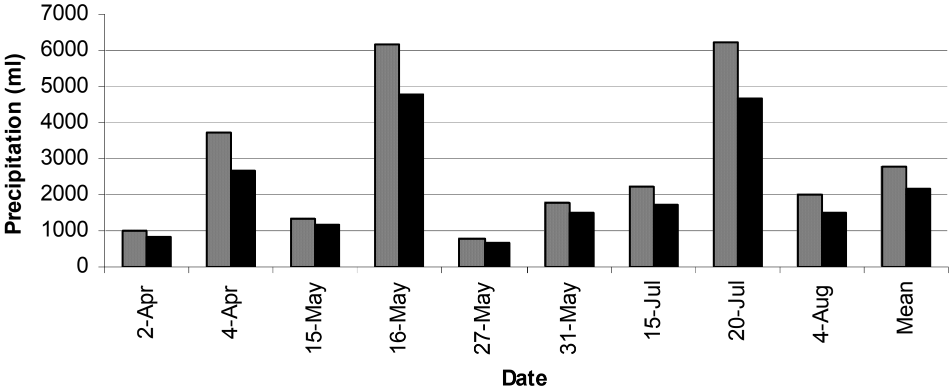


Figure 2. 4 Estimated amounts of rainfall (ml) for the total area inside control plots (grey bars) and open-top chambers (black bars) for nine rain events between April and August 2007.

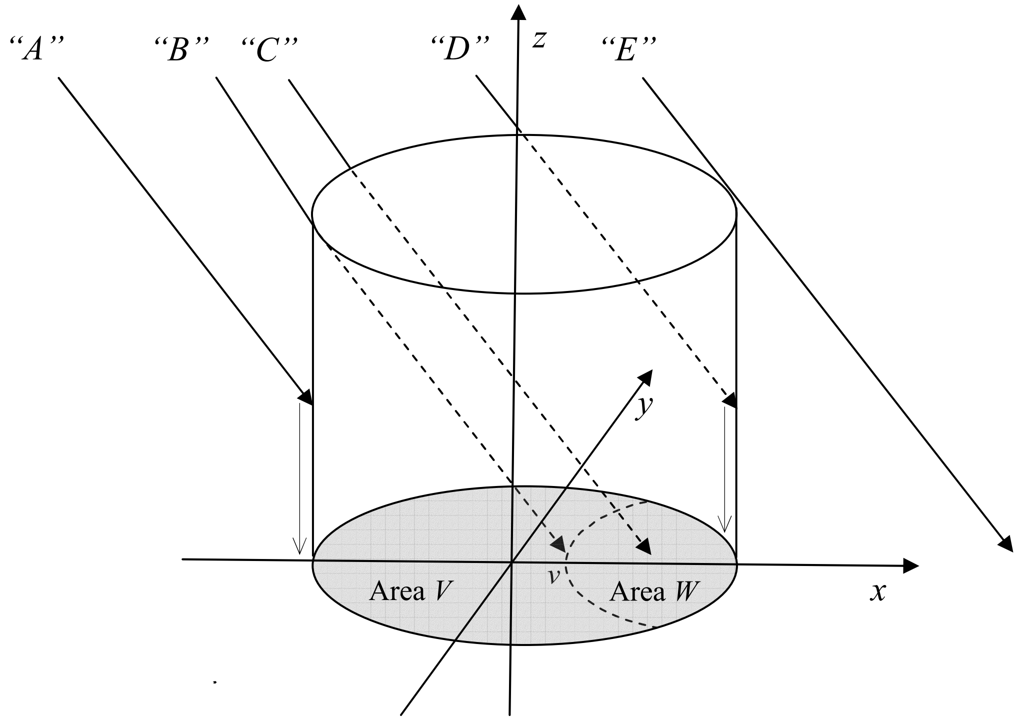


Figure 2. 5 Hypothetical scenario illustrating the effects of a chamber on rainfall patterns, with wind coming along the *x* axis, and raindrops falling with gravity component along *y* axis. Boundary *v* within the chamber separates area *V*, which receives no direct rainfall, from area *W*, which receives a fraction of the rainfall, with the remaining fraction striking the wind-facing inside chamber wall. Assuming the same raindrop sizes, raindrop *"A"* strikes the windward wall of the chamber, raindrop *"B"* enters the chamber and lands at the boundary *v*, raindrop *"C"* enter the chamber and lands within area *W*, raindrop *"D"* encounters the inside chamber wall, and raindrop *"E"* lands on the leeward side of the chamber, without entering it. Dashed line indicates presence of the raindrop inside the chamber, and a whole line indicates presence of a raindrop outside of the chamber.

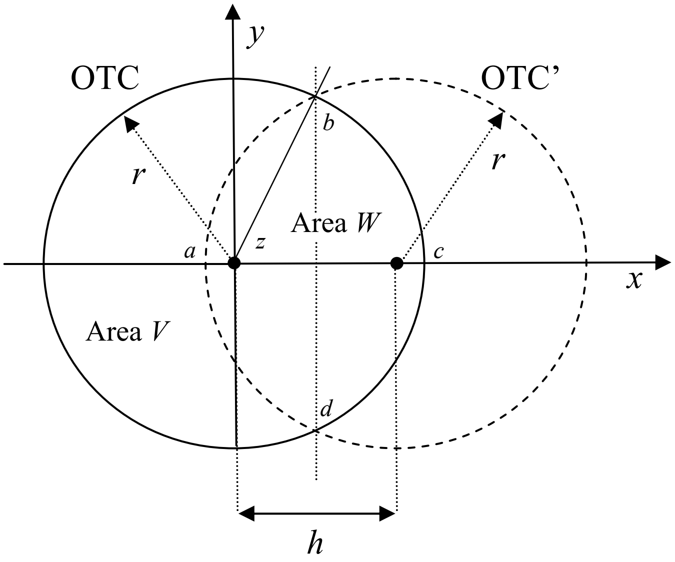


Figure 2. 6 Diagram representing (from top) the area of the chamber (OTC), and hypothetical shift of rainfall (OTC') caused by a wind blowing along *x* axis. All the rainfall will fall beyond the boundary marked by the dashed arc '*dab'*, landing either directly within area *W*, or striking the wall of the chamber along the full-line arc marked '*bcd'*. Area *V* will receive no direct rainfall. Knowing the radius (*r*) of the chamber, the distance (*h*) between the centers of OTC and OTC', and angle *z*, we can calculate area *W*. Multiplying *W* by the total amount of rainfall on a given day, we can find the fraction of total rainfall which reached area *W* inside the chamber; subtracting that amount from the total rainfall will allow for determination of the rain amount which encountered the inside part of wall of the chamber marked '*bcd'*.

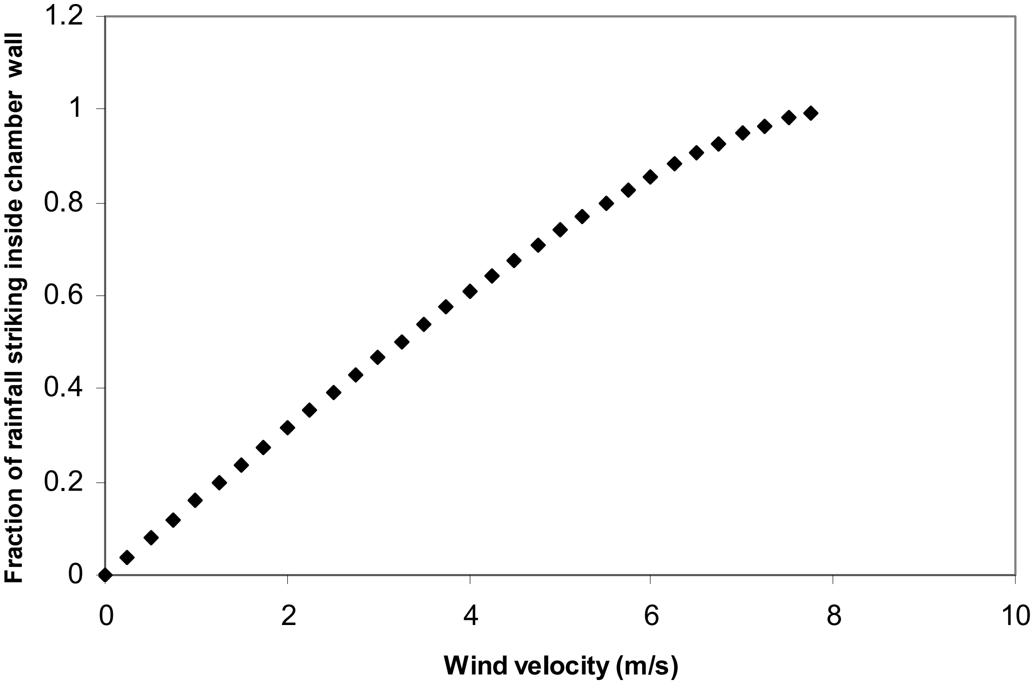


Figure 2. 7 Estimated fraction of incoming rainfall, which would strike the inside wall upon entering the chamber for raindrops of size 1.8 mm.

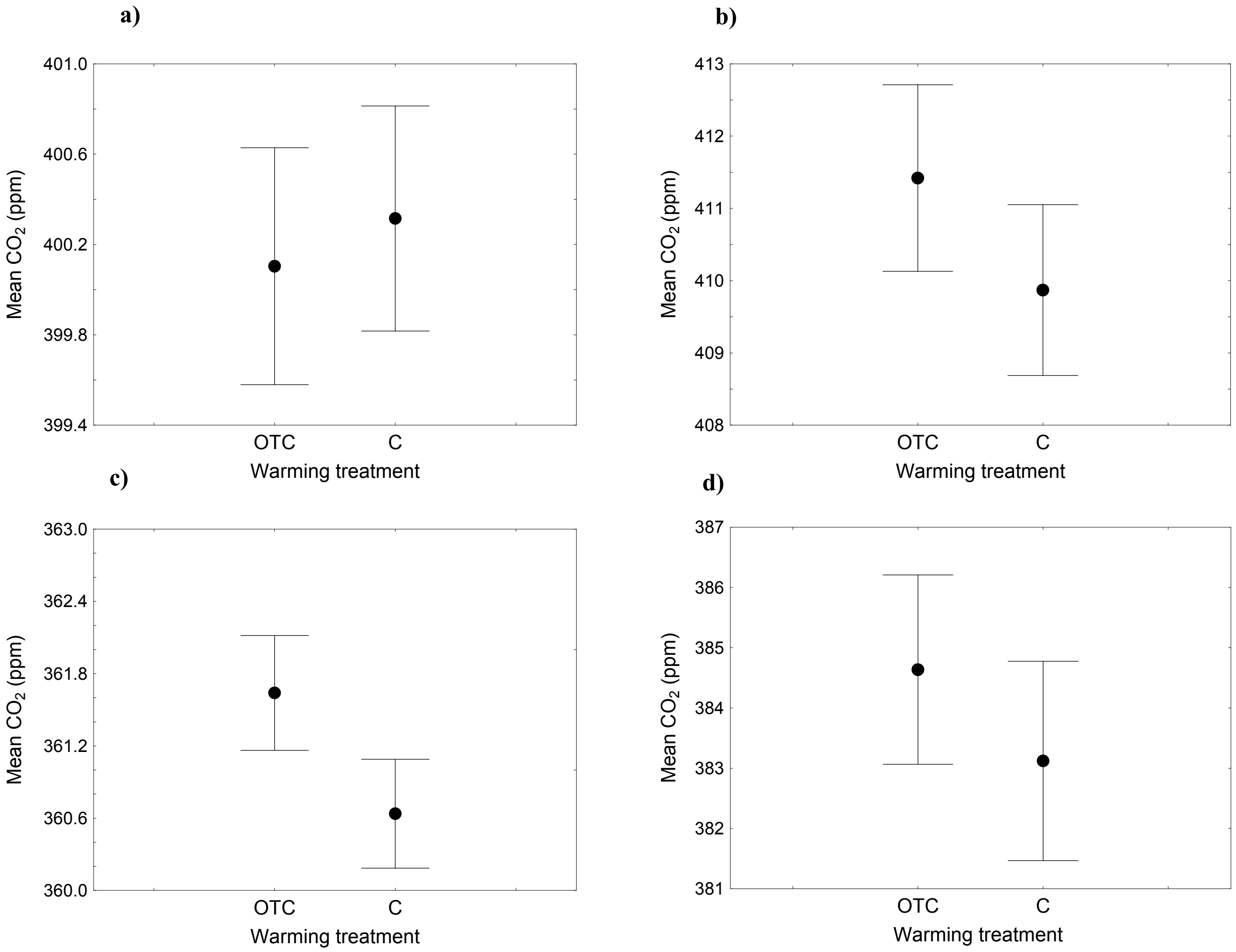


Figure 2. 8 Comparison of means and error bars of continuous CO_2 measurements (ppm) taken inside open-top chambers (OTC) and control plots (C) on March 22-26, 2007 (days 81-85) at Macdonald campus for a) daytime and b) nighttime, and on August 26-September 5, 2007 (days 238-247) for c) daytime and d) nighttime in northern James Bay region.

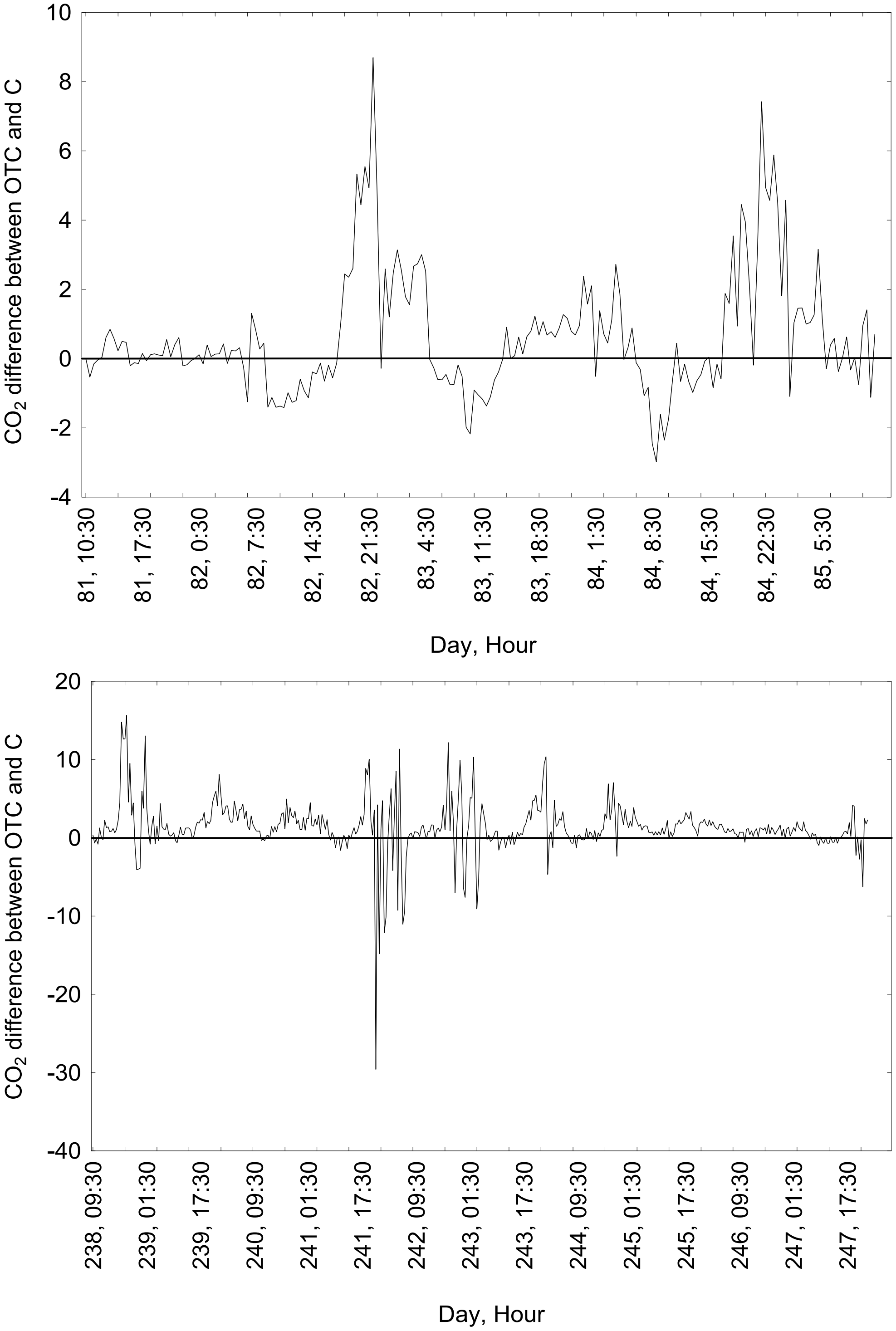
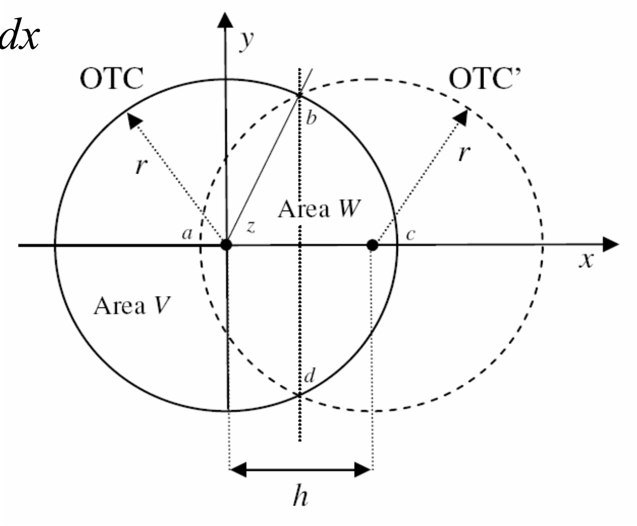


Figure 2. 9 Comparison of patterns for half-hour intervals of CO$_2$ measurements (ppm) showing the differences between the open-top chambers and control plots on March 22-26, 2007 (days 81-85) at a) Macdonald campus, and b) August 26- September 5, 2007 (days 238-247) in northern James Bay region. The scale for day and hour is shown at every 7-hour interval for Macdonald campus site, and every 17-hour interval for northern James Bay site.

Appendix

$$W = 4\int_{\frac{h}{2}}^{r} y(x)\,dx = 4\int_{\frac{h}{2}}^{r} \sqrt{\left(r^2 - x^2\right)}dx$$



$$x = r\cos\theta$$
$$dx = r\sin\theta d\theta$$

$$W = -2r^2\int_{\cos^{-1}\left(\frac{h}{2r}\right)}^{0} \sin\theta\sqrt{\left(1-\cos^2\theta\right)}d\theta$$

$$= -4r^2\int_{\cos^{-1}\left(\frac{h}{2r}\right)}^{0} \sin^2\theta d\theta$$

$$= -2r^2\left[\theta - \frac{1}{2}\sin 2\theta\right]\Bigg|_{\cos^{-1}\left(\frac{h}{2r}\right)}^{0}$$

$$= 2r^2\left\{\cos^{-1}\left(\frac{h}{2r}\right) - \frac{1}{2}\sin\left[2\cos^{-1}\left(\frac{h}{2r}\right)\right]\right\}$$

The final formula for calculating area *W* would be:

$$W = 2r^2\left\{\cos^{-1}\left(\frac{h}{2r}\right) - \frac{1}{2}\sin\left[2\cos^{-1}\left(\frac{h}{2r}\right)\right]\right\}$$

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Connection of Chapter 2 with Chapter 3 and the thesis in general

In **Chapter 2** we tested the effects of OTCs on air temperature and relative humidity, air CO_2 concentrations, soil temperature and soil moisture. Our main findings were that while open-top chambers had little effect on CO_2 concentrations and relative humidity, the air temperature was higher and soil temperature and moisture were lower in the OTCs than in the control plots. We found evidence that these results may in part be due to earlier snowmelt inside the OTCs, and OTCs effects on the distribution of rainfall reaching the ground inside the chambers. We plan to use these results in **Chapter 3**, where we will test the effects of OTCs on biogeochemical processes including soil pH, nutrient supply rates and decomposition rates. Prior understating of the OTC effects on soil temperature and moisture is essential, since biogeochemical processes are strongly related to soil temperature and moisture conditions. In the context of the thesis, understanding the effectiveness and functioning of OTCs as climate change simulators is a prerequisite and crucial basis of our project, since we planned to use OTCs to predict the impact of climate change on growth and performance of aspen and black spruce seedlings regenerating in the mixedwood-boreal zone of northwestern Quebec.

CHAPTER 3: Effects of open-top chambers and substrate type on biogeochemical processes including soil pH, nutrient supply rates and decomposition

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Abstract

Nutrient availability is one of the main factors affecting forest regeneration after disturbance. A changing climate has the potential to impact microbial processes and as such, decomposition rates that affect nutrient availability. Climate change simulation treatment using circular acrylic open-top chambers (OTCs, 1 m in diameter and 0.75 m in height) was applied to explore the potential impact of climatic changes on soil acidity nutrient supply rates and decomposition process, after fire and logging disturbances in the transitional mixedwood-boreal zone in northwestern Quebec. Soil nutrient supply rates and decomposition rates of three litter types (aspen, black spruce, and *Sphagnum*) were measured in response to OTC treatment in the presence or absence of *Sphagnum* moss substrate, under three disturbance types (a fire site, a logging road site, and a logging interval site). Soil pH was significantly lower in the OTCs than in the control plots at the end of the season in 2006 and 2007. The supply rates of Ca and Mg were significantly lower inside the OTCs. There were also significant main effects of substrate type, with Ca and Mg supply rates lower at the *Sphagnum* substrate than non-*Sphagnum* substrate. Furthermore, a significant interaction between the OTC treatment and the disturbance type indicated that the supply rates of N were significantly higher in the control plots at the logging interval site than at any other combination of the OTC treatment and disturbance type. The OTC treatment resulted in lower decomposition rates of the aspen litter after 14 months of incubation. The results suggest that the impact of climatic changes on the soil system is likely to induce a complex web of interacting effects on nutrient supply rates and decomposition processes, potentially affecting regeneration and growth of trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* (Miller) BSP), which are among the most common tree species of our study region. This may lead to possible shifts in plant species composition, and change the relative abundances of deciduous and coniferous trees in the transitional mixedwood-boreal zones of Quebec.

Introduction

One of the major factors limiting forest regeneration after disturbance is soil nutrient availability, determined by atmospheric deposition, microbial processes and decomposition rates (Aber et al. 1991; Saxe et al. 2001). Decomposition is known to be influenced by environmental conditions, with climate, the physical and chemical quality of decomposing litter, and soil organisms as major factors (Swift et al. 1979; Aerts 1997). Global temperatures have increased by $0.74^{o}C \pm 0.18$ over the past ~ 100 years (IPCC 2007), and it has been suggested that in a positive feedback loop, warmer soils may accelerate decomposition processes and the release of CO_2 into the atmosphere, which may, in turn, lead to further temperature increases (Kirschbaum 2000; ACIA 2004; IPCC 2007).

This global warming, especially pronounced at high latitudes, may induce potential shifts of plant community composition and structure (Aerts 2006). Inherent differences with respect to species adaptations to environmental conditions may be beneficial to some species but detrimental to others. Our project investigated the complex network of issues associated with the potential role of climate change on regeneration, growth and performance of young trembling aspen (*Populus tremuloides* Michx.*)* and black spruce (*Picea mariana* Miller (BSP) at disturbance sites along the transitional mixedwood-boreal forest zone in the Abitibi-James Bay region of northwestern Quebec. Should aspen be more benefited by current climatic changes than black spruce, mixedwoods could potentially advance northward, into the boreal forest zones, dominated currently by black spruce. In this study we focused on the effects of potential climatic changes on biogeochemical factors and processes (soil pH, nutrient supply rates and decomposition) within the mixedwood-boreal zone of NW Quebec, and on implications this could have for the community composition of the region.

In general, compared to deciduous broadleaf trees, coniferous trees grow more slowly, and produce more recalcitrant litter (Ågren et al. 1991). In our study, the potential shift from previously coniferous-dominated to mixedwood communities may result in overall changes to the quality of the litter produced, such as a decrease in C:N ratios. This could accelerate decomposition rates at the community level. Indeed, Aerts (2006) claims that changes in litter quality associated with the changes in species community composition may be of greater importance than direct temperature-induced changes in foliar and litter qualities of the native species present within a community.

Ultimately, climate change related alterations in litter quality and thus decomposition rates within a community may be threefold: 1) direct soil temperature and moisture-related effect on chemical litter structure of the native species; 2) relative change in overall litter chemistry at the community level associated with shifting abundances and dominance of native species; 3) and litter changes associated with the advancement of alien species. All may affect the rates of decomposition, and thus, nutrient cycling and nutrient availability within a community. Using a litter bag decomposition method (Trofymow et al. 1998), we explored the first of these three factors, by testing the effects of passive warming treatment using open-top chambers (OTCs), on trembling aspen and black spruce litter. We appreciated nonetheless that the potential effects of climatic change on litter chemistry and decomposition rates may result from all three above-mentioned factors.

Black spruce is identified as one of the dominant tree species of the poorly drained, cool northern peatland habitats with thick *Sphagnum* mats (Van Cleve et al. 1983). Given the abundance of peat moss in the habitats we studied, and its inhibitory effects on decomposition (Turetsky 2003), we also tested the effects of OTC treatment on *Sphagnum* moss decomposition. The effect of potential climatic change on growth and decomposition of the peat moss could have compelling consequences on growth and performance of coexisting vascular vegetation, including trembling aspen and black spruce (Dorrepaal et al. 2006). For example, drying effects of peat due to increased ambient temperatures could potentially accelerate decomposition of water-logged peat mats, leading to accelerated rates of nutrient release, which could be beneficial to coexisting vascular plants.

Intrinsic properties of different litter types are expected to affect decomposition processes, but inherent properties of the habitat including nutrient availability and soil acidity, will also influence decomposition. In an attempt to separate the effects of litter quality from microenvironmental properties on decomposition rates Belyea (1996) concluded that due to their dynamic and complex interactions, the combined effects of both factors must be considered in a proper assessment of decomposition processes. The interaction of site properties, including moisture conditions, microtopography (e.g. Belyea 1996), acidity (e.g. Hobbie and Gough 2004) and nutrient availability (e.g. McClaugherty et al. 1985) are all expected to have a direct or indirect effect on decomposition.

At a larger scale, our experiment encompassed different disturbance types, and included a post-fire site, a post-logging road site and a post-logging interval site. Inherent characteristics of the sites connected to the disturbance history may affect decomposition processes, though in our case they would be context-specific as we did not explore replicates of different disturbance types. At a smaller scale, experimental climate simulation using OTCs was crossed with the effects of substrate type: *Sphagnum*-dominated and non-*Sphagnum*-dominated plots (usually sparse *Polytrichum* moss covered with mixture of humus and mineral soil). The presence of *Sphagnum* was expected to decelerate decomposition rates due decomposition-inhibitory effects of the thick, cool, water-logged conditions associated with peat mats (Belyea 1996; Hobbie 1996; Moore et al. 2007).

Climatic change was simulated using open-top chambers following the modified International Tundra Experiment (ITEX) design of Marion and Pidgeon (1992). In a previous study we determined that the conditions in our OTCs were marked by consistently higher air temperatures (2-3°C), lower relative humidity (up to 3%), drier soil (up to 10% volumetric moisture content) and cooler soil (up to 2.6°C) in comparison to control plots (Chapter 2). In this study our main interest was in determining which microclimatic or chemical soil properties most strongly affect the decomposition process under OTC treatment. Thus, we tested the effects of OTCs and substrate types on soil acidity and nutrient supply rates, and the relation of soil acidity, nutrient supply rates, soil moisture, and soil temperature to the decomposition process. We also explored whether the soil variables which were significantly affected by the chambers (e.g. soil temperature and moisture) contributed with different magnitudes to the decomposition process in the chambers versus control plots. Possible differences in trends and factors affecting decomposition between chambers and control plots could allow us to better project potential effects of climate change on decomposition. Shifts in any one of these factors could cause a chain of reactions that would create more or less environmentally favourable conditions for regeneration of different plant species, and could thus affect community composition and structure.

Our specific predictions were that the drier, cooler soil in the open-top chambers would inhibit microbial activity and thus decomposition rates. Initial rates of broadleaf litter decomposition would likely be faster than those of *Sphagnum* and coniferous litter, with the inhibitory properties of *Sphagnum* substrate decelerating decomposition rates of all three litter types. Soil temperature and moisture would be the limiting factors in decomposition processes in the open-top chambers and the control plots, but their relative importance would probably be different in and out of chambers. The differences in the major factors affecting decomposition between OTCs and control plots could also be reflected by differences in final chemical composition of the litter types, with more recalcitrant qualities (e.g. higher C:N ratio) found in the litter decomposing in chambers versus control plots.

Materials and methods

Study sites

The study area (49° 37’ N; 79° 00’ W) was found in the boreal mixedwood-black spruce transitional forest zone in James Bay, which constitutes part of the Clay Belt physiographic region spanning northwestern Quebec and northeastern Ontario. A detailed description of the region, including geological background, climate, and present vegetation is provided in the general introduction and the first two chapters of this thesis.

We identified three study sites spanning 20 km along the Selbaie road (from 49^{o}37’ N; 78^{o}59’ W to 49 ^{o}45’ N; 79^{o}02’ W) which was constructed between 1977 and 1980 to allow access to Selbaie copper mine located at km 92 (S. Galarneau, personal communication, Ministère des Ressources naturelles et de la Faune du Québec, La Sarre, Quebec). We refer to the Selbaie gravel road as a primary forestry road, while the smaller roads laid out perpendicular to it are secondary forestry roads or logging roads. There were three study sites: a salvage logged post-fire site; a logging road, created to facilitate timber harvest; and a post-logging site, where the timber harvest took place. At all the sites the disturbance occurred in years 1996-1997. Detailed descriptions of the sites, including dominant vegetation and soil texture and drainage information, are provided in the general introduction of this thesis.

Experimental design

In total we established 40 experimental plots: 20 open-top chambers and 20 control plots. At the fire site there were eight OTCs and eight control plots; at the logging road site there were also eight OTCs and eight control plots; and, at the logging interval site there were four OTCs and four control plots. At each site, every OTC was paired with a control plot established in a close proximity.

In order to test the responses to the OTC treatment in the presence or absence of the live *Sphagnum* moss, for the eight pairs of OTC and control plots located at the fire site and logging road site the dominant substrate consisted of *Sphagnum* moss, while for the other eight pairs the substrate was dominated by sparse *Polytrichum* moss growing on a mixture of humus and mineral soil. The substrate and the OTC treatments at the fire and logging road sites were crossed factorial: four OTCs and four control plots at *Sphagnum*-dominated substrates, and four OTCs and four control plots at non *Sphagnum*-dominated substrates, for a total of sixteen plots per site. At the logging interval site, four pairs of OTC and control plots were all set up on live *Sphagnum* moss. In summary, there were 40 plots, and each plot was described in terms of the OTC treatment and the dominant substrate. The four possible combinations were: control plot with non-*Sphagnum* substrate (C_NS), control plot with a *Sphagnum* substrate (C_S), open-top chamber plot with non-*Sphagnum* substrate (OTC_NS), and open-top chamber plot with *Sphagnum* substrate (OTC_S).

At each of the three sites, for the plots receiving an open-top chamber treatment, we constructed a circular enclosure, 1 m in diameter and 0.75 m in height, built of clear transparent 8 mm thick polymethylmethaacrylate (PMMA, commonly known as acrylic) material. The construction of the chambers took place between June 28 and July 1, 2005, and the chambers were not removed until mid-August of 2007. Two flexible PMMA sheets were connected with tie-wraps and supported in two places by plastic stakes inserted in the ground. The walls of the chambers were perpendicular to the ground. A nearby control plot of the same size was not shielded with the acrylic chamber but marked with a nylon thread placed on the ground and secured with metal pegs. Detailed descriptions of the OTC properties, as well as its effects on air temperature, relative humidity, CO_2 concentrations, rain interception, and soil temperature and moisture are given in Chapter 2.

Substrate acidity

Samples for pH measurement were collected from each plot eight times between July 2005 and August 2007. Between 2005 and 2007 samples were collected every early July and late August. In 2006 and 2007 samples were also collected in early May. Usually, each sample consisted of a 20 cm deep core, divided into a surface layer (live green moss), middle layer (brownish-yellow partially decomposed moss) and bottom layer (humus or mineral soil). Three cores were collected randomly from each plot and combined to make one composite sample. The three sampling locations inside each plot were marked during the first collection and each subsequent sample was collected from the same spot. All samples were dried at $65^{o}C$ for 24 hours, mixed thoroughly and a 1.5 g dry sub-sample was suspended in 15 ml of distilled water to determine pH.

Preliminary analysis of the effects of the OTC treatment on substrate pH involved performing analyses of variance (ANOVA) using procedure MIXED in SAS (SAS Institute 2007). Separate analyses were performed for each of the eight sample collections. A complete ANOVA model included explanatory variables of the OTC treatment (OTC or control [C] plot), the substrate type (*Sphagnum* [S] or non-*Sphagnum* [NS]) and the site (treated here as a block in space: fire [F], logging road [LR], logging interval [LI]) as the fixed factors, and all of the interactions among explanatory variables (SAS Institute 2007). The effects of the explanatory variables were tested against the experimental error, and all non-significant interactions ($p > 0.05$) were dropped in the final model. In the case of significant effects of the main factors or significant interactions, least-squares (LS) means were used to determine the levels differing, and the direction of the difference.

As there are no replicates of disturbance sites, no valid generalizations can be made with regard to the overall effects of specific disturbance types on pH conditions;

nonetheless, site must be included as a factor in the model to avoid inflation of the experimental error and thus, the possibility of a Type II error. In general, the effects of sites (disturbance types) and the substrate type (*Sphagnum* or non-*Sphagnum*) in this and all subsequent statistical analyses will be described and interpreted only in the context of how they might have affected, and interacted with the OTC treatment. All data analyses were checked for normality and the homogeneity of variance.

Nutrient supply rates

To determine the dynamics of the soil nutrient supply rates, eight Plant Root Simulator (PRS) resin probes were inserted in each plot for 14 days in July 2005, 21 days in May 2006 and May 2007, and 42 days in July and August 2006. PRS resin probes are plastic probes enclosing an ion exchange membrane with an adsorbing surface area of 17.5 cm^2. After chemical pre-treatment, the membrane inserted in the soil will exhibit characteristics of plant roots, adsorbing available nutrients from the soil solution (PRS^{TM}-Probe Operations Manual 2004). The measurements are recorded as exchangeable ion supply rates per amount of ion exchange surface area over the time of the probe burial at a specified temperature and moisture, and are usually given in units of μg ion/10cm^2/time. Four cation and four anion probes within each plot were combined and analyzed as one composite sample. The probes have been analysed by Western Ag Innovations Inc. in Saskatoon, Saskatchewan. The nutrients were measured in bioavailable forms: NO_3^--N + NH_4^+-N, NH_4^+-N, $H_2PO_4^-$-P, K^+, Ca^{2+}, Mg^{2+}. For simplicity, we will refer to them respectively as available N, NH_4, P, K, Ca and Mg. The supply rates of available N and NH_4 were below method detection levels in May 2007, and were excluded from statistical analyses.

Statistical analyses included ANOVA, using procedure MIXED in SAS (SAS Institute 2007), and were performed separately for every nutrient, with OTC, substrate type and site as explanatory variables. Separate analyses were performed on summer data sets including: July 2005 (J_05, initial conditions, no effects of chambers expected), July/August 2006 (J/A_06), and spring data sets including May 2006 (M_06) and May 2007 (M_07). Data for all the responding variables was checked for normality and homogeneity of variance prior to analysis. For nutrient supply rates, normality was violated for the analysis of Ca and Mg in J_05 and M_06-07 data sets, for P in J/A_06, M_07 and M_06-07 data sets, and for K in M_07 and M_06-07 data sets. In all these cases data were square root transformed to obtain normality. Interactions among all the explanatory variables were tested and dropped in the final model if not significant. In the case of significant effects of the main factors or significant interactions, least-squares (LS) means were used to determine the levels differing, and the direction of the difference.

Decomposition rate and change in litter chemistry

To assess effects of the OTC treatment, substrate type and site on decomposition rates and changes in litter quality, three types of litter (deciduous-aspen, coniferous-black spruce, and *Sphagnum* moss) were buried in litter bags in each OTC and control plot. The first two litter types were collected from aspen-dominated and spruce-dominated stands in two locations: near Beaucanton, Quebec (49°04’N, 79°25’W), and approximately 50 km north of Beaucanton along the Selbaie road (49°39’N, 79°01’W). In July 2004, three litter traps were set up at each of these four stands by suspending 1 m^2 pieces of fabric 1 m above the ground. The fabric was fine enough to hold the leaves, including the coniferous needles, but porous enough to allow rainwater to drain. Litter was collected in October 2004, and oven-dried for four days at 65°C to prevent further decomposition. For each litter type, litter collected from both stands was combined. The *Sphagnum* moss litter was collected and dried in late spring 2005 at the same locations as the other two litter types.

Before litter incubation in OTCs and control plots, initial total N, P, K, Ca and Mg for each litter type were measured following the procedure of tissue digestions by wet oxidation in sulphuric acid and hydrogen peroxide, in a block digestor (Parkinson and Allen 1975). Concentrations of total N and P in litter digests were measured colorimetrically using a Lachat QuickChem autoanalyzer (FIA+8000, Lachat Instruments, Milwaukee, Wisconsin) while concentrations of total Ca, K and Mg were determined with an atomic absorption spectrophotometer (2380, Perkin-Elmer, Waltham, Massachusetts). Twenty replicates were sampled and averaged to obtain one initial value for each litter type and each nutrient. Total % C and % N were determined using NC soil analyzer

(Flash EA 1112 Series, Thermo-Finnigan Carlo Erba Instruments, Milan, Italy), and C:N ratios were calculated for pre-experimental samples of all three litter types.

Litter collection resulted in an abundant amount of aspen and *Sphagnum* moss litter, but a rather limited amount of spruce litter, allowing for more litter samples of the former litter types that the latter. Consequently, twice as many litter bags were made for the aspen and *Sphagnum* litter types than for the spruce litter. Mesh nylon/polyester bags (10 x 10 cm, 1 mm^2 mesh size) were filled with 2.5 g of oven-dry litter. Bag construction was based on a modified design of The Canadian Intersite Decomposition Experiments (CIDET) (Trofymow et al. 1998). In each OTC and control plot six replicate bags each, of aspen and *Sphagnum* litter types, and three bags of spruce litter type were buried vertically with the top of the bag right at the level of ground surface. For the aspen and *Sphagnum* litter types, three out of six litter bags were collected after 14 months of incubation, and were re-weighed and re-analyzed for total N, P, K, Ca, Mg and C:N ratio as above. All remaining samples, including the spruce litter, were collected after 24 months of incubation and analyzed the same way.

We estimated the rate of decomposition by calculating the % of dry mass remaining (% DMR) inside the litter bags after 14 month incubation or 24 month incubation. High % DMR would indicate slow decomposition process, while low % DMR would suggest more rapid decomposition. Statistical analysis of % DMR after 14 months of incubation for aspen and *Sphagnum* litter, and after 24 months of incubation for aspen, *Sphagnum* and spruce litter involved performing analyses of variance (ANOVA) using procedure MIXED in SAS (SAS Institute 2007). For each analysis performed for 14 and 24 month incubations, the effects of the OTC treatment (OTC or C), substrate (S or NS) and site (F, LR or LI, treated as block in space), were tested on the responding variable % DMR. The analyses were performed separately for each litter type: aspen, *Sphagnum* and spruce. Same statistical procedures were followed as for the ANOVAs for soil pH and nutrient supply rates described above.

In order to identify a subset of microenvironmental variables (predictors) which could explain the largest proportion of variance in decomposition rates (represented by % DMR), we ran multiple regression analyses using Maximum r^2 Improvement selection option in SAS (SAS Institute 2007). The MAXR option selects predictor variables which maximize the proportion of variance in the responding variable accounted for by the model, by means of iterative replacement of variables to find the one with the highest overall r^2 (SAS Institute 2007). We built a separate model for each litter type and both incubation periods, with the initial set of variables including soil pH, nutrient supply rates (available N, NH_4, P, K, Ca, and Mg), and spring and summer soil moisture and temperatures over the incubation periods. For each model, we determined the top four predictors affecting % DMR. The assumptions of normality and homogeneity of variance were verified.

For the litter bags that were incubating 14 months, we used the average pH from core samples collected (as described earlier) in July 2005, May 2006, July 2006 and August 2006. For the 24 month incubation period we took the average of the above mentioned core samples plus the samples collected in May 2007 and July 2007. Similarly, nutrient supply rates (by PRS probes) were averaged from the nutrient values obtained in July 2005, May 2006, and July 2006 for the 14 month incubation. For the 24 month incubation additional values obtained in May 2007 were included to determine the mean nutrient supply rates for each plot.

Soil temperature and moisture data were collected in July and August 2005 and 2006 (summer data). Measurements were taken three times a week, for eight consecutive weeks. The 24 measurements were averaged to provide a mean soil temperature and moisture value for every plot. The soil temperature was measured at depth 12 cm with soil probe thermometer (Thermor DT 130, Newmarket, Ontario). For each data-gathering event, three temperature measurements, two taken at the opposite sites of the plot, and one taken in the middle were averaged.

The soil moisture in each plot was measured at the same time as the temperature, using a portable time-domain reflectometry (TDR) instrument (Field Scout TDR-100, Spectrum Technologies Inc., Plainfield, Illinois).The moisture was recorded as % volumetric moisture content measured as an average over the length of the 12 cm long stainless steel rods, with each final measurement represented by an average of six measurements taken randomly over the entire area of the plot.

The spring temperature and moisture data were collected in May 2006 and 2007 from four intervals of three consecutive days of measurements. Each of the four 3-day measurement intervals was separated by one day free of measurements. The data for 12 measurements was averaged, resulting in a mean spring soil temperature and moisture value for each plot. In season 2007, we also collected a set of early summer data (end of June and early July) following the exact same procedures as in the spring, except three, not four 3-day measurement intervals were collected.

To obtain a final summer and spring value for soil temperature and moisture, for each season (summer or spring) we averaged the data collected over the years 2005 to 2007. In summary, for each OTC and control plot we had a soil temperature and moisture value for the summer, averaged from the measurements taken in July-August 2005 and 2006 and June-July 2007, and a soil temperature and moisture value for the spring, averaged from the measurement taken in May 2006 and 2007.

Initial statistical analysis of litter chemistry for every litter type and incubation period involved finding means and standard deviation of final nutrient concentrations (total N, P, K, Ca, Mg) for each of the four combinations of the OTC and substrate treatment: C_NS, C_S, OTC_NS, and OTC_S. Comparisons were made between the initial (i.e. pre-burial) and final (i.e. post-burial) nutrient concentrations and C:N ratios. Analyses of variance were performed in order to assess the effects of the OTC treatment, substrate type, and disturbance site on final nutrient concentrations and C:N ratios for each litter type and incubation period. All the analyses were performed in SAS, separately for each nutrient (total N, P, K, Ca, Mg) and C:N ratio, following the same ANOVA procedure as described earlier for soil pH and nutrient supply rates (SAS Institute 2007). Data for each responding variable were checked for normality and homogeneity of variance prior to analysis.

Results

Effects of OTCs, substrate type, and sites on soil pH and soil nutrient supply rates

Overall, soil pH appeared to follow a trend of low spring values (May), peaks in mid-summer and drops by the end of summer (August) (Table 3.1). There was no effect of OTC treatment on pH in the first season (2005), but in 2006 and 2007, the soil conditions in the chambers by the end of the summer (August) were significantly more acidic than control plots ($p = 0.050$ and $p = 0.030$ for August 2006 and 2007 respectively; Table 3.1). The effect of site was significant for every measurement with the exception of May 2006 and August 2006; the logging interval site was usually the most acidic, and the logging road site the least acidic (Table 3.1). There were no significant effects of substrate type on pH.

As expected, there were no significant effects of OTC treatment on nutrient supply rates for any of the tested nutrients (available N, NH_4, P, K, Ca and Mg) at the start of the experiment in July 2005 (J_05) (Table 3.2). By the following spring (May 2006), nutrient supply rates were significantly lower in the OTCs for Ca and Mg ($p = 0.001$ and $p = 0.007$ for Ca and Mg respectively; Table 3.2). The lower Ca levels persisted inside the chambers throughout the study period ($p = 0.033$ and $p = 0.010$ in July 2006 and May 2007; Table 3.2). Magnesium supply rates were also lower in the summer 2006, although not significantly, but they became significantly lower again in May 2007 ($p = 0.012$; Table 3.2). There were no main effects of OTC treatment on supply rates of any other nutrients for any of the four probe burials between July 2005 and May 2007. There was a significant interaction between the OTC treatment and site in May 2006: the supply rates of available N in the control plots at the logging interval site were significantly higher than at all the other combinations of OTC treatment and site. There was also significantly less Mg at the logging interval than at the logging road site in July 2005, throughout spring and summer 2006, and continuing into spring 2007 (Table 3.2). Also, in the spring of 2007, Mg supply rates became significantly lower at the fire site than at the logging road site (Table 3.2).

Calcium supply rates were significantly lower in the *Sphagnum* substrate plots in July 2005 and continued to be lower into the spring of 2006 (Table 3.2). Magnesium supply rates became significantly lower in the *Sphagnum* plots in spring 2006 and continued to be lower over the summer 2006.

Effects of OTCs, substrate type, sites, and soil properties on decomposition rates

Aspen litter experienced the highest degree of decomposition after the 24 month incubation period, followed by spruce litter, and *Sphagnum* litter. There was only ~ 1%

difference in % DMR of *Sphagnum* litter between 14 and 24 month incubation periods. More than 40% of aspen litter decomposition occurred within the first year of incubation, and decomposition continued at a much slower pace in the second year.

After 14 months the OTC treatment had a significant effect on % DMR of aspen litter, but not *Sphagnum* litter. The % DMR of the aspen litter was about 3% higher when buried inside the chambers (DMR = 58.6%) as compared to control plots (DMR = 55.5%) (p = 0.031), indicating less decomposition inside the chambers (Table 3.3). On the other hand, the difference in % DMR between the chambers (DMR = 81.4%) and control plots (DMR = 81.6%) for *Sphagnum* litter was negligent (p = 0.914) (Table 3.3). Although there were no main effects of substrate type or site on % DMR after 14 months for either of the two litter types tested, there were significant interactions between the substrate and site for both aspen (p = 0.035 after 14 month incubation) and *Sphagnum* litter (p = 0.040 and p = 0.010 after 14 and 24 month incubation, respectively). Decomposition of aspen litter was highest in the non-*Sphagnum* plots of the fire site (DMR = 54.6%), and lowest in the *Sphagnum* plots of the logging interval site (DMR = 58.8%). Decomposition of *Sphagnum* litter was highest at the *Sphagnum* plots of the logging road site (DMR = 76.8% after 14 months and 75.7% after 24 months) and lowest at the non-*Sphagnum* of the logging road site (DMR = 83.7% after 14 months) and *Sphagnum* plots of the fire site (DMR = 79.6 after 24 months) (Table 3.3).

Analysis of aspen litter decomposition after the 24 month incubation revealed that although % DMR of aspen litter was still higher inside the chambers (DMR = 48.8%) than the control plots (DMR = 44.9%), the effects of the OTC treatment were no longer significant (p = 0.079) (Table 3.3). There were also no effects of the OTC treatment on decomposition of *Sphagnum* and spruce litters (Table 3.3). In fact, a comparison of *Sphagnum* and spruce litter % DMR between the chamber and control plots showed less than 1% difference (DMR = 80.6% versus 80.3% in OTC and control plots, respectively for *Sphagnum* litter, and DMR = 50.8% and 50.5% for OTC and control plots, respectively for spruce litter).

Multiple regression analyses revealed that in the chambers, soil temperature was among the four factors explaining the most variance in % DMR for aspen litter after both incubation periods, and for *Sphagnum* litter after 14 months only (Table 3.4). For the control plots, soil temperature was among the four most important factors only for *Sphagnum* litter after 14 month incubation and for spruce litter after 24 months (Table 3.4). Soil % volumetric moisture content (% VMC) was among the four most important factors in OTCs and control plots for all litter types and incubation periods, with the exception of aspen and *Sphagnum* litters after 14 month incubation in the control plots (Table 3.4).

Nutrient supply rates in general appeared to play a more important role in the decomposition process in the control plots than OTCs, especially for aspen and *Sphagnum* litter, while soil pH appeared to be essential in decomposition of black spruce litter in both OTCs and control plots (Table 3.4). Calcium and magnesium, the two basic cations with significantly lower supply rates in the OTCs, did not appear to have a major influence on decomposition in the chambers, but were among the four top factors affecting decomposition in control plots.

The r^2 values were similar for aspen litter in the chambers and control plots after both 14 (0.35 and 0.30 for OTC and C respectively) and 24 (0.47 and 0.48 for OTC and C respectively) month incubation periods (Table 3.4). Only the supply rates of P and K were among the four top factors explaining decomposition of aspen litter in both OTCs and control plots after 14 month incubation. After 24 months, only summer soil % VMC and supply rates of NH_4 were the two overlapping factors in both OTCs and control plots (Table 3.4). The direction of the relation with % DMR (i.e. positive or negative) for the overlapping factors in the OTCs and control plots was generally the same, with the exception of supply rates of NH_4; however, the magnitude of the relation differed between the OTCs and control plots (e.g. summer soil % VMC was relatively more important in OTCs than in control plots after 24 month incubation) (Table 3.4).

The r^2 values were also similar for the OTCs and control plots of *Sphagnum* litter following 14 (0.53 and 0.52 for OTC and C respectively) and 24 (0.27 and 0.31 for OTC and C respectively) month incubations (Table 3.4). However, only spring soil temperature was an overlapping factor after 14 months, having opposite relation with % DMR in the OTCs and control plots, and only summer soil % VMC was a common top factor after 24 months, also having opposite relation with % DMR in the OTCs and control plots (Table 3.4).

Although spring and summer soil moisture and soil pH were among the four top factors affecting % DMR of spruce litter type in both OTC and control plots, there was a striking difference in the r^2 between the two models: in the control plots the r^2 value for these factors, along with soil summer temperature was only 0.15, while in the chambers, along with the supply rates of P, the r^2 was 0.79 (Table 3.4). The relations of the overlapping factors with % DMR were opposite in the open-top chambers and control plots (Table 3.4).

Effects of OTCs and substrate type on change in litter chemistry

The concentrations of N increased in aspen and spruce litters from the initial levels, and decreased slightly in *Sphagnum* litter. For both aspen and *Sphagnum* litters, N levels were lowest in the plots with a combination of OTC_S after 14 months, and lowest in the plots of C_NS after 24 months (Table 3.5). Statistical analysis testing the effects of the OTC treatment on final N concentrations revealed that final N levels were marginally significantly lower in the OTCs for the *Sphagnum* litter after the 14 month incubation ($p = 0.058$) (Table 3.6).

Final P concentrations were marginally significantly lower inside the chambers for aspen after the 14 month incubation ($p = 0.052$), and P levels were the lowest in the OTC_S plots (Tables 3.5 and 3.6). After 24 months, P levels fell lower at the control plots for aspen litter, but there were no significant effects of the OTC treatment (Table 3.6). For *Sphagnum* litter, P levels decreased by up to 30% after both incubation times, but there were no significant effects of the OTC treatment (Tables 3.5 and 3.6). For the spruce litter, levels of P did not change much from the initial levels under any combination of the OTC and substrate treatment, and there were no significant effect of OTC treatment and substrate type (Tables 3.5 and 3.6).

Final concentrations of K decreased drastically in comparison to initial levels for all litter types, both incubation periods, and under all combinations of the OTC treatment and substrate type (Table 3.5). Significant effects of the OTC treatment were observed only for the spruce litter ($p = 0.046$), with final concentrations lower in the chambers than in control plots (Table 3.6). Final K concentrations were also significantly lower for all litter types after the 24 month incubation in the *Sphagnum* substrate plots (*p* = 0.007, *p* = 0.005 and *p* = 0.041 for aspen, *Sphagnum* and spruce litters respectively) (Table 3.6).

Final Ca concentrations increased slightly in the aspen litter incubated for 14 months, and decreased after 24 months, but there were no OTC effects (Tables 3.5 and 3.6). For the *Sphagnum* litter, Ca levels increased after both incubation periods, and were significantly lower in the chambers (*p* = 0.035) than in the control plots after 14 months (Tables 3.5 and 3.6). For the spruce litter, Ca concentrations decreased overall in comparison to initial levels, but there were no significant OTC effects (Tables 3.5 and 3.6).

Overall, when compared to the initial levels, final Mg levels decreased for the aspen and spruce litters, and increased for the *Sphagnum* litter, but the OTC treatment had no effects on the final Mg concentrations for any litter type (Tables 3.5 and 3.6). The main effects of substrate were observed for aspen litter after 14 months, with significantly lower levels at the *Sphagnum* substrate plots (*p* = 0.025; Table 3.6).

In comparison to initial values, the C:N ratio decreased for aspen litter after both incubation times, and was significantly lower in the control plots than OTCs after 14 months (*p* = 0.018; Tables 3.5 and 3.6). For *Sphagnum* litter, the C:N ratio increased after 14 months, but decreased after 24 months compared to the initial value, but there were no main effects of the OTC treatment (Tables 3.5 and 3.6). There was also a significant interaction between the OTC treatment and the substrate type for *Sphagnum* litter after the 14 month incubation, with a lower C:N ratio in the control plots with *Sphagnum* substrate than in the control plots with non-*Sphagnum* substrate (*p* = 0.007; Table 3.6). When compared to initial levels, the C:N ratios decreased in the spruce litter under all combinations of the OTC and substrate type treatments, but there were no significant effects of the OTC treatment on the final spruce litter C:N ratios (Tables 3.5 and 3.6).

Discussion

Effects of OTCs, substrate type, and sites on soil pH and soil nutrient supply rates

Lower Ca and Mg supply rates in spring in the OTCs might have occurred because of increased plant nutrient uptake associated with earlier snowmelt in OTCs (Chapter 2) and earlier initiation of the growing season. Significantly higher ambient temperatures in the chambers (Chapter 2) may have led to accelerated growth rates of the vegetation and thus, increased nutrient uptake. It is possible that the uptake of Ca and Mg in OTCs was higher than in the control plots, and the lower soil levels of these basic cations resulted in lower soil pH (e.g. Alban et al. 1978). This might have been especially pronounced in late August due to cumulative Ca and Mg uptake over the growing season, and it may explain the significantly lower soil pH in August 2006 and 2007 in the chambers (Table 3.2).

The significant interaction between the OTC treatment and site in May 2006, where the supply rates of available N in the control plots at the logging interval site were significantly higher than at any other combinations of OTC treatment and sites, corroborates the fact that the soil was generally warmer in the control plots than in the OTCs (Chapter 2), which might have resulted in increased N mineralization and nitrification (e.g. Van Cleve et al. 1990; Dahlgren and Driscoll 1994; Hobbie 1996; Rustad et al. 2001). However, the available nitrogen levels were generally very low (in 2007 they were below PRS probe detection levels) at all sites, which are generally known to be nutrient poor. Likewise, significantly lower Ca and Mg supply rates in the *Sphagnum* substrate plots could be a reflection of inherently poor nutrient conditions in *Sphagnum* dominated habitats (Sjörs 1959; Bridgham et al.1996).

Decomposition processes in the context of OTC-modified soil conditions

In a recent meta-analysis of experimental warming studies in cold biomes, Aerts (2006) reported that decomposition rates are highly influenced by the warming method used. More precisely, open-top chambers generally led to drier soils and reduced decomposition rates, while over-soil heating with infrared lamps promoted decomposition. Ultimately, Aerts (2006) concluded that soil moisture appeared to be a limiting factor in affecting decomposition, and as such, the prediction that global warming will increase decomposition rates must be considered in conjunction with its effects on soil moisture. Our results corroborate his findings on at least two levels: 1) OTC treatment induced lower soil moisture, which led to slightly lower decomposition rates, (although the differences were detectable only for aspen litter type, and only after the 14 month incubation period); 2) along with the soil temperature, soil moisture was definitely one of the major factors affecting the decomposition processes. However, the magnitude and relative contribution of the major factors affecting decomposition differed substantially between open-top chambers and control plots (Table 3.4).

The inverse relationship of the summer soil moisture in the open-top chambers with % DMR for aspen litter after both incubation periods, *Sphagnum* litter after the 14 month incubation, and spruce litter (Table 3.4), suggest that as the soil dried, the decomposition slowed. That is, the dry summer soil conditions were inhibiting decomposition. At the same time, high spring soil moisture associated with snowmelt appeared to have an inhibitory effect on decomposition of spruce and aspen litter after 24 months, and *Sphagnum* litter after 14 months in the chambers, but this effect was not observed in the generally wetter control plots. In other words, soil moisture does not appear to have the same effect on decomposition in OTCs as in control plots.

It is possible that in the control plots the higher soil moisture conditions in combination with higher soil temperatures were promoting decomposition. Wetter soils in the control plots may have induced higher soil temperatures by increases in thermal conductivity, since heat passes faster through water than air (Rosenberg et al.1983; Hollister 1998; Groffman et al. 2001; Hardy et al. 2001; Kellner 2001). It may be difficult to delineate singularly the effects of soil temperature and moisture on decomposition, but the combination of the two seems to have created overall more favourable conditions for decomposition in control plots, as opposed to chambers. The complexity of interaction between soil temperature and moisture on decomposition was shown by Robinson et al. (1995) who observed that elevated temperatures alone reduced litter decomposition rates, but elevated temperatures plus water addition to soil resulted in significant decomposition rate increase. Likewise, the dry soil conditions might have been limiting decomposition in our chambers, but increased soil moisture and its augmentation of soil temperature were not limiting decomposition in control plots.

Although OTC treatment had a significant effect on soil temperature and moisture, following general trends of cooler and drier soils in OTCs, these differences were always much smaller between the chambers and control plots in comparison to the differences observed across the three disturbance sites (Chapter 2). For example, while the difference in soil % volumetric moisture content for TDR probes of 12 cm length in spring 2006 was only ~ 5% between OTCs and control plots, it was over 18% higher at the logging road site than at the logging interval site (Chapter 2). Highly significant effects of disturbance site on decomposition rates after the 24 month incubation of *Sphagnum* litter (Table 3.3) suggest that the moisture differences across the sites were high enough to affect *Sphagnum* litter decomposition. Furthermore, the significant interaction of disturbance site and substrate type on *Sphagnum* litter decomposition rates indicated that after the 14 and 24 month incubation period, decomposition was fastest at the logging road site with *Sphagnum* substrate. Plots with *Sphagnum* substrate were generally wetter than those with non-*Sphagnum* substrates, but there was little difference in the temperature between them (Chapter 2). This suggests that moisture may have been more limiting in terms of decomposition rates than temperature for *Sphagnum* litter type. The conditions at the logging road site were always the warmest and the wettest of the three sites (Chapter 2), and these seem to be the optimal conditions for *Sphagnum* decomposition. Even though the soil in the control plots was, in general, also warmer and wetter than in the OTCs, the difference was apparently not strong enough to affect decomposition rates of *Sphagnum* litter.

However, OTC treatment was strong enough to significantly decelerate decomposition of aspen litter after the 14 month incubation period, with the difference of over 3% in litter dry mass remaining (Table 3.3). Significant interaction between site and substrate shows that the combined effects of these two factors on decomposition rates are rather complex (Table 3.3). The lack of obviously consistent trends here, reinforces how even subtle microenvironmental differences created by the interaction of moisture and temperature across the disturbance sites affect the decomposition rates of aspen litter. This complexity is further represented by the differences in factors which were most strongly influencing decomposition process in the open-top chambers versus the control plots. Soil temperature, moisture and availability of K and P were the top four factors affecting decomposition rates in the OTCs for aspen litter after the 14 month incubation; in the control plots, availability of N, K and P were most influential, while soil temperature and moisture were not among the four strongest factors after 14 months (Table 3.4).

Whether 3% statistically significant difference in decomposition of aspen litter in OTCs and control plots is biologically significant (e.g. in terms of providing more or less available nutrients for plant uptake) may be debatable; however, it does show that simulated by us plausible scenario of climate change using OTCs is affecting decomposition rates, even after a relatively short duration of the experiment. In the longer term, a cumulative effect of decomposition rate deceleration may have a much stronger biological impact on plant nutrient availability.

For spruce litter, neither OTC treatment, nor the differences between the substrate types or across the disturbance sites had a significant effect on decomposition rates, which suggests that other factors in conjunction with the soil temperature and moisture may have played an essential role in decomposition. Indeed, spruce litter was the only litter type where soil pH was among the four top factors affecting decomposition rates (Table 3.4). Soil pH, which was significantly lower in the chambers by the end of the summer in 2006 and 2007 (Table 3.1) was inversely related to % DMR of spruce litter in the chambers (Table 3.4). This suggests that increased acidity in the chambers may have had an inhibiting effect on decomposition process of spruce litter. On the other hand, in control plots pH was positively related to % DMR (Table 3.4), suggesting that increasing acidity was actually enhancing decomposition. In a comparison of litter decomposition rates at moist acidic and moist non-acidic tundra sites, Hobbie and Gough (2004) found that site-specific decay rates were almost twice as fast under the more acidic conditions. They concluded that a potentially higher abundance of fungi decomposers under more acidic conditions contributed to higher decomposition rates by promoting decay of recalcitrant litter. Since there were no moisture and temperature difference between their sites, the authors concluded that soil pH and its associated effect on decomposing organisms were the deciding factors in decomposition processes. In our case, the inverse relation of soil pH with spruce litter % DMR in the chambers was also most likely an indirect reflection of some interaction of soil pH with another factor that affected the decomposition. For example, an interaction of soil acidity with other factors, most likely availability of nutrients, resulted in different decomposition pathways for the spruce litter in the open-top chambers versus the control plots.

The effects of nutrient availability on decomposition are not resolved. Bokhorst et al. (2007) concluded that local substratum characteristics, especially soil N availability, rather than temperature, played a more important role in affecting decomposition rates of organic matter in their open-top chamber field decomposition experiment. However, the effects of soil nutrient availability on decomposition rates can hardly be separated from the context of soil pH, moisture and temperature, since they all interact in affecting nutrient cycling and soil nutrient levels. Under natural conditions, interaction of numerous biotic and abiotic factors will lead to variations in which factors may limit decomposition. In their study of nutrient cycling in relation to decomposition processes in Alaskan taiga, Flanagan and Van Cleve (1983) found that field fertilization of N, P and K had no effect on microbial activity, although negative effects were found under laboratory conditions. The authors managed to induce some limitations on microbial activity under the artificial conditions, which were not present under a natural setting. By the same token, we managed to sufficiently modify the soil moisture and temperature conditions in the open-top chambers so that they became the most influential and potentially limiting factors on decompositions process (especially for aspen litter) (Tables 3.3 and 3.4).

The open-top chamber treatment resulted in reduced supply rates of Ca and Mg. The higher levels of these nutrients in control plots were respectively, inversely and positively related to % DMR of *Sphagnum* litter, indicating enhancement and inhibition of decomposition. On the other hand, although the nutrient supply rates of these basic cations were reduced in the chambers, they were not among the four top factors affecting % DMR for the aspen and spruce litters in the OTCs or control plots. Likewise, Prescott et al. (1999) found no evidence that a fertilizer with a mixture of nutrients including Ca and Mg had an effect on decomposition rate of aspen litter. Our results suggest that the effects of soil nutrient conditions on decomposition may differ not only under varying soil temperature and moisture for the same litter type, but they will also differ among various litter types.

Soil nutrient levels and decomposition processes are complex and variable, and it is hard to make generalizations about their relationships. Indeed, with respect to soil N availability, evidence for and against the positive effect of available soil N on decomposition have been found, although Prescott et al. (1999) claims that the inconsistencies arise from the fact that the reported increases in decomposition upon higher available soil N levels were likely a response to other, unconsidered factors. Our results likewise show that when the available N and NH_4 were among the four top factors affecting decomposition rate, they were inconsistently related to % DMR. Variations were found depending on available N form, litter type and the presence or absence of the open-top chamber. For example, supply rates of NH_4 were positively and inversely related to % DMR of aspen litter after the 24 month incubation in the control plots and OTCs respectively; for spruce litter available N was not among the top four factors affecting decomposition at all; and, for *Sphagnum* litter it was among the four top factors only in the chambers, and only after the 24 month incubation (Table 3.4). Clearly, consistent trends with respect to N availability and % DMR are difficult to detect.

An indication that N mineralization may not have a direct and consistent effect on early years of decomposition comes from McClaugherty et al. (1985). They found that decomposition rates of litter for several temperate-boreal tree species were positively correlated with N mineralization rates only if the litter originated from the forest stand where the incubation took place, but not for the litter transplanted from other forest stands. This positive correlation was evidently a reflection of the N levels in the litter. Since the litter in our experiment did not originate from the sites where we performed our incubations, perhaps this explains why we did not observe a clear relationship of N availability with decomposition processes (Table 3.4).

Furthermore, although the chambers affected the supply rates of some nutrients (Ca, Mg, N; Table 3.2), this was hardly reflected in the final litter chemistry of the decomposing material. Only in the case of *Sphagnum* litter after the 14 month incubation were the final litter Ca concentrations significantly reduced in OTCs, and the supply rates of Ca were also significantly lower in the chambers (Tables 3.2 and 3.6). However, the supply rates of Mg were also lower in the chambers versus control plots, but there were no effects of OTCs on the final Mg concentrations for any litter type (Table 3.6). It may be that nutrient supply rates influence decomposition only when the litter decomposes at the site from which it originates. Presumably this is because soil nutrient availability affects the chemical composition of the foliage, which later becomes the decomposing litter after natural leaf fall occurs.

Ultimately, the intricate interactions of soil moisture, temperature, acidity and nutrient availability will affect decomposition rates and pathways differently, depending on the inherent properties of the litter. This can be clearly seen by the different rates of decomposition of the three litter types in our study (Table 3.3: aspen< spruce< *Sphagnum* in terms of % DMR). In an attempt to separate the effects of litter properties (i.e. species chemical composition) from the microenvironmental properties on decomposition rates in Scottish peatland, Belyea (1996) concluded that due to their dynamic and complex interaction, the combined effects of both factors must be considered for proper assessment of decomposition processes. Only in the case of aspen these inherent litter qualities were significantly affected by the OTC treatment in terms of decomposition rate. However, for all litter types the presence of OTCs appeared to modify the decomposition pathways, as suggested by different factors playing a key role in decomposition (Table 3.4). This may allow us to project which factors could become of major importance in the future under climatic changes. Clearly, drier soil conditions could become one of the major factors. The significant effect of the OTC treatment on decomposition of aspen litter suggests that the small decline in soil moisture may be enough to affect decomposition rates. On the other hand, soil moisture differences may have to be larger to affect *Sphagnum* litter decomposition, as suggested by the effects of sites (disturbance types) and substrate type, which affected *Sphagnum* decomposition and had larger moisture differences than those between OTC and control plots (Table 3.3). For spruce litter, these differences may have to be even larger, since not even the high soil moisture differences across the sites had a significant effect on spruce decomposition rates (Table 3.3). However, the crucial roles of moisture and temperature on decomposition of spruce may be expressed indirectly, for example by their effects on soil acidity.

Conclusion

In the view that elevated air temperatures in the chambers induced earlier snowmelt and evapotranspiration rates (Chapter 2), creating a plausible climate change scenario of cooler and drier soil conditions (Groffman et al. 2001), we can predict that air temperature increases may in fact lead to *deceleration* of decomposition rates. This challenges the notion of the positive feedback whereby the increased decomposition rates would increase the rate of CO_2 release into the atmosphere leading to further increases in temperature (e.g. Kirschbaum 2000).

The changes of up 2^oC in soil temperature and 10% in VMC (i.e. the differences we observed between OTCs and control plots; Chapter 2) had a small inhibiting effect on decomposition rates, but in the future, the climatic changes may reach levels that will have a much larger direct impact on decomposition. However, the effect of OTCs on decomposition will be species and time specific. In our experiment, the decomposition rate of aspen litter was affected by the presence of chambers in the first year of incubation, but less so in the second year, while the effects of chambers on decomposition rates of *Sphagnum* in the first or second year of incubation, and of black spruce litter after two years of incubation, were not detectable. The relative influences of microclimatic and biogeochemical factors affecting the decomposition rates differed between OTCs and control plots and across litter types. Consequently, as future climate change intensifies or reduces the magnitude of changes of these factors, their relative importance in affecting decomposition process may grow or decline, and this may have profound effects on decomposition rates.

In the case of decomposition processes at post-disturbance sites in transitional mixedwood-boreal forest zone in NW Quebec, substantial differences in soil temperature and perhaps more importantly, soil moisture, would have to occur to induce significant changes in decomposition rates, especially for peat moss. In the event that future climate change does, in fact, lead to cooler and drier soil conditions, the decomposition rates would slow, effectively slowing nutrient cycling and thus, plant nutrient availability. This could have more negative effects on regeneration and growth of trembling aspen, which in comparison to black spruce has generally higher nutrient requirements. In that respect, reduced nutrient availability could limit regeneration and growth of aspen in the northern black-spruce dominated regions. The question remaining is whether the indirect effect of soil temperature and moisture on decomposition processes and nutrient availability will prevail over the direct effects of reduced soil moisture and temperature in promoting or inhibiting regeneration and growth of the two species. Simulation of the climatic changes by OTCs and their effects on performance of the two species e.g. in terms of growth rates, biomass, spring phenology and foliar and root nutrient concentrations, and root mycorrhizal colonization may give more insight into that.

Tables

Table 3. 1 Effects of OTC treatment (open-top chamber [OTC] or control [C]), substrate type (*Sphagnum* [S] or non-*Sphagnum* [NS]) and site (fire [F], logging road [LR], or logging interval [LI]) on soil pH measured from July 2005 to August 2007. Means are provided for comparison.

				Mean OTC		**Mean substrate**		**Mean site**		
		F value	*P*>F	OTC	C	S	NS	F	LR	LI
pH	OTC	1.25	0.271	4.22	4.36					
July 2005	substrate	2.10	0.156			4.39	4.19			
	site	**7.04**	**0.003***					**4.47**	**4.53**	**3.87**
pH	OTC	1.32	0.258	4.15	4.29					
August 2005	substrate	0.05	0.819			4.23	4.20			
	site	**3.33**	**0.047**					**4.35**	**4.37**	**3.94**
pH	OTC	1.01	0.323	4.28	4.41					
May 2006	substrate	0.08	0.778			4.37	4.33			
	site	1.71	0.196					4.40	4.49	4.15
pH	OTC	0.15	0.700	4.48	4.53					
July 2006	substrate	0.04	0.839			4.49	4.52			
	site	2.87	0.070					4.55	4.72	4.25
pH	**OTC**	**4.11**	**0.050**	**4.38**	**4.62**					
August 2006	substrate	1.21	0.278			4.43	4.57			
	site	1.12	0.338					4.37	4.62	4.40

pH	OTC	1.59	0.216	4.13	4.29					
May 2007	substrate	1.06	0.309			4.28	4.14			
	site	**5.88**	**0.006**					**4.35**	**4.44**	**3.84**
pH	OTC	0.53	0.470	4.25	4.36					
July 2007	substrate	0.44	0.513			4.25	4.36			
	site	4.40	**0.020**					4.48	4.54	3.89
pH	**OTC**	**5.13**	**0.030**	**4.10**	**4.39**					
August 2007	substrate	0.12	0.734							
	site	**7.25**	**0.002**			4.27	4.22	**4.55**	**4.35**	**3.83**

*Significant results are in bold.

Table 3. 2 Effects of OTC treatment (open-top chamber [OTC] or control [C]), substrate type (*Sphagnum* [S] or non-*Sphagnum* [NS]) and site (fire [F], logging road [LR], or logging interval [LI]) on nutrient supply rates from July 2005 to May 2007.

		July 2005			**May 2006**			**July 2006**			**May 2007**		
		F value	*P*>F	Means**	F value	*P*>F	Means	F value	*P*>F	Means	F value	*P*>F	Means
Total N	OTC	0.00	0.964	C=OTC	3.63	0.066	OTC<C	0.20	0.660	OTC< C	-***	-	-
	substrate	2.79	0.104	NS< S	1.71	0.200	NS<S	0.23	0.635	NS<S	-	-	-
	site	1.16	0.324	F< LR< LI	**5.96**	**0.006**	**F<LI<LR**	**4.13**	**0.025**	**F<** LI< **LR**	-	-	-
	OTC* site				**6.32**	**0.005**	**F*C,OTC*F, OTC*LR, OTC*LI, C*LR< C*LI**				-	-	-
	site* substrate				**8.90**	**0.006**	**F*S,**LR*NS,F*NS, LI*S< **LR*S**				-	-	-
NH$_4$	OTC	0.01	0.939	C=OTC	0.33	0.572	C<OTC	0.01	0.923	C= OTC	-	-	-
	substrate	3.16	0.084	NS< S	0.06	0.803	S<NS	3.05	0.090	NS< S	-	-	-
	site	0.81	0.454	F< LI< LR	**5.67**	**0.008**	**LI** <LR<**F**	**4.45**	**0.019**	**F<** LI< **LR**	-	-	-
Ca	OTC	2.50	0.123	OTC< C	12.35	**0.001**	**OTC<C**	**4.92**	**0.033**	**OTC< C**	**7.58**	**0.010**	**OTC<C**
	substrate	**3.87**	**0.030***	**S< NS**	**4.68**	**0.038**	**S<NS**	3.43	0.073	S< NS	0.13	0.716	S<NS
	site	2.34	0.135	LI< F< LR	**3.27**	**0.051**	**LI**<F<**LR**	**3.61**	**0.038**	**LI<** F< **LR**	**5.20**	**0.011**	**LI**<F< **LR**
Mg	OTC	2.9	0.098	OTC< C	**8.26**	**0.007**	**OTC<C**	3.36	0.076	OTC< C	**7.07**	**0.012**	**OTC<C**
	substrate	2.59	0.117	S< NS	**5.02**	**0.032**	**S<NS**	**4.20**	**0.048**	**S< NS**	0.54	0.469	S<NS
	site	**5.00**	**0.012**	**LI<** F< **LR**	**5.07**	**0.012**	**LI<F<LR**	**6.08**	**0.006**	**LI<** F< **LR**	**8.33**	**0.001**	**LI<LR, F<LR**
P	OTC	0.24	0.630	OTC< C	2.71	0.109	OTC<C	1.21	0.279	C< OTC	2.00	0.166	OTC<C
	substrate	0.12	0.732	NS< S	3.61	0.066	S<NS	0.01	0.937	S= NS	**6.01**	**0.020**	S<NS
	site	2.85	0.072	F< LR< LI	1.34	0.275	F<LR<LI	**7.01**	**0.003**	**F<** LI< **LR**	**15.3**	**<0.0001**	**F<LR<LI**

K	OTC	3.63	0.065	C< OTC	1.81	0.188	C<OTC	2.81	0.103	C< OTC	0.12	0.727	C<OTC
	substrate	0.00	0.953	S = NS	0.08	0.777	S<NS	0.01	0.926	S = NS	1.14	0.292	S<NS
	site	3.25	0.051	LI< F< LR	1.78	0.185	LI<LR<F	0.69	0.508	LR< LI< F	0.36	0.700	LR<LI<F

*Significant results are in bold.

**Treatment level means showing consistency of general trends. Means with *P*-values > 0.9 are considered identical.

*** Due to low total N and NH_4 (i.e. below PRS laboratory methods detection levels) no analysis for these variables could be performed in May 2007.

Table 3. 3 Effects of OTC treatment (open-top chamber [OTC] or control [C]), substrate type (*Sphagnum* [S] or non-*Sphagnum* [NS]) and site (fire [F], logging road [LR], or logging interval [LI]) on percentage dry mass remaining (%DMR) for three littler types after 14 month incubation (Aspen 2006 and *Sphagnum* 2006 litter) and 24 month incubation (Aspen 2007, *Sphagnum* 2007 and Spruce 2007 litter).

	Aspen 2006			**Aspen 2007**			**Sphagnum 2006**			**Sphagnum 2007**			**Spruce 2007**		
	F value	*P*>F	Means	F value	*P*>F	Means	F value	*P*>F	Means	F value	*P*>F	Means	F value	*P*>F	Means
OTC	**5.07**	**0.031***	C<OTC C= 55.5 OTC= 58.6	3.27	0.079	C<OTC C= 44.9 OTC= 48.8	0.01	0.914	C=OTC C= 81.6 OTC= 81.4	0.05	0.828	C=OTC C= 80.3 OTC= 80.6	0.03	0.870	OTC<C OTC= 50.5 C= 50.8
substrate	0.14	0.712	NS<S NS = 56.7 S= 57.3	0.01	0.905	S=NS S= 46.7 NS= 47.0	1.63	0.211	S<NS NS= 82.9 S= 80.5	3.84	0.058	S< NS S= 80.0 NS= 81.0	0.17	0.681	S< NS S= 50.1 NS= 51.4
site	2.41	0.105	F<LI<LR F= 56.0	0.00	0.997	LI=LR=F LI= 46.7	3.00	0.063	LI<LR<F LI= 80.3	**9.32**	**0.001**	F< LR< LI F= 79.0	0.35	0.706	LI<LR<F LI= 49.0

			LI= 56.8 LR= 59.7			LR= 46.8 F= 47.0			LR= 81.1 F= 83.0			LR= 79.7 LI= 85.0			LR= 50.53 F= 51.5
substrate*site	**4.81**	**0.035**	F_NS< LR_S< F_S< LR_NS< LI_S F_NS= 54.6 S_LR= 54.8 F_S= 57.5 LR_NS= 58.8 LI_S= 59.7	**-**	**-**	-	**4.54**	**0.040**	LR_S< LI_S< F_NS< LR_NS< F_S LR_S= 76.8 LI_S= 81.1 F_NS= 82.0 LR_NS= 83.7 F_S= 83.8	**7.49**	**0.010**	LR_S< F_NS< F_S< LR_ NS< LI_S LR_S= 75.7 F_NS= 78. 3 F_S= 79.6 LR_NS= 83_65 LI_S= 85.0	**-**	**-**	**-**

*Significant results are in bold.

**Treatment level means showing consistency of general trends. Means with *P*-values > 0.9 are considered identical.

Table 3. 4 Multiple regression results for open-top chambers (OTC) and control plots (C). Maximum r^2 indicates the variation explained by the top four predictors of % dry mass remaining (% DMR) for the three litter types and two incubation periods: 14 months (Aspen 2006 and *Sphagnum* 2006 litter) and 24 months (Aspen 2007, *Sphagnum* 2007 and Spruce 2007 litter).

% DMR of Litter types	**Max r^2**	**Intercept**	**Variables and parameter estimates**			
		B_o	B_1*X_1	B_2*X_2	B_3*X_3	B_4*X_4
Aspen 2006- OTC	0.35	57.8	+1.47*soil_P	+1.073*soil_Tspring	-0.10*soil_VMCsummer	-0.02*soil_K
- Control	0.30	58.8	+2.06*soil_P	+ 1.43*soil_NH_4	-0.77*soil_N	-0.05*soil_K
Aspen 2007- OTC	0.47	67.1	-3.33*soil_Tspring	-0.72*soil_VMCsummer	+0.55*soil_VMCspring	-0.40*soil_NH_4
- Control	0.48	64.6	-11.4*soil_P	+1.20*soil_NH4	-0.20*soil_VMCsummer	-0.09*soil_K
Sphagnum 2006- OTC	0.53	-2.05	+5.62*soil_Tsummer	-0.51*soil_VMCsummer	+0.38*soil_Tspring	+0.24*soil_VMCspring
- Control	0.52	97.0	+4.87*soil_P	-4.49*soil_Tspring	+0.15*soil_Mg	-0.03*soil_Ca
Sphagnum 2007- OTC	0.27	79.4	+1.23*soil_N	-1.06*soil_NH_4	-0.32*soilVMCspring	+0.20*soil_VMCsummer
- Control	0.31	88.8	+1.72*soil_P	-0.23*soil_VMCsummer	-0.06*soil_K	+0.02*soil_Mg
Spruce 2007- OTC	0.79	96.9	-8.65*soil_pH	-4.36*soil_P	-0.76*soil_VMCsummer	+0.58*soil_VMCspring
- Control	0.15	56.3	+2.93*soil_pH	-1.37*soil_Tsummer	+0.28*soil_VMCsummer	-0.21*soil_VMCspring

Note: Initial set of predictors included soil pH (soil_pH), nutrient supply rates (soil_NH_4, soil_P, soil_K, soil_Ca, and soil_Mg), and spring and summer soil volumetric moisture content (soil_VMC) and temperatures (soil_T) over the incubation period.

Table 3. 5 Means and standard deviations of nutrient concentrations (g/mg) and C:N ratio for trembling aspen, *Sphagnum* and spruce litter buried in litter decomposition bags under open-top chamber-*Sphagnum* [OTC_S], open-top chamber-non-*Sphagnum* [OTC_NS]),control plot-*Sphagnum* (C_S) and control plot-non-*Sphagnum* (C_NS) treatments. Lowest value among four OTC-substrate type treatment combinations is given in italics and underlined if lower than the initial value.

		Aspen 2006*		**Aspen 2007****		**Sphagnum 2006***		**Sphagnum 2007****		**Spruce 2007***	
Nutrient	Treatment Combination	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation
N	**Initial*****	**8.69**	-	**8.69**	-	**5.93**	-	**5.93**	-	**4.16**	-
	OTC_S	13.92	1.34	14.53	1.47	5.13	0.61	5.04	0.33	*6.48*	0.80
	OTC_NS	*13.52*	1.52	14.69	1.00	*4.78*	0.46	5.67	1.70	6.70	0.69
	C_S	14.67	1.84	15.16	1.66	5.68	1.27	5.96	1.99	7.26	1.33
	C_NS	13.92	1.95	*14.24*	3.59	5.10	0.59	*4.91*	0.40	6.89	0.50
P	**Initial**	**0.70**	-	**0.70**	-	**0.81**	-	**0.81**	-	**0.45**	-
	OTC_S	*0.74*	0.06	0.70	0.08	0.53	0.08	0.49	0.05	*0.45*	0.08
	OTC_NS	0.75	0.09	*0.54*	0.29	*0.49*	0.04	0.56	0.13	0.47	0.05
	C_S	0.82	0.12	0.69	0.22	0.54	0.12	0.56	0.16	0.55	0.15
	C_NS	0.76	0.09	0.62	0.27	0.50	0.03	*0.48*	0.04	0.46	0.03
K	**Initial**	**6.62**	-	**6.62**	-	**4.68**	-	**4.68**	-	**2.30**	
	OTC_S	***0.54***	0.22	*0.31*	0.21	0.75	0.51	*0.25*	0.12	*0.23*	0.15
	OTC_NS	0.62	0.20	0.65	0.40	0.54	0.20	0.57	0.32	0.33	0.14
	C_S	0.67	0.39	0.61	0.68	0.62	0.30	0.31	0.12	0.39	0.29
	C_NS	0.78	0.52	0.59	0.60	*0.53*	0.23	0.48	0.44	0.36	0.10
Ca	**Initial**	**18.46**	-	**18.46**	-	**3.31**	-	**3.31**	-	**10.30**	-
	OTC_S	19.48	4.70	*15.03*	2.92	5.18	1.64	5.06	2.03	7.75	3.48
	OTC_NS	21.49	3.46	16.77	6.30	*5.13*	0.99	7.08	4.27	9.20	3.30
	C_S	***17.92***	4.37	15.47	4.40	7.30	4.90	6.79	3.73	8.05	2.60
	C_NS	19.65	2.80	16.42	3.02	6.45	1.04	*5.05*	0.91	*7.62*	1.58

Mg	**Initial**	**2.42**	-	**2.42**	-	**0.88**	-	**0.88**	-	**0.89**	
	OTC_S	1.61	0.50	*1.21*	0.46	*1.24*	0.39	*1.24*	0.45	*0.53*	0.24
	OTC_NS	2.05	0.39	1.73	0.61	1.42	0.31	1.77	0.80	0.69	0.17
	C_S	***1.50***	0.54	1.33	0.51	1.62	0.77	1.61	0.74	0.64	0.26
	C_NS	2.01	0.35	1.51	0.40	1.54	0.38	1.39	0.45	0.66	0.23
C:N ratio	**Initial**	**43.46**	-	**43.46**		**55.98**	-	**55.98**	-	**88.74**	-
	OTC_S	32.90	1.68	30.44	3.93	70.10	10.82	59.56	7.03	63.81	10.11
	OTC_NS	32.38	2.86	29.61	3.03	72.47	10.20	56.45	6.28	59.42	10.05
	C_S	***30.49***	3.25	*28.63*	5.79	*65.44*	12.38	*51.96*	10.04	*56.23*	9.75
	C_NS	30.90	1.82	30.71	6.22	66.29	7.38	61.48	3.06	57.20	5.94

*14 month incubation.

**24 month incubation

***Initial nutrient concentrations and C:N ratio are given for each litter type in bold

Table 3. 6 Effects of OTC treatment (open-top chamber [OTC] or control [C]), substrate (*Sphagnum* [S] or non-*Sphagnum* [NS]) and site (fire [F], logging road [LR], or logging interval [LI]) on final concentrations of N, P, K, Ca and Mg nutrients, and C:N ratio after 14 month incubation (Aspen 2006 and *Sphagnum* 2006 litter) and 24 month incubation (Aspen 2007, *Sphagnum* 2007 and Spruce 2007 litters).

		Aspen 2006			**Aspen 2007**			**Sphagnum 2006**			**Sphagnum 2007**			**Spruce 2007**		
		F value	*P*>F	Means**	F value	*P*>F	Means	F value	*P*>F	Means	F value	*P*>F	Means	F value	*P*>F	Means
N	OTC	1.38	0.248	OTC<C	1.78	0.191	OTC<C	3.86	0.058	OTC<C	0.00	0.969	OTC<C	2.30	0.138	OTC<C
	substrate	1.16	0.290	NS<S	0.06	0.815	S<NS	0.04	0.841	NS<S	1.37	0.251	NS<S	0.06	0.811	S<NS
	site	0.45	0.639	LR<LI<F	0.11	0.893	LI<F<LR	**8.83**	**0.001**	**F<LR<LI**	0.51	0.605	LI<F<LR	0.10	0.902	F=LR=LI
P	OTC	**4.07**	**0.052**	**OTC<C**	2.53	0.121	OTC<C	0.00	0.967	OTC<C	0.01	0.922	OTC=C	2.54	0.120	OTC<C
	substrate	0.31	0.580	S<NS	1.39	0.247	NS<S	0.02	0.882	S<NS	0.00	0.949	NS=S	0.15	0.697	S<NS
	site	**7.44**	**0.002***	**LR<F<LI**	0.92	0.409	LR<F<LI	**7.49**	**0.002**	**F<LR<LI**	0.91	0.412	LI<F<LR	2.41	0.105	F<LR<LI
K	OTC	1.93	0.174	OTC<C	0.17	0.682	C<OTC	0.03	0.870	C<OTC	0.01	0.939	OTC=C	**4.27**	**0.046**	**OTC<C**
	substrate	2.83	0.102	S<NS	**8.43**	**0.007**	**S<NS**	0.94	0.338	NS<S	**9.01**	**0.005**	**S<NS**	**4.51**	**0.041**	**S<NS**
	site	2.21	0.125	LR<F<LI	**3.19**	**0.055**	**F<LR<LI**	**4.35**	**0.021**	**F<LR<LI**	1.03	0.369	F<LR<LI	**3.67**	**0.036**	**F=LR<LI**
Ca	OTC	1.64	0.208	C<OTC	0.01	0.926	C<OTC	**4.84**	**0.035**	**OTC<C**	0.09	0.764	C<OTC	0.28	0.599	C<OTC
	substrate	1.77	0.192	S<NS	1.07	0.308	S<NS	0.80	0.376	NS<S	0.31	0.583	NS<S	1.75	0.195	S<NS
	site	0.03	0.973	LI<LR<F	0.85	0.436	LR<LI<F	**4.39**	**0.020**	**LI<F<LR**	1.57	0.222	LI<LR<F	**4.29**	**0.022**	**LR<F<LI**
Mg	OTC	0.25	0.619	C<OTC	0.01	0.935	C<OTC	2.19	0.148	OTC<C	0.12	0.730	OTC<C	0.54	0.467	OTC<C
	substrate	**5.53**	**0.025**	**S<NS**	1.59	0.216	S<NS	0.10	0.749	NS<S	0.01	0.903	NS<S	0.07	0.798	S<NS
	site	0.99	0.382	LI<LR<F	2.16	0.131	LI<LR<F	**4.88**	**0.014**	**LI<F<LR**	2.07	0.142	LI<F<LR	2.16	0.131	LI<LR<F
C:N ratio	OTC	**6.16**	**0.018**	**C<OTC**	0.23	0.636	C<OTC	3.46	0.071	C<OTC	0.27	0.605	OTC<C	3.42	0.073	C<OTC
	substrate	0.23	0.637	NS<S	1.91	0.175	S<NS	1.13	0.295	NS<S	1.66	0.208	S<NS	1.07	0.308	NS<S
	site	0.71	0.500	LI<F<LR	**6.98**	**0.003**	**F<LR<LI**	**7.96**	**0.001**	**LI<LR<F**	**4.94**	**0.014**	**LI<LR<F**	0.99	0.381	LI<F<LR
	OTC* substrate	-	-	-	-	-	-	-	-	-	**8.24**	**0.007**	**C_S<OTC_NS <OTC_S<C_NS**	-	-	-

*Significant results are in bold

**Treatment level means showing consistency of general trends. Means with *P*-values > 0.9 are considered identical.

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Connection of Chapter 3 with Chapter 4 and the thesis in general

In **Chapter 3** we tested the effects of OTCs on soil pH, soil nutrient supply rates and decomposition rates, and chemical change of different litter types (aspen, *Sphagnum*, and spruce). We found that the soil in the OTCs was more acidic towards the end of the growing season, the supply rates of Ca and Mg were consistently lower, and aspen litter decomposed slower in chambers compared to control plots. We used the data on the effects of OTCs on soil temperature and moisture from Chapter 2 to interpret these results in order to obtain a more complete assessment of the effects of OTC treatment on soil conditions. Both Chapters 2 and 3, allowed us to assess the effects of OTCs on microclimatic factors, physical soil properties and biogeochemical processes. In **Chapter 4**, we will use this information to test the effects of OTCs on growth rates and final biomass of our experimental aspen and black spruce seedlings. We will also use the results from the previous two chapters to interpret the potential effects of OTCs on abundances of other plant species present in our plots. In the broader context of the thesis, the effects of OTCs on biogeochemical properties will be used to predict which of the two species could potentially be more benefited in terms of regeneration along transitional mixedwood-boreal forest in northwestern Quebec.

Part IV: Biotic responses to simulated climate change

CHAPTER 4: Effects of simulated climatic change on growth and biomass of aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* Miller (BSP)) at different substrates of post-disturbance sites in the mixedwood-boreal zone of northwestern Quebec

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Abstract

In the present study we focused on how complex interactions of aboveground and belowground microclimatic and biogeochemical modifications created by simulated climatic changes, could affect the height growth and biomass accumulation of trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* Miller (BSP)). The broad context of the study dealt with comparison of the growth responses of the two species to anticipated continuation of climatic changes at disturbed sites in the mixedwood-boreal transitional forest zone of northwestern Quebec. To simulate climatic changes, we constructed open-top chambers (OTCs) around pairs of trembling aspen and black spruce seedlings at logging and fire sites and then tested the effects of OTC treatment on the percentage height change, foliage dry biomass, and final total dry biomass of the seedlings after 2.5 growing seasons. As positive or negative responses of other vegetation to OTC treatment could shift the competitive balance against or in favour of aspen or spruce, we also assessed the abundance responses of other plant species to OTC treatment. Higher air temperature and drier soil conditions in the open-top chambers resulted in significantly increased growth in height of trembling aspen, and significantly increased final dry foliage and total biomass of black spruce over the experimental period (July 2005 to August 2007). Inter-seasonal variability affected the patterns of aspen height growth more than black spruce: most of the height increase of aspen growing in OTCs occurred over the 2006 growing season, which had noticeably fewer days with temperatures below the freezing point than 2007. Open-top chamber treatment also noticeably affected plant cover abundances of two species of shrubs (decrease in *Kalmia angustifolia,* and increase in *K. polifolia*), and the sedges (*Carex* species). Shifts in abundances of allelopathic *Kalmia* species could have an important impact on the growth

of black spruce, while an increase in the abundance of several species of *Carex* could particularly affect the belowground competitive balance of regenerating trembling aspen. Overall, trembling aspen appeared to show strong growth responses in terms of stem height increase when the growing conditions were favourable (i.e. OTC treatment in season 2006), but smaller growth responses when the conditions fell below its optimal zone range. In contrast, black spruce appeared to experience small-magnitude but continuous positive growth responses to climate change simulation, and was less affected by inter-seasonal variability in weather conditions. The microclimatic and biogeochemical modifications associated with climatic change, as well as their indirect impact on the competitive balance with vascular and non-vascular species coexisting with aspen and spruce at regenerating post-disturbance sites in NW Quebec, could give aspen an initial short-term growth advantage. However, the more balanced and conservative positive growth responses of black spruce could ultimately prove more beneficial for that species over the long term.

Introduction

Recent global climatic changes, caused in part by rising levels of greenhouse gases, have been marked by unprecedented air temperatures increases, and alterations in precipitation regimes and snowmelt patterns, among other factors (IPCC 2007). These changes are expected to affect soil temperature and moisture as well as carbon balance and nutrient cycling (IPCC 2007). Because of inherent differences in species' environmental preferences based on their evolutionary development of unique physiological and morphological adaptations, climatic changes will be beneficial to some plant species but detrimental to others. This may pertain also to trembling aspen (*Populus tremuloides* (Michx.) and black spruce (*Picea mariana* (Miller) BSP) in the transitional mixedwood-boreal zone of northwestern Quebec. Aspen, found under a wide variety of soil types and often in relatively dry, open conditions (Perala 1990), has a high requirement for nutrients (Alban et al. 1978; Van Cleve et al. 1983), while black spruce is often associated with poorly drained, cool, thick, and nutrient-poor peat moss mats (Van Cleve et al. 1983; Fenton and Bergeron 2007). As the climate changes, the growing conditions of these habitats within the transitional mixedwood-boreal forest zones may change, becoming more favourable to one of these species, and less so to the other.

Changes in environmental conditions leading to shifts in the dominance and abundance of plant species and/or plant forms present within communities have been reported before (e.g. Press et al. 1998; Hollister et al. 2005; Walker et al. 2006). At a larger scale, massive migrations and encroachment of new species from south into northern habitats have also been predicted (Huntley 1991; Prentice 1992; Rizzo and Wiken 1992; Weber and Flannigan 1997; Karnosky et al. 2001; ACIA 2004; Sjögersten and Wookey 2004; Walker et al. 2006). Disturbed sites that are in the process of regenerating may be especially susceptible to shifts in species dominance and colonization of migrating species, as suddenly accessible post-disturbance open habitats may allow advancement of a species into regions beyond its previously defined distributional boundaries. The occurrence of such advanced populations may serve as a nucleus for further species expansion and migration (Prentice 1992). For example, infilling of post-disturbance available habitats, where growing conditions modified by the climatic changes may be closer to the theoretical optimum of trembling aspen, could facilitate further northern expansion of the species. This could lead to a gradual progression of mixedwood forest into the boreal forests – a phenomenon that has already been suggested for these regions under the currently changing climate (Bergeron et al. 2004). Assessment of growth responses to potential climatic changes of trembling aspen and black spruce at a small scale would be a pre-requisite to larger scale studies, which would allow for prediction of shifts in species dominance along the transitional mixedwood-boreal forest zones, such as the one in northwestern Quebec.

Furthermore, climatic changes could affect the growth and performance of other vascular and non-vascular vegetation present at disturbed sites in the transitional mixedwood-boreal zone, which could shift the competitive balance against or in favour of the regenerating aspen and spruce trees. For example, the growth of black spruce seedlings can be negatively affected by competing *Sphagnum* mosses (e.g. Ohlson and Zackrisson 1992; Fleming and Mossa 1994; Groot and Adams 1994). Therefore, potential deterioration of *Sphagnum* under drier climatic conditions (Dorrepaal et al. 2004; Peregon et al. 2007) could become advantageous for the early growth of spruce seedlings, as a result of reduced competitive pressure. On the other hand, higher temperature and precipitation may improve the growing conditions for *Sphagnum*, leading to increased competition between peat moss and coexisting vascular plant species.

The broad scope of our project was to investigate the complex network of issues associated with the role of climate change on the growth and performance of trembling aspen and black spruce seedlings at post-fire and post-logging sites along the transitional mixedwood-boreal forest zone in the James Bay region of northwestern Quebec. The particular focus of this study was to assess the height growth responses and biomass accumulation of the two species at the disturbed sites. The simulated climatic changes were produced through the installation of open-top chambers (OTCs) around pairs of regenerating aspen and spruce seedlings at disturbed sites within our study area. We expected that the microenvironmental modification created by the OTCs would have a direct effect on the growth in height and biomass accumulation of the two species, as well as indirect effects on their performance via the growth and abundance responses to OTC treatment of coexisting vascular and bryophyte vegetation. As such, we monitored not only the growth of our experimental aspen and spruce trees, but also the changes in the cover abundance of all other plant species coexisting within our experimental plots. In addition, to assess the role of the rooting substrate type, we performed the OTC treatment in a factorial design, with plots constructed on *Sphagnum* moss and on non-*Sphagnum* moss (usually a mixture of mineral soil and humus with a sparse *Polytrichum* moss cover). We predicted that the higher air temperature and drier, cooler soil conditions inside the open-top chambers would have a direct effect on the growth of both species, but that these responses may be modified indirectly by the effects of OTCs on the rooting substrate, as well as the responses of other vascular and non-vascular vegetation coexisting within the experimental plots.

Materials and methods

Study sites

The study area (49° 37' N; 79° 00' W) is found in the boreal mixedwood-black spruce transitional forest zone in James Bay, which constitutes part of the Clay Belt physiographic region spanning northwestern Quebec and northeastern Ontario. A detailed description of the region, including geological background, climate, and present vegetation is provided in the general introduction and the first two chapters of this thesis.

We identified three study sites spanning 20 km along the Selbaie road (from 49^{o}37' N; 78^{o}59' W to 49 ^{o}45' N; 79^{o}02' W) which was constructed between 1977 and 1980 to allow access to Selbaie copper mine located at km 92 (S. Galarneau, personal communication, the Ministère des Ressources naturelles et de la Faune du Québec, La Sarre, Quebec). There were three study sites: a salvage logged post-fire site; a logging road, created to facilitate timber harvest; and a post-logging site, where the timber harvest took place. At all of these sites, the disturbance occurred in the years 1996-1997. Detailed descriptions of the sites, including dominant vegetation and soil texture and drainage information, are provided in the general introduction of this thesis.

Experimental design

In total, 40 experimental plots were set up: 20 open-top chambers and 20 control plots. At the fire site there were eight OTCs and eight control plots; at the logging road site there were also eight OTCs and eight control plots; and, at the logging interval site there were four OTCs and four control plots. At each site, every OTC was paired with a control plot established in a close proximity.

To test the responses to OTC treatment in the presence or absence of live *Sphagnum* moss at the fire and logging road sites, eight pairs of OTC and control plots were established on each site where the dominant substrate consisted of *Sphagnum* moss, and another eight pairs where the substrate was dominated by sparse *Polytrichum* moss growing on mixture of humus and mineral soil. The substrate and the OTC treatment at the fire and logging road sites were crossed factorial: four OTCs and four control plots at *Sphagnum*-dominated substrates, and four OTCs and four control plots at non *Sphagnum*-dominated substrates, for a total of sixteen plots per site. At the logging interval site, four pairs of OTC and control plots were all set up on live *Sphagnum* moss.

At each of the three sites, in locations where plots were chosen to receive a climate change simulation treatment, a circular enclosure (open-top chamber), 1 m in diameter and 0.75 m in height, was constructed of clear transparent polymethylmethaacrylate (PMMA, commonly known as acrylic) material of 8 mm thickness. The construction of the chambers took place between June 28 and July 1, 2005, and the chambers were not removed until mid-August of 2007. Two flexible PMMA sheets were connected with tie-wraps and supported in two places by plastic stakes inserted in the ground. The walls of the chambers were perpendicular to the ground. A nearby control plot of the same size was not shielded with the acrylic enclosure, but marked with a nylon thread placed on the ground and secured with metal pegs. Detailed descriptions of OTC properties, and its effects on air temperature, relative humidity, CO_2 concentrations, rain interception, and soil temperature and moisture, are provided in Chapter 2.

Each OTC and control plot was constructed around a pair of aspen and black spruce seedlings, for a total of 80 experimental individuals: 40 per species. At least 40 pairs of trees were identified at each site, from which we chose the experimental pairs and randomly assigned OTC treatment or control plot to each pair. The criteria for choosing the seedling pairs was that the distance between them must range from 10 to 60 cm; that their initial height must be between 20 and 80 cm; and that the difference in height between the seedlings within a pair is no more than 50 cm. The initial heights of all experimental seedlings were measured (cm) at the set up of the experiment in July 2005, and the analysis of variance (ANOVA) using a procedure MIXED in SAS (version 9.1, SAS Institute 2007) detected no initial height differences due to chance between the OTC and control plots. The diameters of the seedlings were initially measured at 5 cm above the ground surface in the summer 2006, and likewise, the analysis of variance detected no differences in diameters at that time between the OTCs and the control plots.

Effects of OTCs on growth in height and biomass of aspen and spruce seedlings

Seedling height data was collected in the spring (after snowmelt in early May) and towards the end of the growing season in late summer (August) of 2006 and 2007. Each seedling was measured from the ground surface up to the terminal tip. Percent change in height (% HC) since the experimental set-up in late June 2005 until the termination of the experiment in mid-August 2007 was calculated. As we were also interested in whether the height growth responses were consistent across the growing seasons, we also determined the % change in height between the initiation of the growing season immediately following the snowmelt, and towards the end of the growing season in August 2006 and 2007 (% HC_06 and % HC_07, respectively).

To compare the % HC responses between aspen and spruce, we performed the analysis of variance (ANOVA) (procedure MIXED in SAS, version 9.1; SAS Institute 2007), testing the effects of the explanatory variables including the OTC treatment (OTC, control), the species (aspen, spruce), the substrate type, (*Sphagnum*, non-*Sphagnum*) and the disturbance site type (fire, logging road, logging interval). The initial model involved testing the main effects and all interactions among the explanatory variables, on the responding variable % HC. All non-significant interactions ($p > 0.05$) were dropped in the final model. In the case of significant effects of the main factors or significant interactions, least-squares (LS) means were used to determine the levels differing and the direction of the difference.

As there were no replicates of the disturbance sites, no valid generalizations can be made regarding the overall effects of specific disturbance types on the growth responses we measured; nonetheless, we included site as a factor in the model to avoid inflation of the experimental error and thus, the possibility of a Type II error.

The same statistical procedures were followed for the responding variables of % HC_06 and % HC_07. Growth changes in the establishment year 2005 were not considered, since the instalment of the OTCs and control plots occurred in the middle of the growing season. Also, a certain time lapse was expected for the effects of OTCs to be manifested in terms of microclimatic conditions, as well as for the plants to respond to the treatment.

In mid-August 2007, all of the seedlings were harvested by clipping at the root collar point. The trees were subsequently dried at 60°C for five days, and the final total aboveground dry biomass, as well as the final total dry foliage biomass, were found for every sample. For spruce samples, we also determined the dry foliage biomass of the needles from the current growing season (2007, new), and of needles produced in previous years (before 2007, old).

The analyses of variance (ANOVA) using procedure MIXED in SAS (SAS Institute 2007), were performed to test the effects of the OTC treatment, the substrate type and the site (disturbance type), all as fixed factors, separately on responding variables including total aboveground biomass, total foliage biomass, and biomass of the new and old spruce needles. We performed these analyses individually for the two species, as we believed that inherent species differences in leaf structure, wood density and the overall morphology of the trees rendered separate analysis more appropriate and informative. Same ANOVA procedures were followed as for the analysis of % HC.

All data analyses were checked for the assumptions of normality and homogeneity of variance prior to analysis (SAS Institute 2007).

Effects of OTCs on abundance of vegetation and ground cover

Data on the vegetation present in each plot was collected at the beginning of July 2005, 2006, and 2007. All vascular plant species were identified at least to a genus level, and ascribed to one of the % cover categories, which included: 0 = absent; 1 = <5%; 2 =

5-25%; 3 = 26-75%; 4 = >75% (a modification of Braun-Blanquet's scale (Mueller-Dombois and Ellenberg 1974)). Percent cover of bryophyte species and humus were also recorded. The data was collected from above (i.e. "bird's eye view") therefore even if the frequency of individual species was low, its % cover and thus, relative influence in terms of e.g. shading effects within the plot, could be high.

As not all the species were present in all 40 plots, the data resulted in large number of zero (i.e. absent) values, leading to non-normal distribution. Accordingly, measurements of central tendency such as mean and median performed for all the plots did not present an optimal approach to reflect the presence and abundances of the species. Therefore, we decided to illustrate the trends of species presence and abundance descriptively, first by indicating the number of OTCs and control plots in which a given species was present, and then by summing the abundance values from all the plots in which the species was present.

Based on these preliminary descriptive analyses, we selected several species for which total abundances (i.e. sum of abundance values (0-4, see above) from all the plots) noticeably changed across the three growing seasons. To detect whether the direction and magnitude of the changing abundances differed in the OTCs and the control plots, and whether the changing abundances differed statistically across the years, we performed non-parametric analysis, with year (2005, 2006, or 2007) as a responding variable. The main goal of the analyses was to infer whether the abundances of the species changed over time, i.e. across the three growing seasons. This was tested separately for the OTCs and the control plots, and the consistency of the results between the OTCs and control plots was then compared. For example, if the abundance of a given species stayed unchanged in the control plots, but increased or decreased in the chambers, we could infer that the environmental modifications created by the chamber treatment contributed to shifting species abundances over time.

The analyses were performed using the NPAR1WAY procedure in SAS (SAS Institute 2007) and were performed separately for the OTCs and control plots as well as for each selected species. Since not all of the species we selected were present in all 40 plots to begin with, only the plots in which the species was present were included in the data analyzed. This was done to avoid large amount of zeros in the data, as it was not logical to assess changes in the abundance of species if it was never present in the plot. Since the data was not normal even upon removing the plots where the species was not present, we chose to perform non-parametric analysis. Wilcoxon scores were used to determine the scores expected under the null hypothesis (Ho, i.e. no differences in abundances across the three years), and the scores that were actually observed. The Kruskal-Wallis test was used to determine if there were any significant differences ($p>0.1$) across the three years.

Results

Growth in height and biomass of experimental aspen and spruce seedlings

In general, the seedlings inside the chambers grew significantly faster than those in the control plots. The final ANOVA model testing the effects of the OTC treatment, species, substrate type, and sites indicated highly significant effects of OTC treatment on the overall % HC since the start of the experiment in 2005 until tree harvest in 2007 ($p = 0.005$), as well as separately in seasons 2006 ($p = 0.004$) and 2007 ($p = 0.007$) (Table 4.1). However, significant interactions between OTC treatment and species revealed more precisely that in 2006, aspen grew significantly faster in OTCs than aspen and spruce in control plots ($p = 0.034$), while there were no significant differences in height increases of aspen and spruce in the OTCs, and no differences between height increase of spruce in the OTC versus both species in the control plots. Meanwhile, in 2007, the aspen in control plots grew significantly slower than any other combination of OTC treatment and species ($p = 0.040$), but there were no other significant differences among OTC treatment and species combinations. Overall, aspen increased significantly less in height in control plots than in chambers between 2005 and 2007 ($p = 0.019$) (Table 4.1).

There were no significant differences between the two species in % HC, though according to the means, the trends reversed from apparently higher growth increase of aspen in 2006 to apparently higher growth increase of spruce in 2007 (Table 4.1).
The *Sphagnum* and non-*Sphagnum* substrate types had no effect on the % HC of species in 2006, but in 2007 the seedlings increased significantly more in height at the non-*Sphagnum* substrate than the *Sphagnum* substrate ($p = 0.009$), and overall, the seedlings

grew more at non-*Sphagnum* substrate between 2005 and 2007 ($p = 0.035$). Finally, there were no differences in % HC between the three disturbance type sites.

There were no effects of the OTC treatment, substrate type, and disturbance site on the total aboveground biomass and total foliage biomass of aspen (Table 4.2). However, for spruce, OTC treatment indicated significantly higher total biomass ($p = 0.015$), total foliage biomass ($p = 0.019$), and biomass of foliage produced in the 2007 season ($p = 0.024$), as well as in the previous years ($p = 0.024$) (Table 4.2).

Changes in vegetation abundances in OTCs and control plots

Overall, we identified 25 vascular plants to species level and six vascular and bryophyte plants to genus level in the 40 experimental plots (Table 4.3; authorities for all species or genera are given in Table 4.3). On average, a given species (or genus) was present in 4.8 (standard deviation, [SD] = 5.2), 5.3 (SD = 5.3) and 5.2 (SD = 5.2) open-top chambers in 2005, 2006 and 2007 respectively. The maximum presence of a species/genus occurred in 17 out of 20 OTCs (*Gautheria hispidula* and *Polytrichum* species). In control plots, the species were present on average in 5.3 (SD = 5.0), 5.5 (SD = 4.8) and 5.4 (SD = 4.8) plots in 2005, 2006, and 2007 respectively. At maximum, *Polytrichum* moss was present in 19 out of 20 control plots. In general, mosses (*Polytrichum* species and *Sphagnum* species) as well as several shrubs of the ericaceous family (*Chamedaphne calyculata*, *Gautheria hispidula*, *Ledum groenlandicum*, and *Vaccinium angustifolium*) were present in most plots, and had among the highest abundances (Table 4.3).

Exploratory analysis of presence and abundance for each species in each year revealed overall minor shifts of species under OTC treatment conditions and in control plots (Table 4.3). Of the *Cyperaceae* (sedge) family, the abundances of *Carex* species in general became relatively higher in both the OTCs and the control plots across the three sampling seasons. In both cases, the number of plots in which *Carex* species were present increased, leading to a higher total abundance (Table 4.3).

Among the low herbaceous species, the abundance of *Cornus canadensis* increased noticeably in both OTCs and control plots, despite the relatively stable number of plots in which the species was detected. The increase in abundance in OTCs appeared to be higher in comparison to control plots. On the other hand, while the number of plots with the species present remained stable, the total abundances decreased for *Equisetum arvense* in OTCs and control plots, with the latter experiencing more noticeable decreases since 2005 (Table 4.3). *Smilacina trifoliata* was found in the same number of OTCs over the three years, but its total abundance increased in these plots over time; in addition, both the number of control plots and total abundance within control plots increased for this species (Table 4.3).

Among the numerous ericaceous shrubs and other low woody species, despite their generally high presence and abundance in plots, only *Kalmia angustifolia* and *Kalmia polifolia* appeared to have experienced noticeable shifts in abundances over the three summers. The presence of *Kalmia angustifolia* was detected in fewer OTCs in 2007 and its total abundance dropped, while the species was found in more control plots, leading to increase in total abundance. *Kalmia polifolia* was found in more OTCs and its total abundance increased, but its presence was detected in fewer control plots and total abundance dropped (Table 4.3).

As the presence and abundance of all the other species changed slightly over the three sampling seasons, we chose to perform non-parametric analysis for all the *Carex* species combined, *Cornus canadensis*, *Equisetum arvense*, *Smilacina trifoliata, Kalmia angustifolia* and *K. polifolia,* in order to determine if the apparent shifts in their abundances (as indicated by the % cover) were statistically significant, and whether they were of the same magnitude and followed the same direction in the OTCs as in the control plots. After removing from the data the plots in which the species was not present, the number of replicates for the selected species varied between five and 12, down from the original 20 replicates each for OTCs and control plots. Overall, the shifts in abundance of the analyzed species were larger in OTCs than in control plots. Out of the six species analyzed four experienced significant shifts in abundance over the three sampling years, while only species showed significant abundance change in the control plots (Table 4.4).

In terms of herbaceous vegetation, *Carex* species increased both in OTCs and control plots over the three years, but there was no significant difference across the three years in OTCs or control plots ($p = 0.316$ and $p = 0.206$ for OTC and control plots respectively). The abundances of the two forbs *Cornus canadensis* and *Smilacina trifoliata* showed opposite trends of response to OTC treatment: the abundance of *C. canadensis* experienced a highly significant increase in OTCs over the three seasons (p = 0.003), but stayed virtually unchanged in control plots (p = 0.767). The abundance of *S. trifoliata* changed slightly over the three years under the OTC treatment (p = 0.486), while in control plots the increase was on the verge of significance (p = 0.126). The abundance of horsetail, *Equisetum arvense*, decreased in the third sampling season, and significant differences were observed in control plots (p = 0.044), but not in OTCs (p = 0.387).

For the woody species, Wilcoxon scores and Kruskal-Wallis test indicated that the abundance of *K. angustifolia* was significantly higher than expected in 2005 and 2006 but lower than expected in 2007 in the OTCs (p = 0.100). In the control plots, the trends indicated lower abundance of *K. angustifolia* in 2005 and 2006, but higher in 2007, though the differences across the three years were not significant (p = 0.130). *Kalmia polifolia* had a significantly higher abundance in 2007 than in 2005 and 2006 in the OTCs, but in the control plots the trends indicated lower abundance in 2007 than in 2006 and 2005, though the differences were not significant across the three years (p = 0.360). Overall, the results for both *Kalmia* species indicate a decrease in the abundance of *K. angustifolia* in the OTCs and an increase in the control plots, while the opposite was true for *K. polifolia* across the three growing seasons between 2005 and 2007 (Table 4.4).

Discussion

Growth and biomass of aspen and spruce experimental seedlings

The growth and performance of a species is determined by its realized niche, curtailed from its unique fundamental niche by numerous complex interactions with abiotic and biotic factors (Hutchinson 1978; Pulliam 2000). Specific predictions of growth responses to open-top chamber treatment and the microenvironmental modifications associated with it, are thus expected to vary among species (Saxe et al. 2001), which is why the predicted climatic changes may be beneficial to some plants but detrimental to others. For example, differences in growth responses to experimental temperature manipulations have been noted between broadleaf deciduous and coniferous species (e.g. Tjoelker et al. 1998; Landhäusser et al. 2001), and among several species of coniferous trees (e.g. Lopushinsky and Max 1990).

In our study, the higher air temperature and drier soil conditions within the open-top chambers resulted in trends of increased height growth of trembling aspen and black spruce seedlings between July 2005 and August 2007. The significant interaction between OTC treatment and species revealed more precisely that the aspen was more responsive to OTC treatment than black spruce in terms of growth in height (Table 4.1). Interestingly, however, while the OTC effects on growth in height were weaker for spruce than for aspen, spruce final total biomass and needle biomass increased significantly under the OTC treatment (Table 4.2).

The differences in responses to OTC treatment in terms of magnitude and growth strategy between the two species are consistent with their inherent life strategies. Based on the classic three-strategy theory of Grime (1977), aspen has some characteristics of species that are competitive (fast growing; clonal perennial) and ruderal (fast growing; adapted to disturbed conditions), while black spruce would fit the description of stress-tolerant species (slow growing; tolerant to harsh environmental conditions). Our responses would support the classification of aspen as a pioneering ruderal species with opportunistic qualities; under the favourable growing conditions in the OTCs, aspen would put most of its resources into increasing the length of its stem, which supports the strategy of pioneer fast growing species competing for light. On the other hand, under the ameliorated OTC conditions, the spruce trees would allocate more energy and resources into producing more branches and foliage, as suggested by the higher final total and foliage biomass (Table 4.2).

The cold spring and cool summer of 2007, in comparison to the mild spring and warmer summer of 2006 (Chapter 2), support the evidence of intense and opportunistic responses of aspen to favourable growing conditions. In 2006, aspen in the OTCs grew faster than any other OTC treatment-species combination. However, in 2007, the significant interaction between the OTC treatment and species revealed that there were no differences between the growth rates of aspen and spruce seedlings in the chambers;

significant OTC effect in 2007 was mostly a result of the lower growth rates of aspen in control plots in comparison to all the other OTC treatment-species combinations.

Despite cooler soil conditions under the OTC treatment (Chapter 2), aspen grew more in the chambers than in the control plots, which suggests that the positive effects of the elevated air temperatures prevailed over the potentially negative effects of cooler soils in terms of aspen growth. Inherently cold, nutrient-poor, and wet *Sphagnum*-dominated habitats are not usually the prime sites for trembling aspen, but they are commonly associated with the presence of black spruce. Consequently, the initially observed positive growth response of aspen to the OTC treatment may be a short term impulse reaction of the generally fast growing and fast responding species to a sudden amelioration of environmental conditions.

Though the positive effects of elevated air temperatures on the growth rate of aspen had initially prevailed, in the long run, cooler soils may ultimately curb this accelerated growth. In comparing growth characteristics (including leader length, dry mass of roots, shoots, and leaves) for aspen and white spruce seedlings grown under 5, 15 and 25°C soil temperatures, Landhäusser et al. (2001) found that cold soils had a more suppressing effect on trembling aspen than they had on white spruce. The authors concluded that spruce is overall more tolerant to low soil temperature, likely due to a more conservative use of non-structural carbohydrate reserves. Overall then, cooler soils may have a much stronger negative effect on aspen than on black spruce, which is also known to be well adapted to cool soil temperatures (e.g. Van Cleve et al. 1983).

On the other hand, decreased soil moisture (observed under the OTC treatment; Chapter 2) in wet boggy habitats may actually become favourable to aspen growth in NW Quebec. In a study of drought impact on forest growth and regeneration in Yukon, Hogg and Wein (2005) concluded that growth of post-fire regenerating aspen is strongly and positively related to precipitation, and thus, the predicted drier climate could significantly slow down its regeneration. However, in the less dry climate of eastern Canada, climate change-related soil drying in wet, boggy habitats may become more suited to the physiological adaptations of aspen. Ultimately, the balance in terms of the negative effects of cooler soil, but potentially positive effects of drier soil and warmer air, will determine the long term responses of aspen to the changing climate of the transitional mixedwood-boreal zone in NW Quebec.

The prognosis of drier soils may also have a positive effect on the growth of black spruce in the future. The lack of strong height growth response of black spruce to microenvironmental modifications supports the stress-tolerant nature of the species. Although black spruce is often associated with poorly drained, cool, thick and nutrient-poor *Sphagnum* mats (Van Cleve et al. 1983; Fenton and Bergeron 2007), the tolerance of species to certain abiotic environmental conditions does not necessarily indicate that these are the optimal conditions for the species' growth. As such, the presence of black spruce in wet, nutrient-poor habitats may indicate its tolerance to such conditions, but this realized niche might not represent the optimal growing conditions of the species. Indeed, Islam and Macdonald (2004) concluded that in comparison to tamarack (*Larix laricina* (Du Roi) K. Koch), another conifer often associated with wet habitats, black spruce was poorly adapted both morphologically and physiologically to prolonged flooding conditions, which are typical of the peatland habitats where black spruce is commonly found. In their experiment assessing the responses of black spruce and tamarack seedlings to flooding conditions, Islam and Macdonald (2004) found that tamarack seedlings developed adventitious roots, whereas black spruce seedlings did not; moreover, black spruce showed lower root hydraulic and stomatal conductance and increased needle electrolyte leakage compared to tamarack. Thus, in the long run, drier soil may actually have a positive effect on growth and regeneration of black spruce.

As a high-stress tolerant and low-nutrient requiring species, black spruce may also cope better with the potentially decreased levels of available nutrients than high-nutrient requiring aspen. The initially strong OTC treatment growth response of aspen, which is generally known to have a high requirement for nutrients, and in particular, calcium (Coyne and Van Cleve 1977; Alban et al. 1978; Alban 1982; Van Cleve et al. 1983; Bates et al. 1992), may be curtailed by nutrient limitations. Lower Ca and Mg levels inside the chambers (Chapter 3) may have been associated with accelerated plant nutrient uptake, which could be reflected in higher growth rates of aspen. However, the cooler and drier soil conditions in the chambers also led to decelerated decomposition rates (Chapter 3), which may ultimately reduce nutrient availability to aspen.

Although aspen is considered an early successional, shade-intolerant colonizer of post-disturbance sites (Perala 1990; Paré et al. 2001), in the mixedwoods of NW Quebec it may essentially become a climax species, with a mixedwood stand structure maintained in a quasi-equilibrium through continuous small-scale disturbances, leading to presence of multiple cohorts of aspen mixed with conifers such as black spruce (Bergeron 2000). However, the presence of aspen at the later stages of succession in the mixedwoods of NW Quebec could be curtailed by anticipated future climatic changes involving cooler and more nutrient-poor soils. The fact that aspen responded with equal magnitude, but the opposite directions to favourable and unfavourable environmental conditions suggests that when the growing conditions deviate from the expected physiological optimum of aspen, the positive responses are no longer observed, leaving the species under physiological stress, and thus making it more prone to secondary negative impacts such as diseases and pest outbreaks. Therefore, in the long run, the slower and less intense responses of black spruce to climatic changes may put this species at an advantage over the rapid positive responses of aspen.

Effects of OTCs on vascular vegetation: potential changes of competitive interactions

Inherent physiological adaptations and plant life strategies will play a major role in the regeneration process of trembling aspen and black spruce under the changing climate. However, interactions with the biotic component of their habitat may greatly modify these responses. This includes competitive interactions of the regenerating seedlings with the coexisting plant species. Competition of young black spruce trees with numerous plant species have been reported before, including shrubs such as *Alnus rugosa* (DuRoi) Spreng. (Walker and Chapin 1986; Munson and Timmer 1989) and *Kalmia angustifolia* L. (Yamasaki et al. 1998); graminoid-like species such as *Carex* (Munson and Timmer 1989); and trees such as *Betula paperifera* Marsh. and *Larix laricina* (Du Roi) K. Koch (Roy et al. 2000). Likewise, trembling aspen trees may compete in the early stages of regeneration with shrubs such as *Rubus idaeus* L. (Roy et al. 2000). All of these species were present at our sites.

We suspected that the competitive interactions among the plant species coexisting with our experimental seedlings may change under the open-top chamber treatment, due to unpredicted shifts in the abundance of other plant species. Such shifts in the dominance and abundance of existing plant species and/or plant forms within a community have been reported in climate change simulation studies. For example, following 5-7 years of experimental warming using OTCs, Hollister et al. (2005) reported decreases between 1.4 and 4.6% in moss species, with simultaneous increases in standing dead plant mass and graminoids. Meanwhile, Jónsdóttir et al. (2005) found that after five years of experimental warming in the dwarf shrub communities of Iceland, evergreen and deciduous dwarf shrubs increased in abundance by 50%, while bryophytes decreased by 18%. Also, a meta-analysis of 11 open-top chamber experiments as part of the International Tundra Experiment (ITEX) revealed that responses of tundra plant communities to 1-3^{o} C temperature increase were observed within two growing seasons, and OTC treatment resulted in increased height and cover of deciduous shrubs and graminoids (Walker et al. 2006). In studies researching abundance shifts along natural environmental gradients, evidence of increases in shrub abundance at high latitudes comes from Alaska, where the air temperatures have increased ~ 6^{o} C over the past 30 years (Sturm et al. 2001, 2005). Overall then, the responses to climate change, or the experimental simulations of it, indicate the most pronounced abundance increases of shrubs and graminoids and decreases of bryophytes and lichens.

However, the artificial modifications introduced by the instalment of open-top chambers had little effect on species abundances over the 2.5 growing seasons in our experiment (Table 4.3). Among the ~ 30 species identified in our plots, noticeable changes in plant cover abundances were observed for the sedges (*Carex* species), two forbs (*Cornus canadensis* and *Smilacina trifoliata*), one fern ally (*Equisetum arvense*), and two shrubs (*Kalmia angustifolia* and *K. polifolia*) (Tables 4.3 and 4.4). The responses of these species to OTC varied, even within the same genus, as seen for the *Kalmia* species.

Often small in stature herbaceous and grassy species of northern habitats may have less of a competitive advantage in aboveground competition for light with the bigger tree seedlings; however, the increased abundance of forbs, grasses and sedges, which often have extensive and dense root systems, may result in more intense competition for belowground resources. This may have a profound impact on high-nutrient requiring species such as aspen. Indeed, Hobbie and Chapin (1998) observed that the growth and survivorship of aspen seedlings transplanted into Arctic tundra increased substantially upon experimental reduction of belowground competition; Landhäusser and Lieffers (1998) reported that root competition of grass species *Calamagrostis canadesis* (Michx.) P. Beauv. significantly reduced the total biomass, plant height, and root collar calliper of aspen; and Landhäusser et al. (2007) claimed that the roots and litter of *Calamagrostis canadesis* reduced or delayed the expansion of aspen suckers.

Increase in abundance of *Carex* species both inside and outside of open-top chambers indicate that although the OTC treatment may not have had a strong positive effect on sedge abundance *per se*, present and potential future climatic changes are within the ranges of positive growth responses of these species. As such, our results are consistent with the numerous reports of positive responses of these plants to climate warming at high latitudes and altitudes (e.g. Arft et al. 1999; Walker et al. 2006). With regard to potential effects of interactions with regenerating aspen and spruce seedlings, this could offset to some extent the accelerated growth rates of aspen under the OTC treatment, likely due to increased belowground root competition. On the other hand, the extensive cover of *Carex* species may interfere with aboveground growth and development of black spruce seedlings (e.g. Munson and Timmer 1989). Inherently slow growing species such as black spruce may be more affected by the potential shading effects of some larger species of *Carex* (Munson and Timmer 1989). Overall, the trends of increases in abundance of sedges could substantially affect the competitive strength of aspen and spruce seedlings, though the ultimate impact of these effects would depend on the relative importance of the underground versus aboveground competition, which in turn depends on soil nutrient and water availability.

Potential warming may also have a positive effect on the growth and abundance of *Equisetum arvense*. A decrease in abundance of *E. arvense* in and out of the OTCs indicates that perhaps the overall cooler night conditions in the spring of 2007 (in comparison to 2005 and 2006; Chapter 2), were detrimental to this species. The weaker negative response in terms of abundance observed in the OTCs than in control plots in 2007 (Tables 4.3 and 4.4) support the evidence of positive effects of higher temperatures on *E. arvense.*

For *Kalmia angustifolia,* it is possible that either the growing conditions under the OTC treatment became less favourable or that the growing conditions in control plots became more favourable. It is also possible that its competitive interactions with closely related *K. polifolia* have changed, with that species becoming a superior competitor under the OTC conditions, and thus causing a displacement of *K. angustifolia.* This could explain the decreases in abundance of *K. angustifolia* and increases of *K. polifolia* in the open-top chambers. Segregation with respect to environmental conditions of closely related species, likely due to competitive interactions, have been reported before, e.g. for *Carex* species in the fens of northeastern Quebec (Dabros and Waterway, in press) or for *Typha angustifolia* and *Typha latifolia* (Grace 1981).

Shifts in the abundance of *Kalmia angustifolia* may have serious effects in terms of competitive interactions with our experimental black spruce seedlings, as it is known that *K. angustifolia* may interfere with the black spruce regeneration process by allelopathic modifications of soil chemistry and microbial activity (e.g. Bradley et al. 1997; Yamasaki et al. 1998). Decreased abundance of *K. angustifolia* in the open-top chambers indicated that potential climatic temperature increases (as simulated by our OTC treatment) would not be favourable for this ericaceous species, and consequently could be beneficial for black spruce regeneration.

The fact that the abundance of the majority of the species we studied were not visibly affected after 2.5 growing seasons under the OTC treatment indicates that the length of the treatment was not long enough, strong enough, or a combination of both, to induce noticeable responses. This suggests that the forest and bog species of the mixedwood-boreal region have a certain degree of resistance to changing growing conditions, as is expected of species residing under harsh environmental settings (Chesson and Huntly 1997), or that they have generally wide environmental tolerance ranges. In that respect, predicted climatic changes may have less of a drastic and immediate effect on these species.

Alternatively, it is possible that the positive or negative responses to the OTC treatment were expressed by life events other than abundance pertaining to plant performance, which we did not measure in this study. Allocation of resources towards reproductive structures, chemical foliar composition, herbivory defence mechanisms, and belowground biomass are some such examples, and depending on plant species, growth responses will be expressed differently in terms of these factors. Differences in responses to our OTC treatment between aspen and spruce seedlings illustrate well that different plant species respond uniquely to changes in environmental growing conditions.

Conclusion

The effects of open-top chambers on the growth and biomass of trembling aspen and black spruce may have captured the initial responses of the two species to potential future climatic changes at post-disturbance sites in NW Quebec. Warm and wet growing seasons (i.e. predicted climatic changes in NW Quebec) appear to present environmental conditions favourable towards the physiological tolerance levels of aspen. However, given the erratic and often unpredictable weather conditions associated with climate change, the restriction of positive growth responses of aspen to only favourable growing condition years may put it at a disadvantage over the long term. On the other hand, less sensitivity of black spruce to both the inter-seasonal weather variations and the simulated climatic changes may ultimately ensure the regeneration success, growth, and persistence of black spruce over the long term. Positive growth responses of black spruce, although perhaps slower and smaller that those observed for aspen, were nonetheless continuous. Ultimately, the future success of the two species will depend on the net outcome of positive and negative growth responses to changing climate, and the inter-seasonal variations associated with it. Due to its greater responsiveness to variations in environmental conditions, the future of aspen in NW Quebec is thus less predictable than that of black spruce.

Tables

Table 4. 1 Effects of the OTC treatment (open-top chamber [OTC], control [C]), species (trembling aspen [ASP], black spruce [SPR]), substrate type (*Sphagnum* moss presence [S] or absence, non-*Sphagnum* [NS]), and site (fire [F], logging road [LR], logging interval [LI]) on % change in height over the growing seasons 2006 and 2007 (May-August), and between July 2005 and August 2007.

	2006			**2007**			**2005-2007**		
	F value	*P*>F	Means**	F value	*P*>F	Means	F value	*P*>F	Means
OTC	**8.78**	**0.004***	**C<OTC**	**7.73**	**0.007**	**C<OTC**	**8.28**	**0.005**	**C<OTC**
species	1.37	0.246	SPR<ASP	2.97	0.089	ASP<SPR	0.45	0.506	ASP<SPR
substrate	2.30	0.134	S<NS	**7.37**	0.009	**S<NS**	**4.62**	0.035	**S<NS**
site	1.42	0.249	LR<LI<F	2.44	0.095	LR<LI<F	0.88	0.420	LR<F<LI
OTC*species	**4.66**	**0.034**	C*ASP<C*SPR <OTC*SPR <OTC*ASP **C*ASP, C*SPR <OTC*ASP**	**4.41**	**0.040**	C*ASP<C*SPR <OTC*SPR <OTC*ASP **C*ASP< OTC*SPR, OTC*ASP**	**5.80**	**0.019**	C*ASP<C*SPR <OTC*SPR <OTC*ASP **C*ASP< OTC*ASP**

*Significant results are in bold.

**Treatment level means, showing consistency of general trends.

Table 4. 2 Effects of the OTC treatment (open-top chamber [OTC], control [C]), substrate type (*Sphagnum* moss presence [S] or absence, non-*Sphagnum* [NS]), and site (fire [F], logging road [LR], logging interval [LI]) on total aboveground dry biomass and total foliage biomass for trembling aspen and black spruce, and, for black spruce only, foliage biomass of season 2007 (new foliage) and before 2007 (old foliage).

		Aspen			**Spruce**		
Responding variable	Explanatory variable	F value	*P*> F	Means	F value	*P*> F	Means
total aboveground biomass	OTC	0.00	0.947	C=OTC	**6.58**	**0.015**	**OTC<C**
	substrate	2.66	0.114	S<NS	1.83	0.185	S<NS
	site	0.41	0.668	LR<F<LI	0.84	0.440	F<LR<LI
total foliage biomass	OTC	0.05	0.823	C<OTC	**6.05**	**0.019**	**OTC<C**
	substrate	1.75	0.196	S<NS	1.40	0.245	S<NS
	site	0.37	0.693	LR<F<LI	0.53	0.593	F<LR<LI
new foliage	OTC	-	-	-	**5.56**	**0.024**	**OTC<C**
	substrate				2.03	0.163	S<NS
	site				0.46	0.638	F<LR<LI
old foliage	OTC	-	-	-	**5.60**	**0.024**	**OTC<C**
	substrate				0.86	0.360	S<NS
	site				0.55	0.579	LR<F<LI

*Significant results are in bold.
**Treatment level means, showing consistency of general trends.

Table 4. 3 Presence and abundance of vegetation and humus (in alphabetical order) in 20 open-top chambers and 20 control plots in July 2005, July 2006 and July 2007 at the fire and the logging sites in NW Quebec. All species (spp.) were identified at least to a genus level, and ascribed into one of the % cover categories including: 0 = absent; 1 = <5%; 2 = 5-25%; 3 = 26-75%; 4 = >75%. Sum total abundance is the sum of values of % cover categories in all the plots in which the species was present.

Species	Open-top chambers						Control plots					
	Number of plots with species present			Sum total abundance in all plots			Number of plots with species present			Sum total abundance in all plots		
	2005	**2006**	**2007**	**2005**	**2006**	**2007**	**2005**	**2006**	**2007**	**2005**	**2006**	**2007**
Alnus crispa (Aiton) Pursh.	0	0	0	0	0	0	1	1	1	1	3	1
Andromeda glaucophyla Link	0	1	0	0	1	0	1	1	1	1	1	1
Carex spp. L.	**4**	**6**	**7**	**9**	**15**	**20**	**6**	**6**	**9**	**16**	**21**	**30**
Carex canescens L.	0	1	3	0	3	3	1	2	4	1	5	8
Carex disperma Dewey	0	1	0	0	2	0	1	1	0	1	1	0
Carex magellanica Lam.	0	1	1	0	1	2	3	2	4	6	2	6
Carex pauciflora Lightf.	1	1	1	2	2	2	2	2	2	4	3	4
Carex trisperma Dewey	3	6	4	11	12	10	4	6	4	11	17	10
Carex vaginata Tausch	0	0	0	0	0	0	1	1	1	1	2	3
Chmaedaphe caluculata (L.) Moench	7	7	6	14	15	14	6	5	5	12	10	11
Cornus canadensis L.	**6**	**6**	**7**	**13**	**11**	**21**	**5**	**6**	**5**	**8**	**10**	**12**
Epilobium anugustifolium L.	2	3	2	2	3	3	4	5	5	7	6	5
Equisetum arvense L.	**8**	**9**	**9**	**25**	**27**	**19**	**11**	**11**	**11**	**29**	**27**	**20**
Equisetum silvaticum L.	1	2	3	3	4	5	3	4	4	3	4	7
Fragaria virginiana Duchesne	0	0	0	0	0	0	1	1	1	2	3	3
Gaultheria hispidula (L.) Mulhl	17	17	15	41	38	36	14	13	13	31	28	31
Poa spp. L.	2	0	0	3	0	0	4	2	4	5	3	5
Humus	9	10	9	25	23	26	9	10	8	21	19	17
Kalmia angustifolia L.	**6**	**6**	**3**	**10**	**10**	**3**	**2**	**2**	**5**	**2**	**2**	**8**
Kalmia polifolia Wangenh.	**5**	**5**	**9**	**5**	**5**	**14**	**4**	**4**	**2**	**7**	**5**	**2**
Ledum groenlandicum Oeder	13	16	15	30	32	30	12	14	12	21	23	24
Petasites palmatus (Aiton) Gray	1	1	2	1	2	2	2	4	1	2	5	3
Polytrichum spp. Hedwig	15	17	15	35	45	34	19	15	19	51	48	60
Rosa acicularis Lindley	1	1	1	2	1	1	1	1	1	1	2	1
Rubus chmaemorus L.	1	5	4	3	6	6	2	2	2	4	4	5
Rubus idaeus L.	1	1	1	1	1	1	1	1	1	4	4	4
Salix spp. L.	6	7	6	9	11	7	10	12	10	19	17	17
Scriptus spp. L.	3	1	1	6	1	3	4	3	2	8	8	5
Smilacina trifoliata (L.) Desfontaines	**6**	**6**	**6**	**12**	**12**	**15**	**3**	**4**	**5**	**5**	**7**	**13**
Sphagnum spp. L.	17	14	16	48	44	52	16	16	13	49	48	44
Vaccinium angustifolium Aiton	13	14	15	23	29	33	13	14	14	22	27	32
Vaccinium oxycocus L.	4	4	4	6	8	12	5	5	5	5	5	8

Table 4. 4 Kruskal-Wallis analysis testing the differences in abundances (measured as % cover categories) over the three sampling seasons in July 2005, 2006 and 2007, at the fire and logging sites in NW Quebec, in open-top chambers and control plots.

			Wilcoxon scores				Kruskal-Wallis Test	
		*n**	Sum of scores under Ho	Sum of scores observed **			Chi-square	*P* > Chi-square
	Species			2005	2006	2007		
OTC	*Carex* spp.	10	155	>126	<158	<182	2.30	0.316
	Cornus canadensis	**7**	**77.0**	**>61.0**	**>51.0**	**<119**	**11.6**	**0.003*****
	Equisetum arvense	10	155	>150	<184	>132	1.90	0.387
	Kalmia angustifolia	**8**	**100**	**<117**	**<117**	**>67.0**	**4.58**	**0.101**
	Kalmia polifolia	**11**	**187**	**>158**	**>158**	**<245**	**6.27**	**0.044**
	Smilacina trifoliata	6	57.0	<51.0	>51.0	<69.0	1.45	0.486
Control	*Carex* spp.	11	187	>151	>183	<228	3.16	0.206
	Cornus canadensis	9	126	>114	<128	<137	0.53	0.767
	Equisetum arvense	**11**	**187**	**<225**	**<208**	**>128**	**6.24**	**0.044**
	Kalmia angustifolia	8	100	>86.0	>86.0	<128	4.02	0.140
	Kalmia polifolia	7	77.0	<88.5	<82.5	>60.0	2.04	0.360
	Smilacina trifoliata	5	40.0	>28.5	>36.0	<55.5	4.14	0.126

*Number of samples used, i.e. the plots (out of possible 20), in which the species was present at least once over the three sampling years.

**Direction and magnitude of the differences across the three years, with '>' and ' <' signs indicating the observed scores to be smaller and larger, respectively, than expected under Ho.

***Significant differences detected at $\alpha = 0.10$ are in bold.

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Connection of Chapter 4 with Chapter 5 and the thesis in general

In **Chapter 4** we assessed the height growth responses and aboveground biomass accumulation of trembling aspen and black spruce seedlings, to the simulated climatic changes provided by open-top chambers. We found that the height growth of aspen in the OTCs was significantly larger than in control plots in the warm growing season of 2006, but the positive growth response was weaker in the cooler growing season of 2007. We also found that the OTCs had no effect on height growth of black spruce in either of the growing seasons, but final dry biomass was higher for spruce growing in the chambers. In **Chapter 5** we explore what factors might have resulted in the observed growth and biomass responses of aspen and spruce seedlings to OTC treatment. Firstly, we compare the timing of spring phenological events inside and out of open-top chambers. Secondly, we explore the effects of OTCs on foliar and root nutrient concentrations of aspen and spruce. Thirdly, we explore the effects of chambers on insect herbivory of aspen leaves, predicting that the change in the quality of aspen leaves in OTCs could alter the magnitude of insect herbivory.

With respect to previous chapters of the thesis, we use the results of the effects of OTCs on microclimatic, soil physical properties and biogeochemical processes to interpret the growth and biomass responses of aspen and black spruce, and try to place them in the larger context of how this may represent a potential scenario of climate change impact on regeneration of the two tree species at disturbed sites in the mixedwood-boreal transitional zone of northwestern Quebec.

CHAPTER 5: Effects of open-top chambers on spring phenology and nutrient concentrations of aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* Miller (BSP)) seedlings at disturbed sites in the mixedwood-boreal northwestern Quebec

Abstract

Open-top chambers (OTCs) were used to investigate the complex network of factors associated with the potential role of climate change on the growth and performance of young trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* Miller (BSP)) regenerating at disturbed sites of the transitional mixedwood-boreal forest zone in the James Bay region of NW Quebec. In this study, we focused on the factors which led to the increased height growth responses of aspen and increased final total dry biomass of spruce growing in OTCs between July 2005 and August 2007. We explored the effects of OTC treatment on spring bud burst, bud and leaf development, as well as foliar and root nutrient concentrations. We also compared the degree of foliar insect herbivory for aspen growing in and out of open-top chambers. Under the OTC treatment (higher air temperatures [2-3°C]; drier [up to 10% volumetric moisture content] and cooler soil [up to 2.6°C]), aspen experienced significantly earlier bud break in spring 2006, but not in spring 2007, which had noticeably more nights with temperatures below the freezing point than did 2006. For black spruce, bud burst and development were advanced by 2-3 days in the open-top chambers in spring 2007. With the exception of higher foliar Ca concentrations and lower root Ca concentrations, there were no effects of OTC treatment on nutrient levels for either species. Foliar insect herbivory was significantly reduced in OTC aspen in 2006 and 2007. Overall, the results of the open-top chamber treatment suggest that the potential climatic changes would likely lead to spring phenological advancement and structurally stronger foliage, resulting in increased growth and performance of both species. However, the growth and performance response of trembling aspen would be less predictable and more variable, ranging from strongly positive to negative, depending on inter-seasonal weather variability. Conversely, black spruce would experience a more balanced and conservative, continuously positive growth response, which could give the species a long term advantage in terms of regeneration at post-disturbance sites of NW Quebec under changing climate conditions.

Introduction

Temperature influences tree growth directly by affecting the physiological processes, and indirectly by affecting decomposition rates and nutrient availability (Kirschbaum 2000; Saxe et al. 2001; Walther 2003). Climatic changes over the last century, marked by a substantial and continuing rise of greenhouse gases, and consequently, global mean temperatures, affect numerous interdependent environmental factors, from rain and snow precipitation regimes and snowmelt and soil freeze-thaw cycles, to soil moisture and temperature, which influence decomposition and nutrient cycling (IPCC 2007). In northern ecosystems, where the climatic changes are expected to be the most pronounced on a global scale (ACIA 2004; IPCC 2007), the warming of the atmosphere is predicted to result in increased growth of northern tree species (Bergh and Linder 1999; Melillo et al. 2002; Strömgren and Linder 2002). Ultimately, however, this phenomenon may be limited by water and nutrient availability, especially nitrogen (Oren et al. 2001; Melillo et al. 2002).

The annual growth of boreal trees is predominantly determined by nutrient uptake in the summer, CO_2 capture in the spring, and the timing of spring thaw and autumn freeze (Jarvis and Linder 2000). Therefore, from a phenological point of view, earlier snowmelt may be considered an extension of the growing season, allowing for earlier bud break and growth initiation, and thus resulting in increased stem growth and biomass accumulation over the season. In a global meta-analysis on climate change impacts on natural systems, Parmesan and Yohe (2003) reported that 62% of the 677 assessed plant and animal species have shown trends of advanced phenology in the spring, with a mean forward shift of 2.3 days in the timing of spring life events. Such advancement of over two days in spring growth initiation may have a profound impact on species performance over the season. Nutrient uptake and the resulting tissue nutrient concentrations and growth could be substantially altered, disrupting the balance of plants' numerous interactions with the surrounding abiotic and biotic factors of their environment, including: water uptake and evapotranspiration processes, quality and quantity of litter produced, subsequent decomposition rates, and plant-insect interactions such as herbivory.

Longer growing seasons could allow for increased nutrient uptake and thus increased growth rates. However, several interactive processes could interfere with plant growth. Firstly, a nutrient dilution effect (Cotrufo et al. 1998; Zak et al. 2000; Johnson et al. 2001) of faster growing trees could lead to decreased leaf litter quality, decomposition rates, and consequently, nutrient availability, thus slowing down increased growth rates over the long term. Secondly, climate change-related tissue nutrient dilution, or increase in tissue nutrient concentrations could alter plant-insect herbivory interactions.

Such a chain of reactions presents one example of the complexity and interdependence of ecosystem responses to changing climatic conditions. Furthermore, the magnitude and nature of these processes will vary among the species, affecting some plants more than others. While for some species, the changing conditions will be detrimental, for others they will be beneficial, promoting their growth and survival. With the climate-related changes affecting microclimatic and biogeochemical factors, the growing conditions of the habitats previously not suited for growth of certain species may now become more favourable. This may result in an increased abundance of existing populations, or the potential expansion of species into new areas.

A changing climate could be one of the factors contributing to such community compositional transformations, which have been predicted and observed already, including in the transitional zones of boreal forest-tundra biomes (e.g. Sturm et al. 2001, 2005; Walker et al. 2006). In northwestern Quebec, populations of trembling aspen are presently regenerating and persisting successfully at the northern extremes of their regional distribution (Toribio Fajardo 2005; Laquerre 2007).With the ongoing climatic warming in this region (Thesis Introduction; Lefort 2003), increase in hardwood species and expansion of mixedwood forests into boreal regions of NW Quebec is possible (Bergeron et al. 2004). Our project investigates the complex network of factors associated with the potential effect of climate change on the growth and performance of young trembling aspen and black spruce at disturbed sites along the transitional mixedwood-boreal forest zone in James Bay region, NW Quebec. Climate change was simulated using open-top chambers (OTCs), following a modified design of the International Tundra Experiment (ITEX) (Marion and Pidgeon 1992).

The general objective of this study was to explore the potential factors which lead to initially higher growth rates of aspen and higher final dry biomass of spruce growing in open-top chambers. Firstly, we considered the possibility that earlier snowmelt in OTCs (Chapter 2) allowed for earlier bud break, presumably prolonging the growing season and resulting in higher stem grown and biomass accumulation of seedlings. Secondly, we explored the effects of OTCs on foliar and root nutrient concentrations of aspen and spruce. Thirdly, we explored the effects of OTCs on insect herbivory of aspen leaves, predicting that the changes in nutrient concentrations, and thus the quality of aspen leaves in OTCs could alter the magnitude of insect herbivory damage.

We discuss our results in the context of potential climatic change impact on growth and performance of trembling aspen and black spruce currently regenerating at disturbed sites in the transitional mixedwood-boreal forest zone of northwestern Quebec.

Materials and Methods

Study site

The study area (49°37’ N; 79°00’ W) was found in the boreal mixedwood-black spruce transitional forest zone in James Bay, which constitutes part of the Clay Belt physiographic region spanning northwestern Quebec and northeastern Ontario. A detailed description of the region, including geological background, climate, and current vegetation is provided in the general introduction of this thesis and the first two chapters.

We identified three study sites spanning 20 km along the Selbaie road (from 49°37’ N; 78°59’ W to 49°45’ N; 79°02’ W) which was constructed between 1977 and 1980 to allow access to the Selbaie copper mine located at km 92 (S. Galarneau, personal communication, Ministère des Ressources naturelles et de la Faune du Québec, La Sarre, Quebec). Our three study sites consisted of a salvage logged post-fire site, a logging road created to facilitate timber harvest, and the actual post-logging site, where the timber harvest took place. At all of the sites, the disturbance occurred in years 1996-1997. Detailed descriptions of the sites, including dominant vegetation and soil texture and drainage information, are provided in the general introduction of this thesis.

Experimental design

In total, 40 experimental plots were set up: 20 open-top chambers and 20 control plots. At the fire site there were eight OTCs and eight control plots; at the logging road site there were also eight OTCs and eight control plots; and, at the logging interval site there were four OTCs and four control plots. At each site, every OTC was paired with a control plot established in a close proximity.

To test the responses to OTC treatment in the presence or absence of live *Sphagnum* moss at the fire and logging road sites, eight pairs of OTC and control plots were established on each site where the dominant substrate consisted of *Sphagnum* moss, and another eight pairs where the substrate was dominated by sparse *Polytrichum* moss growing on mixture of humus and mineral soil. The substrate and the OTC treatment at the fire and logging road sites were crossed factorial: four OTCs and four control plots at *Sphagnum*-dominated substrates, and four OTCs and four control plots at non *Sphagnum*-dominated substrates, for a total of sixteen plots per site. At the logging interval site, four pairs of OTC and control plots were all set up on live *Sphagnum* moss.

At each of the three sites, for the plots receiving an open-top chamber treatment, we constructed a circular enclosure, 1 m in diameter and 0.75 m in height, built of clear transparent 8 mm thick polymethylmethaacrylate (PMMA, commonly known as acrylic) material. The construction of the chambers took place between June 28 and July 1, 2005, and the chambers were not removed until mid-August of 2007. Two flexible PMMA sheets were connected with tie-wraps and supported in two places by plastic stakes inserted in the ground. The walls of the chambers were perpendicular to the ground. A nearby control plot of the same size was not shielded with the acrylic enclosure, but marked with a nylon thread placed on the ground and secured with metal pegs. Detailed descriptions of OTC properties, and its effects on microclimatic conditions including air temperature, relative humidity, CO_2 concentrations, rain interception, and soil temperature and moisture are given in Chapter 2.

Each OTC and control plot was constructed around a pair of aspen and black spruce seedlings, for a total of 80 experimental individuals: 40 per species. At least 40 pairs of trees were identified at each site, from which we chose the experimental pairs and randomly assigned OTC treatment or control plot to each pair. The criteria for choosing the seedling pairs was that the distance between them must range from 10 to 60 cm; that their initial height must be between 20 and 80 cm; and that the difference in height between the seedlings within a pair is no more than 50 cm. The initial height of each experimental seedling was measured (cm) at the set up of the experiment in July 2005, and the analysis of variance (ANOVA) using procedure MIXED in SAS (version 9.1; SAS Institute 2007) detected no initial height differences due to chance between the OTC and control plots. The diameters of the seedlings were initially measured at 5 cm above the ground surface in the summer 2006, and likewise, the analysis of variance detected no differences in diameters at that time between the OTCs and the control plots.

Phenology

Preliminary spring phenological data was recorded in May 2006, during aspen bud burst (defined by us as phenological stage 1 for aspen, see below). The last snowfall and snowmelt of the 2006 season occurred between May 4 and 6, and the presence or absence of bud burst was recorded for every aspen seedling at one week, 10 days, and two weeks following the last snowmelt. The tree was considered to have reached stage 1 if at least one bud burst was observed.

In the 2007 growing season, we observed and recorded bud burst, development, and leafing phenological events for both aspen and spruce on May 12-14, 16-18, 21-23 and 25-27. On May 9, all aspen buds were still closed. We defined four distinctive stages of bud development and leaf emergence for aspen (Table 5.1). To determine the bud developmental stages of black spruce, we followed the six stages identified by Numainville and Desponts (2004) (Table 5.1).

Logistic regression analyses (Hosmer and Lemeshow 2000; McCullagh and Nelder 1985) were performed using procedure LOGISTIC in SAS (version 9.1; SAS Institute 2007) to predict the probability of a positive response for each phenological stage on each given day, as a linear function of explanatory variables of OTC treatment (OTC versus control [C]); substrate type (*Sphagnum* [S] versus non-*Sphagnum* [NS]); and site (logging road [LR], logging interval [LI] and fire [F]). The response for the model was binary, i.e. the phenological stage (e.g. bud burst) was either reached (positive response) or not reached (negative response). The analysis of maximum likelihood estimates yielded parameter estimates for every explanatory variable, and Wald chi-square statistics with associated *p*-values were used to test the null hypothesis of no effects of explanatory variables. Interactions between the three variables were tested and removed from the model if not significant. Exponentiation by *e* of the parameter estimates for explanatory variables gave the odds-ratios, which indicated how many times more likely it was to obtain a positive response in the OTCs versus the control plots and vice versa, and at S substrate type versus NS substrate type and vice versa. We did not report odds-ratios for disturbance site effects, as the differences across the sites were not of our primary interest in this study. In general, the effects of the substrate types (*Sphagnum* or non-*Sphagnum*) and sites (disturbance types) in this and subsequent statistical analyses will be interpreted in the context of how they might have affected and interacted with the open-top chamber treatment.

Lack of adequate convergence for a logistic regression model (i.e. quasi-complete separation of data points indicating that the maximum likelihood estimate may not exist) may occur due to an overwhelming presence of only one of the binary responses. For example, in the later days of May, nearly all the seedlings were at or beyond stage 1, regardless of whether they were in or outside of the chambers, leading to an overwhelming positive response for stage 1 in general. Similarly, in the early days of May, none of the trees had yet reached stage 3, regardless of whether they were growing in or out of the chambers, leading to an overwhelming negative response for stage 3.

For the phenological stage 1 of aspen, adequate fit of data to the logistic regression model occurred only between May 12 and May 22 (dates not presented, i.e. May 13, 15 and 17, indicate either no change in phenological advancement from the previous day, or no data recorded on that day); models for later dates did not result in satisfactory convergence. Similarly, for stage 2, the models converged adequately only between May 18 and 23; for stage 3, adequate convergence was present only on May 25 and 26; and for stage 4 only on May 27. For black spruce, logistic regression resulted in adequate model convergence for stage 1 on May 12 through 14; for stage 2 on May 16 through 21; for stage 3 on May 22 and 23; and for stage 4 on May 25 to 27.

For visual interpretation of the phenological trends of both species, percentages of the trees reaching a given phenological stage inside the chambers and control plots were plotted against the day of the month of May 2007.

Foliar and root nutrient concentrations of aspen and spruce, and aspen leaf herbivory

In mid-August 2007, the experiment was terminated and all seedlings were harvested. The entire foliar component was collected from all of the aspen seedlings, and used for nutrient analysis and herbivory assessment. All of the needles were removed from the spruce seedlings, with current year foliage (i.e. new needles, 2007 season) separated from previous years' foliage (i.e. old needles).

For every seedling, five separate secondary roots branching off from the root crown were identified, and followed down about 30 cm for the longer roots, or to the end of the root tip for the shorter roots. The bottom 10 cm of every 30 cm root piece was collected for the mycorrhizae analysis (Chapter 6), while the remaining top part was collected for nutrient analysis.

Foliage and root samples were dried at 60°C for 5 days, and total concentrations of N, P, K, Ca and Mg were determined, using tissue digestion by wet oxidation in sulphuric acid and hydrogen peroxide in a block digestor (Parkinson and Allen 1975). Concentrations of total N and P in foliage and root digests were measured colorimetrically using a Lachat QuickChem autoanalyzer (FIA+8000, Lachat Instruments, Milwaukee, Wisconsin), while concentrations of total Ca, K and Mg were determined with an atomic absorption spectrophotometer (2380, Perkin-Elmer, Waltham, Massachusetts).

A preliminary assessment of aspen leaf herbivory was made in late August 2006 on all experimental aspen seedlings. Percentage of damaged leaves was determined and recorded as "1" if it exceeded 25% and "0" if it was less than 25%. As we did not want to disturb the experimental seedlings while the experiment was still in progress, we did not perform any destructive sampling that year. After the harvest in August 2007, herbivory assessment was made on 20 random aspen leaves collected from every experimental aspen seedling. The leaves were scanned (using the optical scanner LC4800-II) in a transparent plastic tray filled with water. Total leaf area of the 20 leaves and the % of leaf area estimated as missing (% leaf area missing or % LAM) due to insect herbivory (i.e. holes in the leaves, missing leaf margins) were calculated using WhizRHIZO Pro (Regent Instruments version 2007) and Sigma Scan Proc 5 (SPSS Inc. 2007). After the herbivory assessment, the 20 leaves were combined with the entire remaining collected foliage.

Statistical analysis of the 2006 herbivory assessment was performed by logistic regression (procedure LOGISTC, SAS Institute 2007), following the same procedures as were used for the analysis of spring phenology described above. The effects of OTC treatment, substrate type, and site were tested on the probability of positive response, which was that more than 25% of the leaves on the tree had insect damage at the end of the 2006 growing season. Odds-ratios were calculated to determine how many times more or less likely it was to obtain a positive response in the open-top chamber versus the control plots.

Statistical analyses of the 2007 herbivory and foliar and root nutrient concentrations were performed by ANOVA (procedure MIXED, SAS Institute 2007), testing the effects of OTC treatment, species (aspen versus spruce), substrate type, and site (all as fixed factors), on the responding variables including % LAM, and N, P, K, Ca, and Mg foliar and root concentrations. Separate analyses were performed for leaves and roots and for every responding variable. The initial models included testing for the effects of OTC treatment, species, substrate, site and all of the interactions among the explanatory variables on the responding variables. Non-significant interactions ($p > 0.05$) were dropped in the final model. In the case of significant effects of the main factors or significant interactions, least-squares (LS) means were used to determine the levels differing, and the direction of the difference.

As there were no replicates of the disturbance sites, no valid generalizations can be regarding the overall effects of specific disturbance types on the variables we tested; nonetheless, we included site as a factor in the model to avoid inflation of the experimental error and thus, the possibility of a Type II error. All data analyses were checked for normality and homogeneity of variance.

If the concentrations of any nutrient differed significantly between the control plot and the chamber, we correlated them with the number of days since the occurrence of each phenological stage until the harvest day (procedure CORR, SAS Institute 2007). The analyses were done separately for aspen and spruce and for OTC and C. Our goal was to examine whether higher or lower concentrations of a given nutrient result from the differences in the duration of growth. If, for example, bud break (signifying initiation of growth) occurred earlier inside the chambers, seedlings may have had more days to accumulate a given nutrient in their foliage. Since the "end of season" occurred when we harvested the seedlings, the length of the growing season could vary only through an earlier start (i.e. advanced spring phenology) of the season.

Results

Bud development and leafing phenology of trembling aspen

Spring phenology data recorded in 2006 indicated general trends of earlier bud burst (stage 1) for aspen growing in open-top chambers than in control plots (Tables 5.1 and 5.2). There was a significantly higher probability of reaching phenological stage 1 on May 16 (p = 0.010), and odds-ratios indicated that it was over eight times more likely for bud burst to occur in chambers than in control plots on that day (Table 5.2).

In contrast to spring 2006, spring phenology data from May 2007 showed a general trend of slight delay in bud burst (stage 1) (Table 5.1) in chambers compared to control plots (Fig. 5.1 a). Odds-ratios for May 12 to18 of 2007 indicated that it was 1.6 to nearly five times more likely for aspen trees growing in control plots to reach stage 1. The trend was reversed on May 21 and 22, with a slightly higher probability of aspen reaching stage 1 in the chambers. Despite these biological trends, logistic regression models for May 12 to 22 showed no statistical effect of OTC treatment (Table 5.2, Fig. 5.1 a).

The first observations of phenological stage 2 for aspen (Table 5.1) were recorded on May 12, 2007, but the majority of the trees did not reach that stage until the last week of May (Fig. 5.1 a). Stage 2 was between five to 10 times more likely to occur in control plots between May 18 and 23, and was marginally statistically more probable (p = 0.054) in control plots on May 21 (Table 5.2).

The first account of phenological stage 3 (Table 5.1) for aspen was observed as early as May 13 in chambers, and was followed in control plots four days later. Similar to stage 2, stage 3 was observed in very low numbers overall until May 23. On May 25, it reached 30% in OTCs and 45% in control plots, and was two to three times more likely to occur in control plots, although these differences were not statistically significant (Table 5.2, Fig. 5.1 a).

Phenological stage 4 (Table 5.1) for aspen did not occur in any of the plots until May 22, when we observed it inside one OTC (Fig. 5.1 a). There were no statistically significant effects of OTC treatment on the timing of stage 4 occurrence, but odds-ratios indicated that it was close to seven times more likely for stage 4 to occur in control plots than OTCs (Table 5.2).

Substrate type had no significant effects on the timing of bud burst in 2006. Likewise, substrate type did not have significant effects on reaching stage 1-4 in 2007. There were no significant effects of disturbance site on the timing of reaching stage 1 in 2006, or stage 1 and 2 in 2007. However, site had a significant effect on reaching stage 3 in 2007, with the highest % of seedlings at stage 3 occurring at the logging interval site, followed by the logging road, and the fire site. There were also significant differences in reaching stage 4 across the sites (Table 5.2).

Bud development and leafing phenology of black spruce

In contrast to aspen, black spruce showed overall more advanced bud development in chambers than in control plots in spring 2007. Between May 12 and 27, we observed the progression of bud development from stage 0 to stage 5 (Tables 5.1 and 5.3, Fig. 5.1 b).

OTC treatment was significant on May 12 ($p = 0.040$) and odds-ratios indicated that it was up to about five times more likely for spruce growing in OTCs to reach stage 1 on May 12-14 than it was for spruce in control plots (Tables 5.1 and 5.3). After May 15, trees growing in control plots progressed rapidly in terms of reaching stage 1, and by May 21, all of the experimental spruce trees were at or beyond stage 1 (Fig. 5.1 b).

Phenological stage 2 for spruce (Table 5.1) was evident in one chamber as early as May 12, while in control plots it occurred two days later. By May 16, 50% of OTC spruce and 15% of control plot spruce were at or beyond stage 2 (Fig. 5.1 b). There was a significantly higher probability of reaching stage 2 inside the chambers on May 16, 17 and 21 (Table 5.3). Odds-ratios indicated that it was up to ~ 10 times more likely for OTC trees to be at or beyond stage 2 during this time period. Overall, we can conclude that in comparison to control plots, stage 2 bud development was advanced by about three days inside the open-top chambers.

Phenological stage 3 for spruce (Table 5.1) was not observed until May 22 (Fig. 5.1 b). There was a significantly higher probability (*p* = 0.012) of stage 3 occurrence in OTCs on May 22 (Table 5.3). It was over six times more likely for OTC spruce seedlings to be at or beyond stage 3 on May 22, but only about twice as likely on May 23.Overall, we can conclude that OTC trees were advanced by about two days in reaching stage 3.

In spruce, phenological stage 4 (Table 5.1) occurred in one chamber and one control plot as early as May 23, and by May 27, 80% and 40% reached that stage in OTCs and control plots respectively (Fig. 5.1 b). There was a significantly higher probability of stage 4 occurrence in OTCs between May 25 and 27 (*p* = 0.011, 0.012 and 0.005 for May 25, 26 and 27 respectively, Table 5.3). Odds-ratios indicated that it was between seven and 10 times more likely for OTCs to reach stage 4 on these days.

The earliest account of phenological stage 5 for spruce (Table 5.1) was observed on May 26 for two trees: one in an OTC and one in a control plot. On May 27, stage 5 was recorded for one more tree in the control plot. As the majority of the trees did not reach stage 5 or 6 by May 27, we cannot perform an adequate statistical comparison between OTCs and control plots.

There were no differences between the substrate types or across the disturbance sites for any spruce spring phenological stages (Table 5.3).

Foliar and root nutrient concentrations of aspen and spruce

The open-top chamber treatment had no effect on the foliar and root concentrations of N, but there were highly significant differences between the two species, and marginal differences in terms of substrate type. Foliar N concentrations were lower in spruce than aspen (*p*< 0.0001), but root N concentrations were lower in aspen than spruce (*p*< 0.0001) (Table 5.4). Both foliar and root N concentrations were marginally lower at *Sphagnum* (S) substrate plots than non-*Sphagnum* (NS) substrate plots (*p* = 0.052 and *p* = 0.056 for foliar and root N concentrations respectively) (Table 5.4). Root N concentrations were also significantly lower at the fire and logging road sites than at the logging interval site (*p* = 0.004) (Table 5.4).

There were no effects of OTC treatment or substrate type on foliar and root P concentrations (Table 5.4). Disturbance site had a significant effect on foliar and root P, with foliar P concentrations lower at the logging road than the logging interval site, and root P concentrations lower at the logging road and fire sites than the logging interval site ($p = 0.036$ and $p = 0.0002$ for foliar and root concentrations respectively) (Table 5.4). Also, root P concentrations were significantly lower for aspen than for spruce ($p< 0.0001$) (Table 5.4).

Foliar K concentrations were significantly lower in spruce than aspen ($p< 0.0001$) and marginally significantly lower at the logging interval and road sites in comparison to the fire site ($p = 0.046$) (Table 5.4). The open-top chamber treatment and substrate type had no effect on foliar K levels and OTC treatment also had no effect on root K concentrations (Table 5.4). However, there were significant effects of substrate type on root K concentrations, which were lower on *Sphagnum* substrate than non-*Sphagnum* substrate ($p = 0.015$) (Table 5.4).

There was a marginally significant effect of the OTC treatment on foliar Ca concentrations, which were significantly lower in control plots than in chambers ($p = 0.056$); conversely, root Ca concentrations were significantly lower in chambers than control plots ($p = 0.021$) (Table 5.4). Spruce had significantly lower foliar and root Ca concentrations ($p< 0.0001$ for both foliar and root) than aspen. There were no main effects of substrate or site on foliar and root concentrations, but there was a significant interaction between OTC treatment and substrate ($p = 0.028$), with Ca root concentrations lower in control plots with *Sphagnum* than OTCs with *Sphagnum* (Table 5.4).

Since foliar Ca concentrations were significantly higher in OTCs, we correlated them with the number of days since the occurrence of every phenological stage until the tree harvest, in order to determine whether higher Ca concentrations were due to a longer growing season. There was a weak positive correlation (0. 286, $p = 0.074$, significant at alpha level 0.1) between the number of days since the occurrence of stage 2 (Table 5.1) for black spruce and the concentrations of foliar Ca. There was no correlation between Ca foliar concentrations and the number of days since stage occurrence and harvest for any other phenological stages for black spruce or aspen.

Foliar and root Mg concentrations did not differ between OTC treatment levels, the two substrate types, or across the disturbance sites (Table 5.4). Foliar Mg concentrations were significantly lower for spruce than aspen ($p< 0.0001$), but there were no differences in root Mg concentrations.

Aspen leaf herbivory

Logistic regression models testing the effects of OTCs, substrate type, and site on the probability of occurrence of ≥ 25% of foliage with herbivory damage at the end of summer 2006 converged adequately. Maximum likelihood analysis showed that insect herbivory was significant reduced in the OTCs ($p = 0.0008$), but there were no significant substrate type or site effects ($p = 0.610$ and $p = 0.103$, respectively). Accordingly, odds-ratios showed that aspen seedlings growing in control plots were ~ 55 times more likely to have more than 25% of their leaves damaged by insect herbivory than the aspen growing in OTCs.

The analysis of variance testing the effects of OTC treatment, substrate type, and disturbance site on herbivory in 2007, resulted in highly significant effects of OTC treatment ($p = 0.0005$), but no effects of substrate type ($p = 0.618$) or site ($p = 0.500$) on % leaf area missing (% LAM) for the 20 randomly sampled leaves of every experimental aspen tree. Least square (LS) means analysis indicated that % LAM was significantly higher in chambers than in control plots.

Discussion

Phenological responses in relation to open-top chamber treatment

We observed an increased growth rate in the height of aspen seedlings and a higher total final dry biomass of spruce trees (Chapter 4) under cooler and drier soil conditions inside the open-top chambers, leading us to questions on several levels:

1) What major factors were responsible for the increased growth of trees inside the chambers?

2) How could these observed growth responses be projected into the future with respect to the potential competitive advantage of aspen and black spruce regenerating on post-disturbance sites under the changing climate?

3) Why were the growth response patters different (i.e. height vs. biomass) between the two species?

4) Would the initially observed growth responses persist in the long term; would they reach certain threshold; or would they trigger a negative feedback that could effectively reverse the current trends?

In regions defined by distinct seasonality, such as the mixedwood-boreal forest, one of the major factors contributing to the annual accumulation of growth is the length of the growing season versus winter dormancy. Bud burst and foliage development allow for the initiation of spring growth, and these phenological events are determined predominantly by temperature and water availability (Kramer et al. 2000). We predicted that climatic changes may potentially modify the temperature and moisture of air and soil, thereby affecting the length of the growing season, and the growth patterns of regenerating aspen and spruce seedlings at post-disturbance sites in NW Quebec.

Indeed, under the simulated climate change conditions using open-top chambers, we observed clear trends of advanced bud burst for aspen in 2006 (but less so in 2007), and advanced bud burst and development for spruce in 2007 (Tables 5.2 and 5.3). We believe that a combination of the effects of the chambers on air temperature and the effects of the timing of snowmelt on soil temperature had a differential impact on spring phenology between the two growing seasons and between the two seedling species. Earlier snowmelt under the OTC conditions (Chapter 2) could have been one of the major factors allowing for earlier initiation of growth, thus resulting in the increased height growth of aspen trees and higher total final dry biomass of spruce inside the chambers. Snowmelt is, in fact, considered one of the major environmental cues signalling the start of the growing season, (e.g. Bliss 1956; Kudo 1991; Galen and Stanton 1993; Walker et al. 1995; Price and Waser 1998).

Spring 2007 was marked by below 0°C nighttime temperatures for most days in May, while in May 2006, negative nighttime temperatures very seldom occurred (refer to meteorological data collection described in Chapter 2). Maximum daytime temperatures were on average over 2.5°C higher inside the OTCs than in control plots in 2006, but only less than 2°C higher in OTCs than control plots in 2007 (Chapter 2). Thus, earlier snowmelt in OTCs led to the earlier exposure of soil to frequent freezing night temperatures in 2007, which likely contributed to the delay in bud burst of aspen trees in OTCs. Soil temperatures at rooting depth (12 cm) were lower overall in OTCs versus control plots, and lower in 2007 than in 2006 (Chapter 2). In spring 2006, average soil temperatures were ~ 4°C in OTCs and ~ 6°C in control plots, but in spring 2007 they were ~ 2°C and ~ 3°C in OTCs and control plots respectively (Chapter 2). It is possible that the overall cooler spring soil temperatures of 2007, in combination with the earlier snowmelt, had a potentially damaging effect on plant roots due to early soil exposure to frequent spring frost events, which did not occur in the warmer spring of 2006. Potential frost damage of roots would prevent the plants from water and nutrient uptake, thus inhibiting initiation of spring growth.

As opposed to aspen, black spruce bud burst and bud development (stage 1 to 4) in spring 2007 were generally more advanced in OTCs than in control plots, despite cooler soil conditions inside the OTCs (Tables 5.1-5.3). Accordingly, Slaney et al. (2007) claimed that while the elevated air temperature in whole-tree chambers resulted in earlier bud development and initiation and termination of shoot growth of Norway spruce (*Picea abies* (L.) Karst.), the effects of whole-tree chambers on soil temperature played little, if any, role in timing of these phenological events. On the other hand, Landhäusser and Lieffers (1998) observed that low soil temperatures (6°C and 12°C) had a strong negative effect on aspen growth in general, and the timing of bud flush was not advanced under cooler soil temperature treatments.

The generally higher positive response of spruce than aspen in terms of bud burst under cooler soil conditions is consistent with the frequently-reported better adaptations of northern coniferous species to lower temperatures in comparison to deciduous species (e.g. Landhäusser and Lieffers 1998; Tjoelker et al. 1998). Nonetheless, despite lower soil temperatures in OTCs, the timing of bud burst for aspen seedlings in May 2006 and in the late days of May 2007 (21-22) was advanced in the chambers. This suggests that higher air temperatures, rather than lower soil temperatures inside the OTCs, might have played a more critical role in spring bud burst advancement.

Following a critical chilling period over winter, bud burst occurs as a result of accumulation of high temperature units in spring time, which is specific at the species and genotype level (Hanninen et al. 2007). Clearly, cool spring nights in 2007, with frequent air temperatures below the freezing point, prolonged the accumulation of sufficient heat units, that is, days with temperatures equal or above the commonly used threshold temperature values at northern latitudes such as 0°C or 5°C (Slaney et al. 2007; Wesołowski and Rowiński 2007). It appears that in our case, the threshold temperature for accumulation of heat units was higher for aspen than spruce. A lower heat unit requirement for the commencement and progression of spring phenological events may give spruce a competitive advantage over aspen in terms of early spring growth and nutrient uptake. The fact that spruce already has foliage from previous seasons, and thus may become photosynthetically active even before bud burst and new leaf development, gives it yet another advantage in terms of early spring growth. Such a head-start in early spring growth may also give spruce an advantage in growth and performance for the remainder of the season.

Indeed, advanced early spring phenology of spruce in chambers may explain the higher final biomass of spruce growing in OTCs. Bud burst and development in conifers is not equal across the branches of an individual; rather, it starts with the bottom lateral buds and progresses up towards the terminal shoot (Slaney et al. 2007; personal observation). In determining the phenological stage, we recorded the most advanced stage – likely the lateral bottom buds. Such a pattern of bud burst progression is significant as it may indicate that the lateral shoots of spruce trees growing in chambers had a longer growing season than in control plots, thus producing longer branches. The advanced growth of the lateral shoots may have resulted in higher overall biomass accumulation over the growing season. It is very likely that by the time the bud burst stage reached the terminal bud, the spruce trees growing in control plots might have "caught up" phenologically, since the advancement of warmer spring weather would result in the accumulation of a sufficient number of heat units to allow for the rapid progression of phenological events. A longer growing season for lateral branches would be consistent with our observations of significantly higher final biomass of spruce in chambers, and no differences in final heights in chambers and control plots.

In the case of aspen, the cooler spring of 2007 in comparison to 2006 led to later leaf emergence in 2007 in both control plots and OTCs, with general trends of delayed bud and leaf development in OTCs in 2007 (with the exception of stage 1 on May 21-22) (Table 5.2). Accordingly, increased growth in the height of OTC aspen occurred mostly in the 2006 season, but was less obvious in 2007 (Chapter 4). Jarvis and Linder (2000) argue that the timing of spring thaw and autumn freeze are among the predominant factors determining the annual stem growth of boreal trees. It appears then, that the advancement in bud burst in early spring 2006 and thus the prolongation of the growing season, might have contributed to the significantly higher growth increase in height for aspen growing in OTCs. However, a longer growing season was likely not the sole advantageous factor for aspen growth in OTCs; Jarvis and Linder (2000) also state that nutrient capture in the summer time is another major factor contributing to stem growth of the boreal forest trees. As such, increased allocation of Ca into the foliar component of aspen growing in OTCs may also have played a role in the higher growth of OTC seedlings.

Open-top chamber effect on nutrient concentrations and aspen foliar herbivory

With the exception of marginally higher Ca concentrations in aspen leaves and current-year spruce needles in chambers, we observed no effects of OTCs on foliar nutrient concentrations (Table 5.4). Interestingly, the root concentrations of Ca were significantly lower in chambers for both species, suggesting that OTC treatment affected the allocation of Ca, with the chamber seedlings showing an increased aboveground allocation of this nutrient. This could have contributed to higher growth in the height of aspen and a higher final dry biomass of the spruce growing in chambers (Chapter 4). Indeed, a positive relationship between available soil Ca and aspen growth and survival have been reported by van den Driessche et al. (2005), while Lu and Sucoff (2001) observed significant elongation of shoots and roots of aspen seedlings with increasing levels of Ca in nutrient solutions. Among other factors, calcium availability may be important to plant growth in general because of its effects on soil pH and availability of other essential nutrient such as P (e.g. van den Driessche et al. 2005), or because increased levels of Ca as a component of cell walls may reduce plant susceptibility to fungal diseases (e.g. Elad 1997).

It is possible that the actual nutrient uptake of seedlings under the OTC treatment was in fact higher, since the growth was also higher, and the overall amount of acquired nutrients would be elevated. Indeed, consistently lower Ca supply rates in OTCs over the 2006 and 2007 growing seasons (Chapter 3) suggest a potentially higher uptake of this nutrient. Elevated Ca uptake likely contributed to increased growth of aspen inside the OTCs, since aspen is generally known to have a high requirement for this nutrient in particular (Coyne and Van Cleve 1977; Alban et al. 1978; Alban 1982; Van Cleve et al. 1983; Bates et al. 1992; Frey 2001). In comparison to other boreal trees, spruce likewise may have a higher Ca requirement, as shown by Alban et al. (1978) in their investigation and comparison of biomass and nutrient distribution in adjacent stands of red pine (*Pinus resinosa* Ait.), jack pine (*Pinus banksiana* Lamb.), white spruce (*Picea glauca* (Moench) Voss), and aspen, where they found that Ca levels were much lower in soils under aspen and spruce in comparison to the pines. This is consistent with our results of lower Ca supply rates in soils, and increased foliar Ca concentrations for both aspen and spruce in OTCs.

Since Ca is not resorbed from the foliage, elevated Ca concentrations by the end of the season may also have resulted from a longer growing season, which we observed inside the chambers. Earlier snowmelt and advanced phenology could allow more time for Ca uptake and allocation to foliage. Indeed, when we correlated foliar Ca concentrations with the number of days since bud tip emergence for black spruce (Stage 2; Table 5.1), there was a positive correlation between the two. Since phenology of aspen was not particularly advanced in the chambers in 2007, we found no correlation between the number of days since phenological stage occurrence and the harvest of the trees for any of the stages.

The lower soil Ca supply rates, which may partially be a result of increased Ca uptake by black spruce under the OTC treatment, may also be a representation of luxury consumption - a phenomenon observed in black spruce (Malik and Timmer 1995, 1996). As a highly stress-tolerant species, but a rather poor competitor in terms of nutrient uptake, black spruce is known to be efficient at internal nutrient cycling (Malik and

Timmer 1996). Thus, uptake and storage of available nutrients when the growing conditions are favourable and competitive pressure is low, may be a strategy for increased competitive performance in the future, when nutrient availability is lower and competing pressure is higher.

Slower-paced, gradual, and more conservative nutrient uptake, use, and growth responses may protect spruce from reaching sudden thresholds (i.e. boundaries of physiological tolerance for nutrient levels, temperature etc.), for which the species may have had no time to develop physiological adaptations. On the other hand, Tolvanen and Henry (2001) suggested that some woody species' slower response to OTC treatment in terms of nutrient uptake and growth may put them at a competitive disadvantage over the plastic and rapid responses to sudden environmental changes exhibited by faster growing species. We argue however, that plastic and rapid responses of fast-growing species such as aspen may be beneficial in the short term, but may not necessarily put the species at an advantage over the long term. Seeing as aspen appears to be quite sensitive to sudden changes in environmental conditions, if the negative growth responses associated with climate change outweigh the positive growth responses, the species may be weaken physiologically to the point where they become a prime target of insect outbreaks, diseases or fires (Bhatti et al. 2003).

Indeed, in western Canadian boreal forests, where increases in temperatures and fire frequency have been recorded, recent dieback and reduced growth of aspen have been observed (Hogg and Wein 2005). It is possible that the changes in the interdependent factors associated directly (greenhouse gas levels, temperatures) and indirectly (fire, diseases, pests, droughts) with the global climate change are progressing too fast for the physiological adaptations of western Canadian aspen. Likewise, interactions of defoliation by forest tent caterpillar (*Malacosoma disstria* Hbn.), drought history, and poor soil structure, among other factors, have been reported to contribute to the extensive decline of aspen in northeastern Ontario (Candau et al. 2002). This suggests that not only western, but also eastern Canadian aspen stands, may be prone to declines due to the direct effects of sudden climatic changes, which may be further amplified by indirect interacting factors such as herbivore pest outbreaks.

Changes in nutritional leaf quality associated with OTC treatment may affect the magnitude of insect herbivory. Increased growth could result in a nutrient dilution effect, lowering the quality of leaves and thus reducing herbivory rates, as insects might choose to search for better quality food. On the other hand, increased nutrient concentrations and higher foliar quality may also decrease herbivory rates, as herbivores would need to consume less matter to meet their nutritional demands (Lincoln et al. 1993).

In our case, OTC treatment did not change the foliar concentrations of any nutrients with the exception of Ca; nonetheless, we did observe reduced foliar herbivory of aspen growing in chambers. It is possible that the higher allocation of Ca to the foliage of both species, with concurrent reduction of root Ca concentrations, reflects an investment in secondary metabolite foliar defence mechanisms. This would be consistent with the reduced foliar herbivory of OTC aspen. However, as calcium is generally not known to be a structural component of major defensive compounds in aspen (phenolic glycosides, condensed tannins) (Lindroth 2001), the contribution of foliar Ca to the reduction of herbivory would likely be indirect and mechanical rather than chemical, i.e. better overall performance and higher levels of foliar Ca could lead to the production of structurally tougher leaves in the OTCs.

Direct investment of elevated foliar Ca into defense compounds in OTCs could be reflected in higher calcium oxalate crystal levels, which have been shown to function as an important antagonist to beetle attacks of conifers (Hudgins et al. 2003). We did not measure foliar calcium oxalate levels in our species, or the herbivory rates in black spruce, but it is possible that the increased foliar Ca allocation in spruce in fact resulted in higher calcium oxalate, which likewise reduced foliar herbivory and contributed to the higher final dry biomass of OTC spruce.

The higher likelihood of spruce over aspen to invest luxury levels of foliar Ca into chemical herbivore defence compounds is also supported by the slow versus fast-growing strategies of the two species. According to the hypothesis of resource-availability, under harsh environmental conditions such as inherently nutrient-poor, cool, and often water-logged disturbed sites of our study region, slow-growing species would be more likely to allocate resources into chemical defences rather than faster-growing species, for which it may be more beneficial to allocate nutrients and energy into structural components, e.g.

the production of tougher leaves (Coley et al. 1985; de Jong 1995). It is also possible that for fast-growing species, it may be less energetically expensive to re-grow new leaves to compensate for herbivory rather than to invest in preventative chemical defence mechanisms. This appears to be the case in our study, since despite higher herbivory levels of aspen growing in control plots, our exploratory analysis indicated no differences in total foliar biomass (Chapter 4) and average leaf area between OTCs and control plots.

It is also possible that the modification of microclimatic conditions by our OTC treatment may no longer have fit the life strategies and/or resource requirements of certain major aspen herbivores. In a factorial OTC-nutrient fertilization experiment in a sub-Arctic heath community, Richardson et al. (2002) observed that certain taxa of herbivores were present exclusively under a certain combination of their OTC-fertilization treatment. For example, some levels of fertilization treatment resulted in a 400% increase in abundance of herbivores of certain herbivore species of Homoptera.

In our study, the patterns of herbivory consisted primarily of small holes (~ 1-3 mm in diameter) in the leaf; consumption of leaf margins and skeletonizing were observed less frequently. Cases of rolled leaves with silk webbing inside, or several leaves clustered together by silk webbing were also observed, but extensive silk webs were not present. Such herbivory patterns led us to suspect that various species of leafrollers and leaf beetles (family *Chrysomelidae* Latreille) were the primary herbivores of aspen foliage at our sites. Indeed, during the inspection of over 150 aspen seedlings and saplings at our sites in early June 2008, about 4-5 days after leaf emergence, we discovered the presence of beetles and/or small holes on leaves of nearly all observed samples. The most frequently encountered beetle species were identified by us as a flea beetle *Crepidodera populivora* Parry and gray willow leaf beetle *Tricholochmaea decora* Say of the family *Chrysomelidae*. Many chrysomelid beetles feed on plant genera of *Populus, Salix* and *Alnus* (Brown 1956), which were abundant at our sites. Some beetle species even show specific preferences toward one genus or even one species of plant, e.g. *Chrysomela crotchi* Brown and *Crepidodera populivora* Parry feed preferentially on the foliage of trembling aspen (Brown 1956; Parry 1986).

The physical barrier of the OTC wall may be considered a methodological constraint in terms of preventing insects from entering the chambers (Richardson et al.

2000, 2002). However, it is worth noting that this barrier would mostly affect flying insects, and even then, the open top of the chambers would still allow their entrance. As the primary herbivores of the aspen seedlings included beetles which fly and often crawl on the ground, the open top of the chamber and the gap of 2-5 cm between the ground and the base of the chamber would allow their entrance.

The decreased herbivory of seedlings inside the chambers may also have resulted from the decreased overwinter survival of herbivores present in the chambers. For example, the adults of chrysomelid beetles, including the species we frequently encountered at our sites, overwinter in the ground or under debris and litter below their host plants, and climb up the tree to deposit eggs on leaves; breeding adults are known not to disperse away from their food-plants (Brown 1956; Smereka 1965; Parry 1986; Ives and Wong 1988). Presumably, the same number of adult beetles was present in the ground and on the leaves of our experimental trees in chambers as in the control plots at the start of our experiment. However, the survival of adult chrysomelid beetles overwintering in the ground within our chambers might have been affected by significantly earlier snowmelt and exposure of soils to frequent early spring freezing episodes, which did not occur in the control plots due to the longer presence of insulating snow cover. Overall, significantly colder and drier soils in springtime inside the chambers (Chapter 2) might have reduced not only the survival of the beetle herbivores, but also their reproductive fitness, leading to fewer eggs deposited on the leaves, and fewer larvae feeding on the leaves. Lower night air temperatures in chambers due to night inversions (Chapter 2; Marion et al. 1997), and lower soil temperatures might also have affected the survival of the eggs and larvae themselves. Indeed, Burkot and Benjamin (1979) reported that temperature-related mortality was the highest for egg and first instar stages of chrysomelid beetles.

The drier soils inside the chambers, resulting in part from higher evapotranspiration (Chapter 2), probably affected the water content of aspen leaves in OTCs, which might also have reduced the growth and survival of herbivores. Rank (1994) reported that the low water content of *Salix* host plants significantly affected the larval growth and survival of *Chrystomela* species beetles. Also, Lawrence et al. (1997) observed that high leaf water levels and low foliar Ca concentrations in white spruce

(*Picea glauca* (Moench) Voss) increased the probability of herbivory by spruce budworm (*Choristoneura fumiferana* (Clemens). By reverse reasoning, potentially lower water leaf content and the observed higher foliar Ca concentrations of aspen growing inside the OTCs, may therefore have had a negative effect on insect herbivory.

Prolonged thawing and cooler soils inside the chambers might also have resulted in an asynchrony of phenological events of herbivores and aspen trees. If the overwintering beetles emerged from hibernation later due to the soil being cooler for a longer time in the OTCs, the aspen may have been at a different phenological stage than if the insects had emerged from hibernation earlier. For example, newly produced leaves may have a higher nutrient concentration due to early spring nutrient uptake compared to foliar concentrations later in the season, when the tree may relocate resources to other plant parts. Indeed, upon their emergence from hibernation, chrysomelid beetles feed gregariously and extensively on young foliage (Brown 1956; Parry 1986; Ives and Wong 1988; personal observation). In that case, it is possible that due to their later emergence from hibernation, the insects consuming the foliage of the trees growing in chambers missed the period when the leaves were at their highest nutritional quality.

The effects of climate change-related phenological asynchrony across trophic levels is a common phenomenon, affecting numerous biotic relationships, including insect-plant interactions, mammal herbivore-plant interactions, predators-prey interactions and parasitoid-host interactions, among others (see reviews by Harrington et al. 1999; Visser and Both 2005; Parmesan 2006). The magnitude of changes in hibernation, migration, pollination, flowering and leafing patterns as a response to changing environmental conditions such as temperature increase, depends on the species. Some species will be more responsive than others, in which case coordination of interdependent life events will be out of balance. Potential delay in the timing of overwinter emergence of herbivore insects with simultaneous advancement in timing of aspen bud burst due to higher air temperatures would leave the former species at disadvantage and the latter benefiting from the changing environmental conditions.

We concentrated our discussion on beetles, which were most likely the prime herbivores in our plots. However, our arguments with respect to the effects of cooler, drier soil on the survival of insects, lower night temperatures in chambers on the development and survival of eggs and insect larvae, and asynchrony of phenological events induced by the OTC effects on both the herbivores and host plants, likely extends partially or fully to other potential insect herbivores.

Conclusion

Our study suggests that the effects of climatic changes on aspen regeneration and growth in NW Quebec, would be positive in favourable weather years in terms of advanced phenology, higher growth rate, and reduced herbivory. However, the initially increasing growth rates of aspen would likely be limited at some point by nutrient availability, particularly in the inherently nutrient poor sites of boreal regions (such as NW Quebec), where nutrients are already scarce (Lefort 2003; Oren et al. 2001; Melillo et al. 2002). Furthermore, assuming the plausible representation of OTCs as climate change simulation devices, deceleration of decomposition rates (Chapter 3) could further limit nutrient resources. The reduced herbivory may actually result in a positive feedback of OTC effects on drier and cooler soil conditions. The less insect-damaged the leaves are, the higher the water uptake and transpiration rates would be, leading to even drier soil conditions (for reversed effects, see Brown 1994). Less insect leaf damage could also provide more shade, leading to cooler soils (Classen et al. 2005). Direct strong negative effect of cool soil conditions on aspen growth and performance have been reported before (Landhäusser and Lieffers 1998; Landhäusser et al. 2001.) In that respect, climatic changes may be progressing too fast for the physiological adaptations of the rapidly-growing, nutrient-demanding aspen, putting the slower growing black spruce, with its conservative use of nutrients and better adaptation to cooler soils at a long term advantage. In particular, due to less sensitivity in terms of responsiveness to sudden environmental changes, black spruce has a smaller chance of being physiologically weakened to the point where it becomes prone to secondary negative effects associated with climate change, such as insect outbreaks, diseases and fires. In contrast to black spruce, the increased growth rate and advanced phenology of aspen appears to occur largely under favourable weather conditions, which under the erratic weather patterns often associated with climate change, makes the overall positive future of aspen in NW Quebec more unpredictable.

Tables

Table 5. 1 Spring phenological stages defined for bud burst and development, and leaf emergence of trembling aspen and black spruce.

Phenological Stage	**Species**	
	Aspen	**Spruce***
0	Bud closed, dark brown or purple, no green leaf tissue visible.	Buds completely closed.
1	Bud burst at the tip, green leaf tissue visible.	Visible bud opening at the tip; internal bud scales visible but no bud tip elongation present.
2	Buds opened at the tip, separate leaves visible within the opening, but still tightly rolled.	Tip of the bud covered by internal scales, protruding slightly from the opening but its diameter no larger than that of the external scales surrounding it.
3	Buds fully open, leaves distinctly visible, but still mostly rolled.	Bud swollen, protruding visibly from the opening of external scales surrounding it; bud diameter larger than the external scales, but the opaque internal bud scales still covering the bud and no leaves visible.
4	At least one leaf on the tree completely unrolled.	Leaves visible through the translucent internal scales covering the bud.
5	-	Breaking of the internal scales; leaves out but still rolled tightly.
6	-	New growth elongating visibly; leaves unrolling around the axis of new growth.

*Based on the six phenological stages identified for black spruce by Numainville and Desponts (2004).

Table 5. 2 Logistic regression analysis testing the probability of occurrence of phenological stages: bud break (stage 1), bud opening (stage 2), leaf visible but rolled (stage 3), and leaf unrolled (stage 4) of trembling aspen seedlings under OTC treatment (open-top chamber [OTC] or control [C]), substrate type (*Sphagnum* [S] or non-*Sphagnum* [NS]), and site (fire, logging road, logging interval). Observations recorded on three days in year 2006 for stage 1 only, and on 11 days in May 2007, for stages 1-4.

		OTC treatment		**Odds-ratios** for OTC treatment**		**Substrate type**		**Odds ratios for substrate type**		**Site**	
Stage	Date	Wald chi-square	*P*> chi-square	OTC vs. C	C vs. OTC	Wald chi-square	*P*> chi-square	S vs. NS	NS vs. S	Wald chi-square	*P*> chi-square
1	May 14, 2006	1.19	0.275	**2.30**	0.44	2.52	0.112	0.23	**4.38**	1.91	0.385
1	**May 16, 2006**	**6.65**	**0.010**	**8.29**	0.12	2.61	0.106	0.23	**4.35**	2.61	0.271
1	May 18, 2006	1.29	0.256	**2.48**	0.40	2.74	0.098	**5.15**	0.19	2.75	0.253
1	May 12, 2007	1.79	0.182	0.20	**4.97**	0.39	0.531	**2.28**	0.44	0.85	0.653
1	May 14, 2007	1.69	0.194	0.26	**3.90**	0.39	0.531	**2.27**	0.44	3.64	0.162
1	May 16, 2007	0.62	0.431	0.50	**2.01**	0.00	0.960	**1.06**	0.95	3.36	0.186
1	May 18, 2007	0.44	0.507	0.62	**1.62**	0.58	0.447	0.52	**1.92**	2.63	0.269
1	May 21, 2007	0.18	0.671	**1.33**	0.75	0.37	0.544	0.63	**1.58**	2.59	0.274
1	May 22, 2007	0.61	0.435	**1.72**	0.58	1.69	0.194	0.37	**2.74**	3.93	0.140
2	May 18, 2007	2.80	0.094	0.13	**7.98**	0.40	0.529	**2.30**	0.43	2.22	0.330
2	**May 21, 2007**	**3.68**	**0.054**	0.10	**10.13**	0.00	0.994	**1.01**	0.99	2.81	0.245
2	May 23, 2007	2.60	0.107	0.20	**5.10**	0.00	0.990	**1.01**	0.99	4.16	0.125
3	May 25, 2007	1.96	0.161	0.33	**3.07**	0.63	0.426	0.50	**2.01**	**6.39**	**0.041**
3	May 26, 2007	1.20	0.274	0.41	**2.45**	0.61	0.434	0.51	**1.97**	**7.74**	**0.021**
4	May 27, 2007	2.64	0.100	0.15	**6.74**	0.00	0.990	**1.01**	0.99	**7.36**	**0.030**

*Significant results are in bold.

**Odds-ratios indicate how many times more likely is it for the event to occur in OTCs or control plots, and at *Sphagnum* or non-*Sphagnum* substrate types. In comparing OTC to C, log-odds with a higher value are in bold.

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Table 5. 3 Logistic regression analysis testing the probability of the occurrence of phenological stages: bud break (stage 1), bud elongation (stage 2), bud swelling (stage 3), and 4) leaves visible, for black spruce seedlings under OTC treatment (open-top chamber [OTC] or control [C]), substrate type (*Sphagnum* [S] or non-*Sphagnum* [NS]), and site (fire, logging road, logging interval). Observations recorded on 11 days in May 2007.

		OTC treatment		**Odds-ratios for OTC treatment**		**Substrate type**		**Odds-ratios for substrate type**		**Site**	
Stage	Date	Wald chi-square	*P*> chi-square	OTC vs. C	C vs. OTC	Wald chi-square	*P*> chi-square	S vs. NS	NS vs. S	Wald chi-square	*P*> chi-square
1	**May 12, 2007**	**4.22**	**0.040**	**5.36**	0.19	1.39	0.238	**2.67**	0.37	0.71	0.703
1	May 13, 2007	1.27	0.260	**2.46**	0.41	0.00	1.000	1.00	1.00	0.50	0.778
1	May 14, 2007	1.54	0.215	**3.18**	0.31	0.85	0.356	0.40	**2.49**	1.41	0.495
2	**May 16, 2007**	**5.40**	**0.020**	**7.90**	0.13	0.00	1.000	1.00	1.00	4.00	0.135
2	**May 17, 2007**	**5.21**	**0.022**	**6.08**	0.17	0.68	0.410	0.50	**2.01**	3.89	0.143
2	May 18, 2007	2.89	0.089	**3.55**	0.28	0.58	0.448	**1.80**	0.56	1.00	0.607
2	**May 21, 2007**	**4.34**	**0.037**	**10.7**	0.09	0.22	0.641	**1.55**	0.64	0.39	0.822
3	**May 22, 2007**	**6.28**	**0.012**	**6.53**	0.15	1.37	0.241	0.38	**2.62**	2.79	0.248
3	May 23, 2007	1.31	0.252	**2.55**	0.39	0.69	0.405	0.49	**2.06**	1.69	0.430
4	**May 25, 2007**	**6.42**	**0.011**	**7.06**	0.14	0.00	1.000	1.00	1.00	2.77	0.251
4	**May 26, 2007**	**6.34**	**0.012**	**7.06**	0.14	0.17	0.682	0.71	**1.40**	3.84	0.147
4	**May 27, 2007**	**7.77**	**0.005**	**10.1**	0.10	1.48	0.224	**2.87**	0.35	0.30	0.859

*Significant results are in bold.

**Odds-ratios indicate how many times more likely is it for the event to occur in OTCs or control plots, and at *Sphagnum* or non-*Sphagnum* substrate types. In comparing OTC to C, log-odds with a higher value are in bold..

Table 5. 4 Effects of the warming treatment (open-top chamber [OTC] or control [C]), species (trembling aspen [Asp] or black spruce [Spr]), substrate type (*Sphagnum* moss presence [S], or absence, non-*Sphagnum* [NS]), and site (fire [F], logging road [LR], or logging interval [LI]) on foliar and root nutrient concentrations of aspen and back spruce seedlings**.**

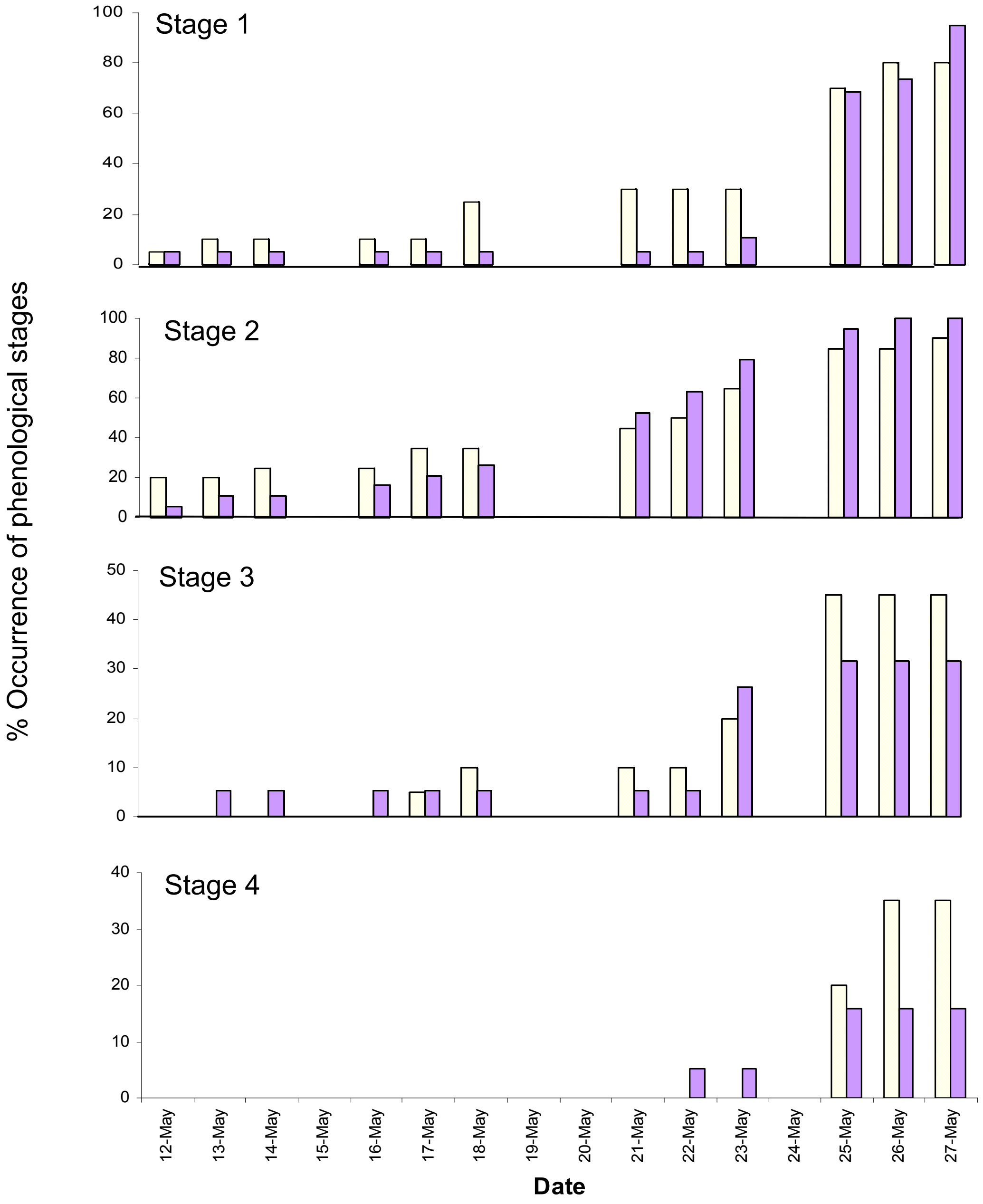
		Foliage			**Roots**		
Responding variable	Explanatory variable	F value	*P* >F	Means	F value	*P* >F	Means
N	OTC	0.56	0.458	C< OTC	1.26	0.265	OTC< C
	species	**133**	**<.0001***	**Spr< Asp**	**44.7**	**<.0001**	**Asp< Spr**
	substrate	**3.90**	**0.052**	**S< NS**	3.78	0.056	S< NS
	site	2.47	0.092	LR<F<LI	**5.93**	**0.004**	**F=LR<LI**
P	OTC	2.33	0.131	C< OTC	1.44	0.234	C< OTC
	species	0.64	0.428	Asp< Spr	**23.8**	**<.0001**	**Asp< Spr**
	substrate	0.38	0.537	S< NS	1.34	0.251	S< NS
	site	**3.48**	**0.036**	**LR**<F<**LI**	**9.71**	**0.000**	**LR<LI, F<LI**
K	OTC	0.00	0.976	OTC = C	2.90	0.093	C< OTC
	species	**44.6**	**<.0001**	**Spr< Asp**	3.28	0.074	Spr< Asp
	substrate	0.03	0.854	S = NS	**6.26**	**0.015**	**S< NS**
	site	**3.21**	**0.046**	**LI<LR<F**	1.64	0.202	LR<F<LI
Ca	OTC	**3.76**	**0.056**	**C< OTC**	**5.53**	**0.021**	**OTC<C**
	species	**56.9**	**<.0001**	**Spr< Asp**	**24.7**	**<.0001**	**Spr< Asp**
	substrate	0.23	0.632	S< NS	2.80	0.099	S< NS
	site	0.70	0.499	LI<LR<F	0.18	0.835	F=LI=LR
	OTC*substrate	**-**	**-**	-	**5.06**	**0.028**	**C*S< OTC*S**
Mg	OTC	0.94	0.337	C<OTC	3.64	0.060	OTC< C
	species	**120**	**<.0001**	**Spr< Asp**	3.17	0.079	Asp< Spr
	substrate	1.27	0.264	NS< S	1.64	0.205	S< NS
	site	0.25	0.781	LI<LR<F	1.93	0.15	LI< F< LR

*Significant results are in bold.

**Treatment level means, showing consistency of general trends. Means with *P*-values > 0.8 are considered identical

Figure

a)



Stage 1
Stage 2
Stage 3
Stage 4
% Occurrence of phenological stages
0
20
40
60
80
100
0
10
20
30
40
50
12-May
13-May
14-May
15-May
16-May
17-May
18-May
19-May
20-May
21-May
22-May
23-May
24-May
25-May
26-May
27-May
Date

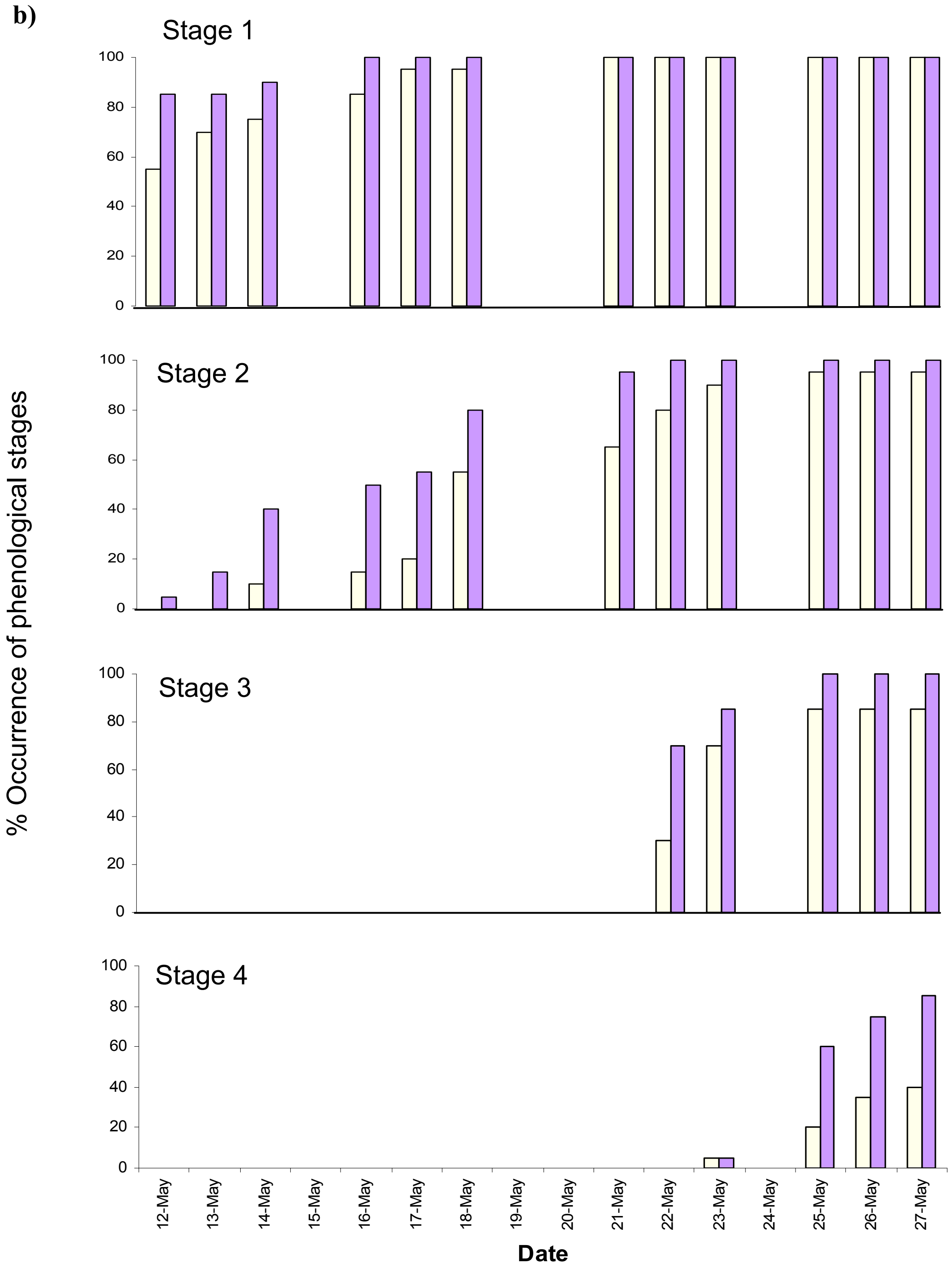


Figure 5.1 Comparison of % occurrence of phenological stages 1 to 4 (see Table 5.1) for a) aspen and b) black spruce from May 12 to May 27, 2007 for seedlings growing in open-top chambers (dark bars) and control plots (light bars) at disturbed fire and logging sites in northwestern Quebec.

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Connection of Chapter 5 with Chapter 6 and the thesis in general

In **Chapter 5** we compared the foliar and root nutrient concentrations of aspen and black spruce growing inside the open-top chambers and control plots, and we assessed how these effects might have contributed to growth responses of the seedlings. We also explored whether the effects of OTCs on spring phenological events may explain increased growth in height of aspen and increased final dry biomass of spruce growing in chambers. We found that spring bud burst was indeed advanced in the chambers for both species, and that both species had elevated concentrations of Ca in leaves but lower root Ca concentrations. Our findings addressed predominantly the aboveground responses of seedlings to OTC treatment; in **Chapter 6**, we continue our investigation, this time concentrating on the belowground plant responses, including the effects of open-top chambers on root tip numbers and percent colonization of root tips by ectomycorrhizae (ECM) of aspen and black spruce seedlings. In order to form an above and belowground assessment of plant responses to our climatic simulation, we compare the relationship of root tip numbers and % ECM colonization with growth responses and root and foliar nutrient concentrations of aspen and spruce (Chapter 5), as well as soil acidity, temperature, moisture, and nutrient supply rates in open-top chambers and control plots (Chapter 2 and 3). This completes our investigation of the OTC effects on the microclimatic and soil physical properties and biogeochemical processes, and the above and belowground responses of trembling aspen and black spruce seedlings to the open-top chamber treatment. We put the overall results in perspective of prediction of climate change impact on the future of trembling aspen and black spruce in the mixewood-boreal zone of northwestern Quebec.

CHAPTER 6: Comparison of simulated climatic change effects on root systems of aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* Miller (BSP)) at different substrates of post-disturbance sites in the transitional forest zone of northwestern Quebec

Abstract

The effects of potential climatic change on aboveground and belowground processes associated with growth of trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* Miller (BSP) at mixedwood-boreal post-disturbance sites in northwestern Quebec were addressed using open-top chambers. In this study we focused on the relationship of the number of root tips and the percent root tip colonization by ectomycorrhizae (% ECM colonization) with the aboveground growth responses (height, aboveground biomass), foliar and root nutrient concentrations, and soil acidity, temperature, moisture and nutrient supply rates. There were no significant effects of OTC treatment on root tip number or % ECM colonization, but both species showed similar trends in responses: higher root tip number in the open-top chambers was marked by lower % ECM colonization, and lower root tip number in control plots was marked by higher % ECM colonization. This suggests that under cooler, drier soil conditions inside the open-top chambers, ECM colonization may be inhibited, resulting in the production of more fine roots as a compensation strategy for increasing nutrient uptake. A significant negative correlation of root tip number with soil moisture content for aspen but not spruce growing in control plots suggests that aspen roots are more sensitive to excess soil moisture than root systems of black spruce. A significant positive correlation between soil moisture and % EMC colonization of black spruce in control plots, suggests that mycorrhizal colonization was enhanced under wetter soil conditions for black spruce. Drier soils induced by the OTC treatment and predicted as one of the potential future climate scenarios, could lead to eventual decrease in % ECM colonization of black spruce. Although calcium concentrations were higher in leaves and lower in roots of both species in OTCs, there was a positive correlation of foliar Ca concentration with % ECM for aspen in OTCs, but no foliar or root Ca concentration correlated with % ECM of spruce. This suggests that despite higher Ca demand in the foliar component of both

species growing in the OTCs, ECM appeared to play a more important role in Ca supply to aspen leaves than spruce needles. Overall, in comparison to black spruce, trembling aspen, appears to be more responsive to and dependent on the presence of ECM. The balance between costs associated with maintenance of ECM and benefits provided by the ECM will determine if the potential changes in ECM root colonization will be negative or positive under the changing climate. The relative impact of these costs or benefits may be greater for aspen than spruce. We expect that higher dependence of trembling aspen on ECM symbiosis can make the species more vulnerable to the often unpredictable impacts of climatic changes. With the frequently volatile inter-seasonal variations in weather conditions further compounded by trends of global climatic changes, the prognosis of black spruce regeneration and growth may be more secure at disturbed sites in northwestern Quebec.

Introduction

The unprecedented and continuous increases in concentration of greenhouse gases over the past century are very likely one of the major causes of an increase in global average air temperature of 0.74°C between 1906 and 2005 (IPCC 2007). The climatic changes are predicted to be among the strongest in northern ecosystems, with annual average temperatures projected to increase ~ 3-5°C over the land area (ACIA 2004), affecting the complex interactive biotic and abiotic processes both below and aboveground.

Numerous methods have been employed to study the potential effects of rising levels of greenhouse gases and global temperatures on ecosystems. The most common experimental methods of climatic change simulation include electrical heating of the soil (e.g. Bergh and Linder 1999), the use of infrared heaters (e.g. Bridgham et al. 1999) and passive treatments such as open-top chambers (OTCs) (e.g. Marion et al. 1997). The major limitation of experimental warming techniques is that the majority of studies focused on either the aboveground plant or belowground soil responses of the system Rustad et al. (2001). As such, only fragments of the system responses to the climate simulation treatment are considered.

Our research addressed the effects of potential climatic changes on below and aboveground processes within the mixedwood-boreal post-disturbance sites in northwestern Quebec. Using open-top chambers, we investigated the potential climate change scenario with regard growth and performance of young trembling aspen and black spruce seedlings at disturbed sites. The regeneration of these two species may be affected and shaped by the ongoing climatic changes within that region (Thesis Introduction; Lefort 2003).

While studies involving open-top chambers and aboveground plant growth responses in northern ecosystems have been widely carried out (see reviews of meta-analysis by Arft et al. (1999), Aerts (2006), Walker et al. (2006)), there are few studies on the effects of OTCs on root systems. Sullivan and Welker (2005) observed that root growth was higher, maximum root growth rates occurred earlier, and root biomass was greater for arctic sedges growing in the open-top chambers, while Björk et al. (2007)

reported evidence of OTC effects on root morphology and root mass distribution of tundra vegetation in Swedish Lapland. With respect to root-associated fungal responses, open-top chamber treatment increased the density of different fungal genotypes in Canadian tundra communities (Fujimura et al. 2008). Belowground fungal communities, including mycorrhizae, modify the architecture of roots, the structure of soil, and act as a storage and a potential sink of carbon, which in the future may have a profound effect on belowground processes under the continuously changing climate (Fitter et al. 2000; Treseder and Allen 2000; Kubiske and Godbold 2001; Söderström 2002; Staddon et al. 2002; Fitter et al. 2004; Pendall et al. 2004; Treseder 2004).

Ubiquitous and mutually beneficial, symbiotic associations of mycorrhizal fungi with the roots occur in the vast majority of vascular plants (Johnson et al. 1999). Breaking down complex organic matter polymers into plant-available monomer forms (Schimel and Bennett 2004), and transferring essential nutrients from the soil solution (Johnson et al. 1999), rocks (Jongmans et al. 1997) and mosses (Carleton and Read 1991), mycorrhizae play a vital role in plant growth and performance. In the northern forest systems, ectomycorrhizae (ECM) in particular, are prevalent in major families of tree species, including *Pinaceae* for conifers, and *Fagaceae, Betulaceae*, and *Salicaceae* for deciduous species, although endommycorhizae (EDM) are also present, e.g. in trembling aspen (Cripps and Miller 1993; Neville et al. 2002). Recently, Kernaghan et al. (2003) explored the biotic and abiotic factors affecting ECM diversity in mixedwood-boreal region of NW Quebec, while DeBellis et al. (2006) addressed the relationship between stand composition and ECM community structure in this region. However, the potential effects of climate change on colonization of ECM have not been investigated.

The objective of this study was to examine the effects of open-top chambers on root tip numbers and percent colonization of ECM for young trembling aspen and black spruce at post-disturbance sites in the mixedwood-boreal zone in NW Quebec. As *Sphagnum* moss constitutes one of the major components of the disturbed sites within our study area, we investigated the OTC effects on root tip numbers and ECM colonization on both *Sphagnum* dominated and non-*Sphagnum* dominated plots. We expected that the presence of peat moss may substantially modify the effects of OTCs on root ECM colonization, since moss can act as a major nutrient reservoir, and it can interact directly with ECM in providing nutrients for plant root uptake (Carleton and Read 1991). To explore both the above and belowground responses of the investigated ecosystem, we also compared the relationship of root tip numbers and % ECM colonization with growth responses and root and foliar nutrient concentrations of aspen and spruce, as well as soil acidity, temperature, moisture, and nutrient supply rates in soils within the open-top chambers and outside (control plots).

Materials and methods

Study sites

The study area (49° 37’ N; 79° 00’ W) was found in the boreal mixedwood-black spruce transitional forest zone in James Bay, which constitutes part of the Clay Belt physiographic region spanning northwestern Quebec and northeastern Ontario. A detailed description of the region, including geological background, climate, and current vegetation is provided in the general introduction and the first two chapters of this thesis.

We identified three study sites spanning 20 km along the Selbaie road (from 49°37’ N; 78°59’ W to 49 °45’ N; 79°02’ W) which was constructed between 1977 and 1980 to allow access to Selbaie copper mine located at km 92 (S. Galarneau, personal communication, Ministère des Ressources naturelles et de la Faune du Québec, La Sarre, Quebec). There were three study sites: a salvage logged post-fire site; a logging road created to facilitate timber harvest; and a post-logging site, where the timber harvest took place. At all sites the disturbance occurred in years 1996-1997. Detailed descriptions of the sites, including dominant vegetation and soil texture and drainage information, are provided in the general introduction of this thesis.

Experimental design

In total, 40 experimental plots were set up: 20 open-top chambers and 20 control plots. At the fire site there were eight OTCs and eight control plots; at the logging road site there were also eight OTCs and eight control plots; and, at the logging interval site there were four OTCs and four control plots. At each site, every OTC was paired with a control plot established in a close proximity.

To test the responses to OTC treatment in the presence or absence of live *Sphagnum* moss at the fire and logging road sites, eight pairs of OTC and control plots were established on each site where the dominant substrate consisted of *Sphagnum* moss, and another eight pairs where the substrate was dominated by sparse *Polytrichum* moss growing on mixture of humus and mineral soil. The substrate and the OTC treatment at the fire and logging road sites were crossed factorial: four OTCs and four control plots at *Sphagnum*-dominated substrates, and four OTCs and four control plots at non *Sphagnum*-dominated substrates, for a total of sixteen plots per site. At the logging interval site, four pairs of OTC and control plots were all set up on live *Sphagnum* moss.

At each of the three sites, for the plots receiving an open-top chamber treatment, we constructed a circular enclosure, 1 m in diameter and 0.75 m in height, built of clear transparent 8 mm thick polymethylmethaacrylate (PMMA, commonly known as acrylic) material. The construction of the chambers took place between June 28 and July 1, 2005, and the chambers were not removed until mid-August of 2007. Two flexible PMMA sheets were connected with tie-wraps and supported in two places by plastic stakes inserted in the ground. The walls of the chambers were perpendicular to the ground. A nearby control plot of the same size was not shielded with the acrylic enclosure, but marked with a nylon thread placed on the ground and secured with metal pegs. Detailed descriptions of OTC properties and its effects on microclimatic conditions including air temperature, relative humidity, CO_2 concentrations, rain interception, and soil temperature and moisture are given in Chapter 2.

Each OTC and control plot was constructed around a pair of aspen and black spruce seedlings, for a total of 80 experimental individuals: 40 per species. At least 40 pairs of trees were identified at each site, from which we chose the experimental pairs and randomly assigned OTC treatment or control plot to each pair. The criteria for choosing the seedling pairs was that the distance between them must range from 10 to 60 cm; that their initial height must be between 20 and 80 cm; and that the difference in height between the seedlings within a pair is no more than 50 cm. The initial height of each experimental seedling was measured (cm) at the set up of the experiment in July 2005, and the analysis of variance (ANOVA) using procedure MIXED in SAS (version 9.1; SAS Institute 2007) detected no initial height differences due to chance between the OTC and control plots. The diameters of the seedlings were initially measured at 5 cm above the ground surface in the summer 2006, and likewise, the analysis of variance detected no differences in diameters at that time between the OTCs and the control plots.

Determination of seedling growth, biomass and foliar and root nutrient concentrations

Seedling height was measured at the start of the experiment in July 2005 and right before the harvest in mid-August 2007. Each seedling was measured from the ground surface up to the tip of the terminal branch. Percent change in height (% HC) between the start of the experiment in early July 2005 and the termination in mid-August 2007 was calculated.

In mid-August 2007 all the seedlings were harvested by clipping them at the root collar point. For every tree, the root system was uncovered, and five separate lateral roots branching off from the primary root were identified, and followed down about ~ 30 cm, usually to the root tip. The bottom 10 cm of each of the five lateral roots was collected for mycorrhizal analysis, and all samples were placed in 100 ml plastic vials filled with water, and stored at 4^{o}C for a maximum of 7 days. The remaining top part was collected for nutrient concentrations analysis.

The aboveground parts of the tree were dried at 60^{o}C for 5 days, and final total aboveground dry biomass was determined for every sample. The entire foliar component was collected from all aspen seedlings, and used for nutrient analysis and herbivory assessment (Chapter 5). All the needles were removed from the spruce seedlings, with current year foliage (i.e. new needles: 2007 season) separated from previous year foliage (i.e. old needles).

Foliar and root nutrient concentrations were determined in September 2007 following the procedure of tissue digestions by wet oxidation in sulphuric acid and hydrogen peroxide, in a block digestor (Parkinson and Allen 1975). Concentrations of total available N and P in foliage and root digests were measured colorimetrically using a Lachat QuickChem autoanalyzer (FIA+8000, Lachat Instruments, Milwaukee, Wisconsin), while concentrations of total Ca, K and Mg were determined with an atomic absorption spectrophotometer (2380, Perkin-Elmer, Waltham, Massachusetts). For black spruce, separate nutrient analyses were performed for new needles and old needles.

Percent ectomycorrhizae colonization

All root samples were scanned (using optical scanner LC4800-II) in a transparent plastic tray filled with water, and total number of root tips for every 10 cm root piece was determined using WhizRHIZO software (Regent instruments, version 2007). Through visual inspection of every root sample using a Leica MS5 dissecting microscope (5-10x magnification) and an Ancansco compound microscope (up to 1000x magnification), as well as digital images of roots scanned at high-resolution (6400 dots per inch [dpi]) and magnified by up to 1000% (Adobe Photoshop Elements 2.0.2, 2002), we determined the number of root tips colonized by ectomycorrhizae.

For each tree, we also recorded the approximate number of different types of mycorrhizae observed, based on morphological characteristics including colour and texture (Goodman et al. 1998). This allowed us to identify the presence of the most abundant and/or easily identifiable genera such as the black, woolly fungal species of genus of *Cennococum*, the bright yellow or white species of genus *Piloderma*, and the light yellowish-brown species of genus *Russula*.

Soil acidity, temperature, moisture and nutrient supply rates

Soil acidity properties were measured by collecting a soil sample at the time of tree harvest and root collection. All samples were dried at 65^{o}C for 24 hours, mixed thoroughly and 1.5 g dry sub-sample was dissolved in 15 ml of distilled water to determine pH.

The soil temperature and moisture data were collected at the end of June and early July 2007, from three intervals of three consecutive days of measurements. Each of the three 3-day measurement interval was separated by one day free of measurements. The data for 9 measurements were averaged, resulting in a mean soil temperature and moisture value for each plot.

Soil temperatures were measured at depth 12 cm with soil probe thermometer (Thermor DT 130, Newmarket, Ontario). For each data-gathering event, three temperature measurements, two at the opposite sites of the plot and one taken in the middle, were averaged. The soil moisture in each plot was measured at the same time as the temperature, using a portable time-domain reflectometry (TDR) instrument (Field Scout TDR-100, Spectrum Technologies Inc, Plainfield, Illinois). The moisture was recorded as % volumetric moisture content measured as an average over the length of the two 12 cm long stainless steel rods, with each final measurement represented by an average of six measurements taken randomly over the entire area of the plot.

To determine the dynamics of the soil nutrient supply rates, eight Plant Root Simulator (PRS) resin probes were inserted in each plot for 21 days in May 2007. PRS resin probes are plastic probes enclosing an ion exchange membrane with an adsorbing surface area of 17.5 cm^2. After chemical pre-treatment, the membrane inserted in the soil will exhibit characteristics of plant roots, adsorbing available nutrients from the soil solution (PRS^{TM}-Probe Operations Manual 2004). The measurements are recorded as exchangeable ion supply rates per amount of ion exchange surface area over the time of the probe burial at a specified temperature and moisture, and are usually given in units of μg ion/10cm^2/time. Four cation and four anion probes within each plot were combined and analyzed as one composite sample. The probes have been analysed by Western Ag Innovations Inc. in Saskatoon, Saskatchewan. The nutrients were measured in bioavailable forms: NO_3^--N + NH_4^+-N, NH_4^+-N, $H_2PO_4^-$-P, K^+, Ca^{2+}, Mg^{2+}. We will refer to them respectively as total available N, NH_4, P, K, Ca and Mg. The supply rates of total available N and NH_4 were below method detection levels in May 2007, and were excluded from statistical analysis.

Statistical analysis

The analyses of variance (ANOVA, procedure MIXED in SAS version 9.1; SAS Institute 2007) were used to test the effects the explanatory variables including OTC treatment (OTC or control), substrate type (*Sphagnum* or non-*Sphagnum*), tree species (spruce or aspen), and site (fire, logging road, logging interval) on responding variables including the total number of root tips for five 10 cm-root pieces collected for each tree, and the percent of root tips colonized by ectomycorrhizae (% ECM). All non-significant interactions among the explanatory variables ($p > 0.05$) were dropped in the final model. In the case of significant effects of the main factors or significant interactions, least-squares (LS) means were used to determine the levels differing, and the direction of the difference (e.g. significantly higher or lower % ECM colonization under a given treatment or interaction of treatments). In all cases, data were checked for normality and homogeneity of variance.

Pearson correlation (procedure CORR in SAS; SAS Institute 2007) analyses were run for each species, and OTCs versus control plots separately. The relationship between the root tip number and % EMC colonization with % HC, total aboveground dry biomass, and foliar and root nutrient concentrations for aspen and spruce, as well as soil pH, temperature and moisture, and soil nutrient supply rates were found. For black spruce foliar concentrations from needles of season 2007 were used in these analyses. For the purposes of interpretation of significance of correlations, we consider $p< 0.05$ to be significant at the level of individual correlations.

Results

Overall we inspected 63 787 root tips: 31 274 for aspen and 32 513 for spruce (Table 6.1). The total number of root tips for five 10 cm-long-root segments averaged just over 800 for both aspen and spruce, and was higher, although not significantly, in chambers compared to control plots for both species (Tables 6.1 and 6.2). The overall variability for root tip number was high but consistent for both species, with maximum values ranging from 1432 to 1803 and minimum values ranging from 232 to 253 (Table 6.1). For aspen, ~ 39% and ~ 35% of roots tips were colonized by ECM in control plots and OTCs respectively, and for spruce ~ 56% and 50% of root tips were colonized by ECM in control plots and OTCs respectively (Table 6.1). There were no significant differences in % ECM colonization between the OTCs and control plots, but spruce had a significantly higher % ECM colonization compared to aspen (Table 6.2). Both species had significantly fewer root tips on *Sphagnum* substrate than non-*Sphagnum* substrate (~740 vs. ~ 900), but % ECM colonization did not differ between the two substrate types (Table 6.2). The root tip number was lower at the fire site than at the logging road and logging interval sites, but again, % ECM colonization did not differ across the sites (Table 6.2). There was a significant interaction of OTC treatment, substrate and site, where the trees in control plots with *Sphagnum* substrate at the fire site had significantly less root tips than those in the OTCs with non-*Sphagnum* substrate at the logging road site (Table 6.2).

Root tip number did not correlate with % ECM colonization for either species in control plots and OTCs (Table 6.3 a). In terms of growth parameters, the number of root tips was positively correlated with the aboveground biomass of aspen in the control plots, while the % height change between 2005 and 2007 was negatively correlated with root tip number for spruce in OTCs (Table 6.3 a). Neither growth parameter was correlated with % ECM colonization for aspen or spruce in OTCs or control plots (Table 6.3 b).

Root N concentrations were positively correlated with root tip number for aspen in control plots and OTCs. For spruce, concentrations of Ca in roots and foliar concentrations of N were negatively correlated with root tip number in the OTCs (Table 6.3 a). There was a negative correlation of Mg root concentration with % ECM for aspen in control plots, and a positive correlation of K root concentration with % ECM for aspen and spruce in OTCs. There was also a weak positive correlation of foliar Ca concentration with % ECM for aspen in OTCs (Table 6.3 b).

Soil pH was positively correlated with % ECM colonization of aspen roots in the OTCs (Table 6.3 b). Soil moisture in control plots was negatively correlated with root tip number for aspen, and positively correlated with % ECM colonization of spruce roots (Table 6.3 a, b). For soil nutrient supply rates there was a weak positive correlation of P supply rates and % ECM colonization of spruce roots in control plots (Table 6.3 b).

Discussion

Increase in root growth in terms of fine-root tips and root length is commonly believed to result in higher nutrient absorption due to more efficient root exploration capabilities (Kubiske and Godbold 2001). However, the investment in producing a more extensive root system may outweigh the benefits of improved soil nutrient exploration and nutrient uptake capacity. Indeed, despite high variability, trembling aspen and black spruce seedlings in our experiment produced more root tips in open-top chambers than in control plots, but nutrient concentrations were generally not higher in their roots or foliage (Tables 6.1 and 6.3 a; Chapter 5). In fact, there was a negative correlation between root tip number and root concentration of Ca and foliar concentration of N for spruce in OTCs (Table 6.3 a). This also reflects different allocation patterns of nutrients to aboveground and belowground plant components.

With respect to belowground plant response to OTC treatment, there were no direct and statistically significant main effects of OTC treatment on root tip number or % ectomycorrhizae colonization. However, from a point of view of biological significance, both species showed the same trends: higher root tip number and lower % ECM colonization in the open-top chambers, and lower root tip number and higher % ECM colonization in control plots (Table 6.1). Under drier and cooler soil conditions in the OTCs (Chapter 2), the plants were developing more fine roots, but simultaneously, they were forming less symbiosis with ECM. This may be a reflection of negative effects of cooler, drier OTC soil conditions on ECM, with the production of more fine roots presenting a compensation strategy required for increasing nutrient uptake.

In general, the soil temperatures over the growing season in our study area were relatively low with respect to the physiological optimum of trembling aspen (e.g. Landhäusser and Lieffers 1998; Landhäusser et al. 2001). It is possible that as the aspen trees at our sites are growing within their lower ranges of soil temperature tolerance zone, the slightly higher soil temperatures in the control plots than in the OTCs (up to ~ 2°C) are still well below the optimum physiological threshold, which could be expressed in positive root growth responses. The average soil temperatures in spring 2006 and 2007 were 2-4°C in OTCs and 3-6°C in control plots, while in the summer 2006 they reached 14°C in both OTCs and control plots, and in summer 2007 they were 10°C and 11.5°C in OTCs and control plots respectively (Chapter 2). Landhäusser et al. (2001) have shown that at a soil temperature of 5°C aspen experienced no root growth and limited leaf growth and shoot mass increase, while at 25^{o}C there was a large leaf growth and shoot mass increase. In contrast, white spruce (*Picea glauca* (Moench) Voss) still experienced shoot growth at 5°C, and grew well at 25°C, although more moderately than aspen at that temperature. Also, Landhäusser and Lieffers (1998) found that lower soil temperature (6°C and 12°C) had a strong negative effect on aspen growth, producing shorter shoots and reducing leaf area by half, which lowered light harvesting capacity and consequently, the amount of carbohydrates produced for root, shoot and leaf growth.

Root responses under the modified microclimatic conditions are further suggested by significantly different results in terms of root tip number at different substrate types, disturbance sites, and a combination of OTC treatment, disturbance site and substrate type. Root tip number was significantly lower at the *Sphagnum* plots than non-*Sphagnum* plots, and significantly lower at the fire site than at both logging sites (Table 6.2). Soil moisture was always significantly higher at the *Sphagnum* plots (up to 13%, Chapter 2), and soil temperature was consistently lower at the fire site (up to 2°C, Chapter 2), indicating that a combination of wetter and cooler soil conditions may inhibit root tip production. The magnitude of differences in soil moisture between *Sphagnum* and non-*Sphagnum* plots, and soil temperatures across the sites was about the same as the soil moisture and temperature differences between OTC and control plots; however the combination of cooler but *drier* soil conditions inside the OTCs versus the control plots, had no effect on root tip number, suggesting that soil moisture might have been more limiting in terms of root tip number.

Indeed, we found a negative correlation between root tip numbers of aspen with % VMC measured as an average over the 12 cm TDR probe length in control plots, i.e. under wetter soil conditions, in comparison to OTCs. At the same time soil temperature was not correlated with root tip number for either species in OTCs or control plots (Table 6.3). Similarly, Tryon and Chapin (1983), in their study of temperature control over root growth and biomass in taiga forests, found that root elongation was slower for black spruce than aspen in the laboratory, but was faster for black spruce in the field. The authors suggested that limitations of factors other than temperature, most likely moisture, were responsible for these root growth patterns.

Interactions of soil temperature and moisture can affect plant growth directly, such as low soil temperatures reducing root water flow (Wan et al. 1999, 2001) and root metabolism (Wan et al. 2001). Indirectly, effects on interaction with surrounding biotic environment include fungal (e.g. mycorrhizal) and bacterial relations. A significant positive correlation in our study between soil moisture and % EMC colonization of black spruce in the control plots suggests that mycorrhizal colonization was enhanced under wetter soil conditions. It also suggests that drier soil conditions induced by the OTC treatment (and predicted as one of the future climate scenario in certain regions), could lead to eventual decrease in % ECM colonization of black spruce.

Potentially detrimental moss-drying effects associated with climatic changes (e.g. Dorrepaal et al. 2004; Hollister et al. 2005; Walker et al. 2006) could have a further negative effect on ECM relationship with boreal tree species. Ectomycorrhizae is known for its significant function in nutrient transfer from mosses to tree roots (Carleton and Read 1991; Chapin et al. 1987). In fact, in black spruce forests of Alaska, mycorrhizae constitute one of the major means of P transfer from mosses to tree roots (Chapin et al. 1987). Accordingly, we observed a significant positive correlation of P supply rates and % ECM colonization of spruce roots, but only in the control plots, where the soil was more moist than in the OTCs (Table 6.3 b). This suggests that under the drier soil conditions in the OTCs, the potentially beneficial role of mycorrhizae in the uptake of immobile nutrients such as P may be diminished.

Whether or not changes in ECM associations with spruce roots will prove to be advantageous for regeneration and persistence of spruce versus aspen at the disturbed sites in the wake of climatic changes, depends on the relative importance of ECM in plant performance in the first place, and the resilience of ECM species associated with each tree species to potential changes in soil temperature and moisture. A study comparing the effects of ECM between aspen and white spruce (a close relative of black spruce), reported that that the presence of ECM in association with aspen resulted in larger root mass at a soil temperature of 4^{o}C, and lower root mass at 8^{o}C, while root growth of spruce did not respond to either soil temperature or presence of ECM (Landhäusser et al., 2002). This indicates firstly that aspen is more responsive and dependent on ECM in terms of root growth, and secondly, that the ECM associated with aspen might be more affected by soil temperature changes than the ECM associated with spruce.

Depending on mycorrhizal species, host plant species, and soil properties, (including temperature, moisture and pH), the process of nutrient uptake may differ, even with similar nutritional demands of different plant species. In our study this may be illustrated by relations of foliar and root Ca, Mg and K concentrations in aspen and spruce trees with ECM. While for aspen there was a positive correlation of foliar Ca concentration with % ECM, there was no correlation between foliar or root Ca concentrations and % ECM of spruce (Table 6.3 b). However, Ca concentrations were higher and root concentrations were lower for both species in OTCs (Chapter 5). Ultimately, it appears that under the OTC conditions, the acquired Ca was allocated in the foliar tissues of young trees, both aspen and spruce. However, despite higher Ca demand in the foliar component of both species growing in the OTCs, the means of Ca uptake appeared to differ: ECM appeared to play a more significant role in Ca allocation to the leaves of aspen than the needles of spruce (Table 6.3 b). On the other hand, ECM appeared to play an important role in the uptake of K under the OTC soil conditions for both, aspen and spruce (Table 6.3 b). In contrast to other nutrients, including N, the acquisition of K appeared to be more dependent on ECM associations under OTC treatment. In other words, under drier and cooler soil conditions, ECM may be an important factor in the root uptake of K.

In summary, the balance between the costs associated with maintenance of ECM and the benefits of the services provided by ECM, will determine if the potential changes in ECM root colonization will be negative or positive. For example, Corrêa et al. (2006) found that depending on the nutritional status and age of plant, ECM may have a detrimental effect on a plant's productivity during early establishment and developmental stages, but increased soil N availability may reduce this negative impact. In the inherently nutrient-poor habitats of bog-like *Sphagnum* dominated disturbed sites, where the available N supply rates are very low (Chapter 3), carbon demands of ECM may outweigh the benefits of ECM maintenance (Kubiske and Godbold 2001).

Changes in relative abundance of mycorrhizae species may also affect the balance of costs and benefits associated with ECM root symbiosis. For example, ECM genus *Piloderma*, commonly encountered in southern boreal forests of Quebec (DeBellis et al. 2006), and easily identifiable due to its bright yellow colour (Goodman et al. 1998; Arocena et al. 2001), was observed with a high degree of certainty in only two of our 40 plots. It has been shown that *Piloderma* may play an important role in the acquisition of basic cations, especially Ca (Arocena and Glowa 2000), which is known to be crucial to aspen growth and performance (Alban et al. 1978; Alban 1982; Frey 2001), and was one of the few nutrients responding significantly to our OTC treatment, both in terms of nutrient supply rates and tree root and foliar concentrations.

Cenococcum, an ECM genus frequently encountered in our study, is a drought tolerant species (Cripps 2001), known to be negatively affected by high soil moisture (Wright 1963). With the prediction of potentially drier soil conditions, the relative abundance of *Cenococcum* may increase, potentially outcompeting other mycorrhizae species with different levels of beneficial symbiotic potentials. A potential increase in *Cenococcum* abundance may also visibly affect aspen morphology: inoculation of aspen seedlings with a range of mycorrhizal species demonstrated that seedlings infected with *Cenococcum* were tall and pale with narrow leaves (Cripps 2001).

Conclusion

Overall, trembling aspen, appears to be more responsive and dependent on ECM than black spruce. Therefore, climate change related modifications of soil temperature and moisture may have a larger effect on aspen ECM associations. With the possibility that the climatic changes may result in drier soil conditions, which according to our results, may decrease ecotomycorrhizal colonization of young black spruce (Table 6.3 b), lesser dependence of black spruce will have a weaker overall impact on spruce performance, positive or negative. On the other hand, higher dependence of trembling aspen on ECM symbiosis makes the species more vulnerable to often unpredictable impacts of climatic changes on the biotic components of its environment. In that respect, the prognoses of regeneration and performance of trembling aspen at the post-disturbance sites in northwestern Quebec are more uncertain. Combined with the fact that the growth of aspen appears to be more responsive (negatively and positively) to volatile inter-seasonal differences in weather conditions often associated with climate change, this may suggest that in the long term the future of black spruce may be more secure than that of aspen in NW Quebec.

Tables

Table 6. 1 Means, standard deviations (SD), maximum (Max) and minimum (Min) for the total number of root tips of five lateral root segments (10 cm long), and percentage of these root tips colonized by ectomycorrhizae (% ECM) for aspen and spruce growing in open-top chambers and control plots at post-disturbance sites in James Bay area of NW Quebec. Sums of root tips investigated are also included.

Species		**Control plots**		**Open-top chambers**		**Open-top chambers and control plots**	
		Root tip number	**% ECM colonized**	**Root tip number**	**% ECM colonized**	**Root tip number**	**% ECM colonized**
Aspen	**Mean**	783.4	39.0	821.4	35.0	801.9	37.1
	SD	316.9	13.3	388.1	13.9	349.2	13.6
	Max	1432.0	70.0	1514.0	55.7	1514.0	70.0
	Min	253.0	19.3	232.0	14.8	232.0	14.8
	Sum	**15668**		**15606**		**31274**	
Spruce	**Mean**	756.9	55.8	868.8	50.0	812.8	52.9
	SD	366.03	16.51	422.94	18.31	394.49	17.46
	Max	1467.00	92.05	1803.00	86.98	1803.00	92.05
	Min	253.00	30.05	249.00	7.22	249.00	7.22
	Sum	**15138**		**17375**		**32513**	
Both species	**Mean**	770.15	47.38	845.67	42.69	807.43	45.06
	SD	338.22	17.06	398.25	17.79	370.46	17.48
	Max	1467.00	92.05	1803.00	86.98	1803.00	92.05
	Min	253.00	19.30	232.00	7.22	232.00	7.22
	Sum	**30806**		**32981**		**63787**	

Table 6. 2 Effects of the open-top chamber treatment ([OTC] or control [C]), species (Aspen or Spruce), substrate (*Sphagnum* [S] or non-*Sphagnum* [NS]), and site (fire [F], logging road [LR] or logging interval site [LI]) on total number of root tips from five 10 cm long lateral root segments, and the percentage of ectomycorrhizae colonization of these root tips (% ECM).

		F-value	P>F	Means
Root tip number	OTC	1.01	0.319	-
	species	0.03	0.862	-
	substrate	**6.06**	**0.016***	**S< NS**
	site	**8.21**	**0.001**	**F< LI; F<LR**
	OTC*substrate* site	**2.51**	**0.038**	**C_S_F< OTC_NS_LR**
% ECM colonization	OTC	0.76	0.387	-
	species	**21.8**	**<0.0001**	**Aspen<Spruce**
	substrate	0.01	0.938	-
	site	0.08	0.924	-

*Significant results are in bold.

**Treatment level means, showing consistency of general trends.

Table 6. 3 Pearson's correlation coefficients and associated probabilities (*P*-values) for: 1) growth parameters including total aboveground biomass, and % change in height between July 2005 and August 2007; 2) root and leaf nutrient concentrations and, 3) soil nutrient supply rates, soil % volumetric moisture content (%VMC), soil temperature, and soil pH), with a) root tip numbers of five 10 cm root segment and b) % ectomycorrhizae colonization of root tips, for trembling aspen and black spruce roots in control plots and open-top chambers (OTC). Correlation between root tip number and %ECM is also included.

a)

		Aspen				**Spruce**			
		Control		**OTC**		**Control**		**OTC**	
		Correlation coefficient	*P*-value	Correlation coefficient	*P*-value	Correlation coefficient	*P*-value	Correlation coefficient	*P*-value
Growth parameters	% ECM	-0.38	0.101	0.15	0.534	-0.42	0.063	0.07	0.759
	Biomass (g)	**0.45**	**0.049***	0.04	0.876	-0.01	0.953	-0.12	0.613
	%HC	0.16	0.512	-0.38	0.107	-0.04	0.873	**-0.47**	**0.036**
Root nutrient concentration	N	**0.48**	**0.033**	**0.60**	**0.006**	-0.25	0.282	-0.35	0.134
	P	0.26	0.273	0.30	0.208	-0.21	0.372	-0.26	0.270
	K	0.30	0.195	0.30	0.220	0.06	0.798	-0.24	0.310
	Ca	-0.12	0.611	0.05	0.843	-0.04	0.851	**-0.46**	**0.044**
	Mg	0.08	0.724	0.37	0.116	-0.36	0.114	-0.32	0.165
Leaf nutrient concentration	N	0.37	0.105	0.18	0.450	-0.21	0.386	**-0.46**	**0.043**
	P	0.14	0.565	0.01	0.952	-0.14	0.547	-0.06	0.790
	K	0.20	0.408	-0.13	0.582	-0.17	0.472	-0.03	0.900
	Ca	0.08	0.752	0.08	0.749	-0.04	0.862	-0.17	0.483
	Mg	-0.02	0.925	0.21	0.382	-0.40	0.078	-0.14	0.554
Soil nutrient supply rates	P	-0.05	0.831	0.00	0.989	0.00	0.997	0.14	0.544
	K	-0.03	0.895	0.02	0.925	-0.08	0.722	-0.18	0.456
	Ca	-0.12	0.612	0.11	0.645	0.01	0.963	-0.31	0.187
	Mg	-0.15	0.531	0.23	0.342	0.09	0.692	-0.26	0.267
Soil moisture, temperature, and acidity	% VMC	**-0.44**	**0.052**	-0.25	0.300	-0.20	0.389	0.39	0.089
	ST (cm)	-0.02	0.918	0.39	0.100	0.29	0.211	0.31	0.188
	pH	-0.25	0.280	-0.04	0.880	-0.32	0.162	-0.47	0.036

b)

		Aspen				Spruce			
		Control		OTC		Control		OTC	
		Correlation coefficient	*P*-value	Correlation coefficient	*P*-value	Correlation coefficient	*P*-value	Correlation coefficient	*P*-value
Growth parameters	Biomass (g)	-0.10	0.669	-0.01	0.970	-0.15	0.524	-0.09	0.721
	%HC	0.21	0.372	0.27	0.272	-0.04	0.873	0.05	0.834
Root nutrient concentration	N	0.14	0.551	0.05	0.845	0.32	0.173	0.14	0.545
	P	0.27	0.246	-0.03	0.917	0.29	0.210	0.14	0.544
	K	-0.17	0.488	**0.63**	**0.004**	-0.08	0.751	**0.64**	**0.003**
	Ca	-0.28	0.233	0.35	0.142	-0.25	0.299	-0.26	0.265
	Mg	**-0.52**	**0.019**	0.34	0.156	0.26	0.269	0.15	0.536
Leaf nutrient concentration	N	-0.09	0.719	0.10	0.675	0.29	0.215	-0.08	0.730
	P	-0.12	0.627	-0.09	0.713	0.25	0.282	0.01	0.974
	K	-0.37	0.114	0.30	0.216	0.00	0.990	0.36	0.121
	Ca	0.24	0.310	**0.45**	**0.056**	0.17	0.483	0.30	0.205
	Mg	0.12	0.614	0.23	0.349	0.13	0.600	0.23	0.331
Soil nutrient supply rates	P	0.23	0.322	-0.07	0.790	**0.44**	**0.054**	0.21	0.386
	K	0.26	0.265	0.13	0.585	0.27	0.256	0.17	0.482
	Ca	-0.05	0.826	0.41	0.079	0.18	0.453	-0.01	0.971
	Mg	-0.16	0.509	0.38	0.113	0.15	0.530	0.07	0.762
Soil moisture, temperature, and acidity	% VMC	-0.01	0.964	0.01	0.962	**0.57**	**0.009**	0.20	0.408
	ST (cm)	-0.04	0.878	0.24	0.318	0.01	0.982	0.00	0.998
	pH	-0.03	0.915	**0.52**	**0.022**	0.08	0.743	0.22	0.347

*Significant results are in bold.

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Part V: CONCLUSION

Summary and concluding remarks

Transitional mixedwood-boreal forests in northwestern Quebec: changing dynamics

Global warming may cause shifts in the reciprocal effects between boreal forests and climate; for example, changes in albedo and net radiation could lead to further warming, affecting decomposition processes, carbon balance and nutrient dynamics (Walker et al. 2006). These changes can affect competitive interactions among species, which could lead to shifts in community composition. Subsequent feedback of climate change-related factors may cause some plant species to eventually reach their physiological thresholds, leading to their decline. A meta-analysis of 143 studies dealing with species' responses to global warming showed that 80% of species experienced migratory range boundary expansions and phenological shifts, as expected based on their present physiological tolerance constraints (Root et al. 2003).

We suspected that the abundant establishment of trembling aspen along the northern extremes of its regional distribution in the mixedwood-boreal transitional zone of NW Quebec, may present an example of such species responses to steadily increasing annual average temperatures and total annual precipitation (Thesis Introduction; Lefort 2003). Therefore, the general goal of this project was to characterize and compare the mechanisms responsible for the growth and performance of trembling aspen and black spruce seedlings at the disturbed sites under different climatic scenarios.

The use of open-top chambers (OTCs) allowed us to simulate climatic changes and observe the potential future responses to elevated temperatures, of trembling aspen and black spruce, which are among the most prominent representatives of the mixedwood-boreal transitional forest zone not only in Quebec, but across North America. Investigation of these species' young-stage regeneration at post-disturbance sites may allow for prediction of species composition in their later stages, when, depending on their relative abundances, they will become part of a mixedwood or a boreal forest. As noted by Davis (1981) in her extensive research of tree migration patterns after the start of the termination period of Wisconsin glaciation approximately 16 000 years ago, the survival ability of the advancing seedlings may have played the most critical role in successful spread of the species into new areas. The potential for successful growth of the seedlings into the adult stage should give us an indication of future species composition and dynamics in the transitional zones of the boreal forests.

Warmer air but cooler and drier soil in our open-top chambers, likely a result of earlier snowmelt in springtime and increased evapotranspiration (Chapter 2), made for a plausible representation of the potential changes in the soil conditions associated with the global temperature increase. These soil conditions likely contributed to the observed deceleration of aspen litter decomposition and decrease in supply rates of calcium. Decreased soil Ca supply rates may also have resulted from increased plant Ca uptake, since we observed a marked increase in the height growth rate of trembling aspen in OTCs, especially in the first full growing season (2006) following the experimental establishment. Spring bud burst for aspen was also significantly advanced in the chambers in 2006, indicating that earlier snowmelt and higher air temperatures led to a longer growing season allowing for increased seedling growth. Overall, these observations suggest a positive growth response of seedlings in the early regeneration process at post-disturbance sites in a changing climate scenario.

The advantages of OTC conditions for the growth of trembling aspen were less significant in the second full growing season (2007). Thus, the initial positive growth response of aspen to climatic changes may indicate a short-term impulse response of an opportunistic species to sudden amelioration of the growing conditions. Such rapid responses to changing environmental conditions may upset the equilibrium of plant interactions with other organisms. For example, we inferred that phenological asynchrony between herbivorous beetle insects and advanced spring phenology of aspen in OTCs may have contributed to significantly lower herbivory rates of aspen seedlings growing under simulated climate change conditions.

It is possible that positive responses of aspen to a sudden amelioration of growing conditions may only occur if the amelioration is indeed significant, as might have been the case in the 2006 growing season, which counted among the warmest summers of the last 45 years, with higher precipitation than in 2005 and 2007 (Environment Canada, Climate Normals 2008). Following the overall cooler and drier growing season of 2007, the positive growth response and advancement of spring phenological events of aspen in the chambers was less noticeable, as the species appeared to be particularly sensitive to cold spring marked by frequent night frosts, and drier conditions of 2007, in comparison to 2006. Therefore, it appears that advanced spring phenology and longer growing season would only be advantageous to aspen if the other conditions are favourable in terms of physiological tolerance ranges of aspen.

On the other hand, black spruce responded positively to the OTC treatment in 2007, particularly through advanced phenology in the springtime. The rate of its growth in height in 2006 was much less affected by the OTC treatment than it was for aspen, but its growth in height was also little affected by OTCs in 2007. Therefore it appears that in contrast to aspen, the seasonal growth response of the black spruce was not affected by the overall weather differences between the 2006 and 2007 growing seasons. As with aspen, the foliar Ca concentrations of spruce growing in OTCs were higher than of those growing in control plots, suggesting the superior quality of spruce foliage under climate change simulation treatment. However, in terms of belowground processes, such as % ectomycorrhizae colonization, black spruce seemed to be less affected by the OTC treatment. Overall, it appears that black spruce is less influenced by the erratic inter and intra seasonal weather conditions than aspen. Less sensitivity with respect to environmental variations may leave black spruce with an advantage over trembling aspen in the long term.

Our research indicated that in the transitional mixedwood-boreal forest zone of northwestern Quebec, both trembling aspen and black spruce are currently within the range of positive response to the changing climate. While positive reaction to warmer growing conditions may be more pronounced for aspen than spruce, aspen’s negative response to less-than-optimal environmental conditions associated with inter-annual weather variations will likewise be proportionally greater. In the long term, trembling aspen can be susceptible to a multitude of secondary negative climate change effects such as pest outbreaks and diseases, which may ultimately prove detrimental to the species. Balance between these negative responses versus positive responses to climate change, such as increased growth or decreased insect herbivory, will determine the future of trembling aspen in NW Quebec.

Summary of contributions to knowledge

The nature of responses of trembling aspen and black spruce to climatic changes and the secondary effects associated with it could affect the future structure and function of Canada's mixedwood and boreal forests, which are of critical importance not only because they affect ecological, biogeochemical and climatic processes, but also from the socio-economic perspective in terms of resource utilization on a global and regional scales. Situating the findings of my investigation in the larger context of related research may lead to a formulation of a more precise prognosis with respect to the future of trembling aspen and black spruce under changing temperature and disturbance regimes across North America.

Contribution to general knowledge of ecology, biogeochemistry and climate

1) I advanced the knowledge of potential impact of climate change on community responses.

2) I demonstrated the systemic effects of climate change involving multiple interactions among the microclimatic variables, soil properties, plants, herbivors and mycorrhizae.

Contribution to the knowledge of ecology of trembling aspen and black spruce

1) I found that root differentiation likely facilitates this coexistence of trembling aspen and black spruce seedlings at a small spatial scale (i.e. as small as <1 m apart), at post-disturbance sites in NW Quebec. The possibility of coexistence of the two species is important, as it may contribute to determining whether the presently regenerating forests in NW Quebec will become black spruce-dominated boreal forests or mixedwood forests.

3) I found that the climate change, as simulated by OTC treatment, will affect growth of aspen and black spruce seedlings differently: aspen is more likely to grow in height, and spruce is more likely to produce more leaves and branches but not necessarily grow taller.

4) I found that climate change, as simulated by OTC treatment, can modify biogeochemical processes by leading to more acidic soils, lower supply rates of nutrients (e.g. Ca and Mg) and slower decomposition. This suggests that climate change will impact plant nutrient availability, and therefore, regeneration and growth of different plant species. Specifically, more acidic soils and lower supply rates of Ca can have a stronger negative impact on nutrient-demanding trembling aspen than less nutrient-demanding black spruce.

5) I found that the climatic simulation of drier and cooler soils, as well as increased air temperatures can accelerate spring phenology of trembling aspen and black spruce. Evidence of accelerated snowmelt and advanced spring phenology in the OTCs suggests that the changing climate may prolong the growing season of these two species in NW Quebec.

6) I found that the climate change, as simulated by OTC treatment, can affect foliar and root calcium concentrations (i.e. increasing foliar Ca concentrations and decreasing root Ca concentrations).

7) I found that the climate change, as simulated by OTC treatment, may reduce insect herbivory of aspen foliage. In that respect, climate change can have a positive impact on aspen growth and performance.

8) I found that in general, the overall performance and growth responses to simulated climate change are less predictable and more variable for trembling aspen than they are for black spruce. The latter species experienced smaller magnitude, but continuously positive growth response to simulated climate change.

Contribution to research methodology knowledge

1) I found evidence that the effects of OTCs on snowmelt can have a profound impact on modification of soil temperature and moisture inside OTCs. More precisely, establishing

OTCs after snowmelt and before snowfall is likely to result in increasing soil temperatures in the OTCs. On the other hand, leaving OTCs year-round is more likely to result in accelerated snowmelt, exposure of soil to frequent freezing temperatures of the early spring, and decreased soil temperatures inside the OTCs.

2) I have empirical and theoretical evidence that OTCs with walls perpendicular to the ground should not affect the amount of rainfall interception, but the distribution of rainfall reaching the ground within the chambers will be affected. This can, in the long term, affect soil moisture inside the OTCs.

3) I have empirical evidence that OTCs have little impact on CO_2 concentrations. To my knowledge, the effects of passive OTC treatment on CO_2 concentrations have not been directly addressed before.

4) I concluded that the functioning of OTCs can be adjusted according to the desired climate change simulation effects. For example, cooler soils within the chambers can be achieved by leaving the OTCs year-round, and warmer soils, by constructing them in the summertime only; rainfall interception can be decreased by building OTCs with inwardly inclined walls, whereas OTCs with walls perpendicular to the ground should not affect rainfall interception.

5) I found that the OTCs have impact on soil acidity, nutrient supply rates and decomposition rates. More precisely, OTCs can lead to more acidic soils, lower supply rates of cations including Ca and Mg, and deceleration of decomposition of deciduous litter.

6) I concluded that OTCs present a plausible representation of climate change scenario, and as such, they are currently among the most optimal means of simulating climate change in the field. This applies both to their efficacy and logistic convenience.

7) I successfully used Plant Root Simulator probes (PRS^{TM}) in my research. My project is currently among the four other projects in North America, which used PRS probes in conjunction with the open-top chamber treatment, and a first one which used the probes in climate change study taking place in a forested boreal system (A. Redman, personal communication).

Socio-economic and ecological implications

This research advanced the understanding of the optimal microclimatic and biogeochemical conditions for growth and persistence of trembling aspen and black spruce in NW Quebec, and made some specific predictions with respect to how the two species may respond to climate change in the future. From a socio-economic perspective, changes in relative abundance of trembling aspen and black spruce may have important implications for the forest industry. Since black spruce has a high economic value in terms of wood resources (Lefort 2003), a better understanding of the optimal microclimatic and biogeochemical conditions for its regeneration and persistence could point policies towards sustainable management of northern spruce forests, especially with regard to fire management and use of forest resources, such a harvest of timber.

On the other hand, the potential of mixedwoods to provide ecosystem services is currently being recognized across scientific and industrial communities, leading to ongoing development of sustainable ecosystem management plans aimed at maximizing wood production and simultaneously preserving biodiversity (e.g. Bergeron and Harvey 1997; Legaré et al. 2004; Comeau et al. 2005; Martin 2005; Burton et al. 2006). Ecologically, the presence of a species such as trembling aspen is considered to positively affect nutrient cycling in mixedwood forests due to its rapid growth rate, capacity to accumulate large amounts of nutrients, and high decomposition rates of both leaf litter and wood tissue (Alban 1982; Brais et al. 1995; Chen et al. 1998; Van Cleve et al. 1983). From an economic point of view, there is currently a growing interest in fast-growing tree species such as trembling aspen as a potential source of high quality fibre for the pulp and paper industry (Liang and Chang 2004). A better understanding of the optimal growing conditions for the species might raise the productivity of plantations of aspen, hybrid aspen, hybrid poplar, and native aspen stands (Brown and van den Driessche 2002;

DesRochers et al. 2006; van den Driessche 1999; van den Driessche et al. 2003, 2005). Climate change may affect the growing conditions for aspen in a positive or a negative way, and aspen growth responses to simulated climatic changes may help determine whether the future growing conditions within a given region will approach or deviate from the optimum.

Future research directions

Continuation of this research over several growing seasons would allow us to confirm our theory that inter-annual weather variation has a proportionally stronger positive and negative effect on the growth and performance of aspen than it does on black spruce. In continuing this research, the effects of OTCs on decomposition dynamics and growth responses of trembling aspen and black spruce should be studied over a longer time period. Further research into this topic should continue investigation of the complex effects of OTCs on snowmelt as well as their connection to soil temperature, moisture and potential spring leaching of Ca and Mg cations, in order to better understand their role with respect to growth responses of aspen and black spruce. Phenological responses to OTC treatment should be replicated over several seasons, especially for black spruce, for which we only have one season of data. The effects of OTCs on aspen herbivory should be addressed in more depth; i.e. our theory of decreased herbivory due to phenological asynchrony between the chrysomelid beetles and aspen leaf development created by microclimatic modifications should be examined in more detail. Open-top chamber effects on herbivory of black spruce should also be addressed. Identification and measurements of concentration of chemical defence compounds, and their possible link to higher foliar Ca levels and lower herbivory in OTCs should be tested for both species. Similarly, identification of mycorrhizal species associated with the roots of both species should be performed, and the OTC effect on individual mycorrhizal species should be assessed in the context of how this might impact nutrient and energy budget of the host plant species.

Finally, it would be beneficial to replicate the project on a larger spatial scale and for other tree species. Replicates of fire and logging disturbance sites should be located, preferably along several mixedwood-boreal transitional zones across Canada. Comparison of responses to OTC treatment of other tree species with inherent life strategies similar to those of aspen and black spruce could provide valuable insight into our theory of OTC impact on fast-growing and highly responsive species versus less responsive slow-growing, stress-tolerant species. This could reinforce and extend the applicability of our findings, and allow future research to make plausible predictions regarding the effect of potential climate change on plants based not on individual species identity, but on their life strategies.

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