UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

BOREAL AND TEMPERATE TREE SPECIES MIGRATION IN RESPONSE TO CLIMATIC CHANGE: BEYOND THE "CLIMATIC ENVELOPE"

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Abstract

Plant species distribution and plant community composition vary along environmental gradients. At the continental scale, climate plays a major role in determining plant distribution, while at local and regional scales vegetation patterns rely more on edaphic and topographic factors. The projected global warming and alteration of the water regime will influence plant physiology and phenology, and is likely to promote northward migration of forest tree species. However the influence of soil factors on tree species migration remains unknown. The objective of this work is to investigate the effects of soil factors and processes, as mediate by climate change, on the migration of tree species of the boreal and temperate forests of northeastern North America. In addition, because of their importance in shaping tree communities and their possible influence on tree species migration, other biotic and abiotic are considered.

The projected climate change is expected to increase soil temperature and alter water availability, which control many terrestrial biogeochemical processes such as soil respiration, litter decomposition, nutrient mineralization, fine root dynamics, and plant nutrient uptake. Because tree species respond individually to environmental factors, it can then be speculated that altered soil factors will influence different species in different ways. Ultimately, these differences could be translated in different colonization abilities and migration rates, which will likely alter current tree communities. Furthermore, other biotic and abiotic factors such as genetic adaptation, disturbance regime, habitat fragmentation, and competition are known to influence tree species establishment and tree community composition.

Considering the broad tolerance of most tree species to soil factors, soils should not represent major constraint for the northward shift of populations located at the southern limit or at the center of their distribution range. For populations located at the northern limit of their distribution range, short-distance (e.g. <10 km) migration should be possible as soil factors do not vary much over these distances, while long-distance (e.g. >100 km) migration, could be constrained by soil factors that prevent seed germination and seedling establishment. Because the presence of soil is a prerequisite for the establishment of

trees, the absence of soil or its low development may be the most important factor constraining the establishment of trees in the tundra, along with climate variables and genetic adaptation. The relative importance of soil factors should thus be high in the tundra. In contrast, in the boreal and temperate forests because soils are already developed, soil relative importance for tree establishment should be lower. In these last biomes, other factors, such as competition and disturbance regime should be as important for tree species migration. The migration of tree species is thus highly probable within the area currently occupied by the boreal and temperate forest, but will be restricted to the more favorable sites in the tundra because of the absence of extended soils. However, during pedogenesis, soils may develop properties that can be favorable or detrimental for some plant species. For instance, podzols of boreal forests are generally low in nutrient content compared to hardwood forest brunisols. Thus, nutrient-demanding species typical of hardwood forests may not be able to thrive in podzols following their establishment. Moreover, some parent materials may lead to the development of soils, such as serpentine, which support unique type of vegetation. Locally or regionally, such irreversible soil development processes may hinder tree migration in response to climate change. Thus, while climate change has the potential to improve soil conditions for plant growth, this forcing will have cope with soil properties inherited from slow pedogenic processes that started at the end of the last ice age and that are still in progress today. These antagonistic forces are likely to slow down potential tree migration in response to climate change.

Contents

1.0 Introduction

It has been long recognized that plant species distribution and plant community composition vary along environmental gradients (Allen and Hoekstra, 1990; Levin, 1992). Furthermore, several community and landscape studies have linked species responses to environmental gradients at different spatial scales (Raisa, 1999; Hollingsworth et al., 2006). At the continental scale, climate plays the largest role in determining plant distribution and community composition, (Woodward, 1987; Neilson, 1995; Box et al., 1999), while at the local and regional scales vegetation patterns rely more on edaphic and topographic factors (Ertsen et al., 1995; Iverson et al., 1997). However, at all scales, temperature and the balance between precipitation and evapotranspiration are particularly important, as they largely control the rate of biological and chemical reactions. For instance, both plant net primary productivity (NPP) and microbial decomposition of organic matter are temperature- and moisture-dependent (Hobbie, 1996; Moore et al., 1999; Nemani et al., 2003).

According to the most recent report of the Intergovernmental Panel on Climate Change, warming of the climate system is unequivocal (IPCC, 2007). Most of the globally observed increase in average temperatures since the mid-20th century is attributed to the anthropogenic emission of greenhouse gases. Since ca. 1850 the global atmospheric concentrations of carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) have increased markedly as a result of human activities and now exceed pre-industrial values over the past 650 000 years (IPCC, 2007). For instance, CO_2 concentration increased by 31% (from 278 ppm pre-industrial values to 383 ppm in 2007), and that of CH_4 by 150% (from 700 ppm to 1745 ppm). Due to the radiative forcing of these greenhouse gases, world surface temperatures have increased by 0.74°C between 1906 and 2005, and are projected to rise by between 1.1 and 6.4 °C by the end of the 21st century (IPCC, 2007). Even if greenhouse gas concentrations were to be stabilized, anthropogenic warming is projected to continue for centuries due to the timescales associated with climate processes and feedbacks, and to the atmospheric lifetime of the greenhouse gases (CO_2 > 1 000 years, CH_4 ~ 12 years; IPCC, 2007). Thus, both past and future anthropogenic CO_2 emissions are susceptible to continue to contribute to global warming for more than a millennium. In northeastern North America, warming is projected to be somewhere between 3-4°C and precipitation is projected to increase by 10-20% by the end of the 21st century (IPCC, 2007). The warming is expected to be largest in winter, and snow season length and snow depth are expected to decrease, except in the northern part of the boreal forest where maximum snow depth is likely to increase.

According to many scientists, the increase in atmospheric CO_2 concentration and the concomitant warming and modifications of the water regime will, in all likelihood, influence plant physiology (Keeling et al., 1996; Myneni et al., 1997; Cannell, 1998) and phenology (Olszyk et al., 1998; Raulier and Bernier, 2000; Delbart et al., 2008), and modify the future range and dynamics of many plant species and ecosystems (Emanuel et al., 1985; Overpeck et al., 1991; Rizzo and Wiken, 1992; Hansen et al., 2001; Neilson et al., 2005; Hamann and Wang, 2006; McKenney et al., 2007). Changes in physiology, phenology, and distribution of individual plant species will inevitably alter competitive and other interactions between species, with consequent feedbacks to local abundance and community composition. Moreover, it is also likely that some species will become extinct (Thomas et al., 2004), either as a direct result of physiological stress or via interactions with other species. These extinctions could possibly reduce the functional resilience of ecosystems in response to altered environmental conditions and have consequences for ecosystem functions such as carbon storage capacity (Thomas et al., 2004). Recent analyses of long-term data sets indicate that some tree species are already responding to the recent anthropogenic climate change, especially at the northern treeline of the boreal forest (Payette and Filion, 1985; MacDonald et al., 1998; Lloyd and Fastie, 2003; Gamache and Payette, 2005; Caccianiga and Payette, 2006).

Furthermore, it is widely accepted that projected global warming is susceptible to impact soil factors and processes, such as litter decomposition (Hobbie, 1996) and N mineralization (MacDonald et al., 1995). In turn, these modifications are susceptible to influence plant migration.

Although temperature and precipitation are often regarded as being the major factors determining plant species and ecosystem distributions, other factors such as dispersal ability, competition, predation, disturbance regime, and rate of genetic adaptation are also considered important. Despite the fact that these factors are acknowledged to have the potential to influence the success of species migration (e.g. McKenney et al., 2007), they are rarely included in models that simulate the effects of climate change on plant species migration. Similarly, although soil factors, such as nutrient and water availability, are known to influence seed germination, seedling survivorship and growth, and hence the probability of successful colonization of a plant species, soils are overlooked in most models simulating plant species migration.

Considering that projected climatic changes are (i) expected to promote northward migration of forest tree species and communities, and (ii) will in all likelihood modify soil biochemical properties, the main objective of this synthesis is to investigate how soil biochemical properties will respond to global warming and altered water regime, and how these soil alterations could influence the migration of tree species across several biomes of northeastern North America (i.e. from the boreal forest to the tundra, and from the temperate forest to the boreal forest). In addition, because of their importance in shaping tree communities and their likely influence on tree species migration and establishment, other biotic and abiotic factors, including atmospheric CO_2, will also be considered. I will first review tree migration in response to past, recent, and projected climate change. Then, I will review how soils currently limit tree species distribution. Next, I will review the responses of soil factors and processes to projected climate change, and then the potential responses of tree species to altered soil properties as mediated by climatic change. Finally, I will discuss the potential migratory responses of trees to other biotic and abiotic factors. Although this work focuses on the migration of trees in response to climate change in northeastern North America, results from studies held in Scandinavia and Alaska will be used to exemplify the views supported by this work.

2.0 Past, current, and future response of vegetation to climate change

2.1 Response of boreal and temperate tree species to past global warming

The last ice age, the Wisconsin, began about 100 000 BP, and glaciers expanded to reach their maximum 18 000 to 20 000 BP. At its maximum, the ice sheet extended over half of North America, from the Canadian Rockies, across the northern plains, to southern New England. The region immediately south of the ice sheet was dryer and cooler than today (Webb, 1988), and was occupied by the arctic tundra, boreal and deciduous forests arranged in sequence farther to the south. The Wisconsin ended at the start of the Holocene (ca. 12 000 BP) with a sudden and rapid warming that melted the ice sheet in a few thousand years (Dyke and Prest, 1987; Vincent and Prest, 1987). The increasing global temperature and retreating ice sheet then initiated a period of rapid adjustment of species ranges to new prevailing climatic conditions. Based on pollen and plant macrofossils (e.g. seeds, fruits, leaves, twigs and wood) preserved in sediments found in wetlands, peatlands and lakes, several authors have reported evidence of past migration of trees.

As early as 15 000 years ago, changes began in what is now southeastern U.S., where boreal species were replaced by hardwood species (Webb, 1988). Spruce (*Picea* spp.) moved into the tundra, and tundra species established where the retreating ice sheet left newly exposed soils. *Picea* spp. were rapidly migrating into the tundra and became established in parts of the Great Lakes region only a few years after glacial retreat (Webb, 1988). In New England, however, where the melting of the ice sheet was very rapid, ca. 2000 years elapsed between the time the ice left and spruce arrived (Davis et al., 1980). Species identifications based on pollen morphology (Watts, 1979; Birks and Peglar, 1980) suggest that white spruce (*Picea glauca*) established first, followed by black spruce (*Picea mariana*), and in the East, by red spruce (*Picea rubens*). Pollen records suggest that the spruce forests were then open, similar to the forest-tundra region north of the boreal forest in Quebec.

Thus, most of the tree species now found in the North American boreal forest was able to track the warming trend of the Holocene. Some species like black spruce, eastern larch

(*Larix laricina*), and balsam poplar (*Populus balsamea*) were able to develop widespread populations during that period (Jackson et al., 1997), so that they are now among the tree species that show the northernmost range (Burns and Honkala, 1990; Thompson et al., 1999). Paleoecological records show that, south of the Laurentian ice sheet, *Picea* spp. were abundant and widespread and reached their current northern range limit about 3 000 years ago (Jackson et al., 1997). According to Davis (1983), balsam fir (*Abies balsamea*) reached southern Quebec around 10 000 BP, while white pine (*Pinus strobus*) reached its current northern limit in Quebec about 9 000 years ago. Deciduous species reached southern Quebec a few thousand years later (e.g. *Quercus* spp. 7 000 BP; *Fagus grandifolia* 6 000 BP; *Ulmus* spp. 8 000 BP). Adjustments to changing climates have continued to the present, with the westward expansion of several species (e.g. white pine) in the last 2000 to 3000 years in response to increased precipitation (Jacobson, 1979). Similarly, the American beech (*F. grandifolia*) has expanded 70 km westward in upper Michigan within the last 500 years in response to climatic changes associated with the Little Ice Age (ca. 1300 to 1850; McLachlan et al., 2005). Holocene pollen records thus show an increase through time in the number of tree genera present in northern North America. The increase in diversity was caused by successive immigrations of trees moving northward behind the retreating glacier. According to these records, tree species moved at different rates, reinforcing Gleason's (1926) idea of individualistic view of plant succession and chance combinations of species assemblages.

Therefore, numerous studies have shown that tree species both typical of present temperate and boreal forests have been able to track past global warming by rapid migration. It is estimated that some species have been able to migrate as fast as 10-100 km/century during the Holocene warming (McLachlan and Clark, 2004; McLachlan et al., 2005). Our current knowledge of seed dispersal mechanisms and current observations of seed dispersal distances, often not extending beyond the edge of the tree and rarely exceeding 100 m, cannot explain such rapid migration rates. It is often suggested, however, that with the projected warming for the next 100 years, migration rates of over 100 km/century will be required for trees to track future climate change (Malcolm et al., 2002). Thomas et al. (2004) and Hansen et al. (2006) suggest that species which will be unable to migrate fast enough could become extinct. The discrepancy between our knowledge of past migration rates with current observations gave rise to extensive debates and research to resolve what is termed as the Reid's paradox (Clark et al., 1998). Many studies have shown that various mechanisms, like long-distance seed dispersal by wind and animals, or the existence of isolated populations near the ice sheets during the last glacial period (Kullman, 1995, 2002a, 2004) could explain the rapid migration rates observed in the paleoecological records.

Although none of the paleoecological studies cited above mention soil factors or processes as having had influence on tree establishment, it can be speculated that following the retreat of the glacier, soil factors were not constraining seed germination and seedling establishment, allowing for rapid colonization of newly available sites and for rapid species migration. It can also be speculated that colonization and migration were facilitated by the absence of competition for habitats resources. Thus, it can be hypothesized that following the retreat of the glacier at the end of the last ice age, adaptation to cold climate and dispersal capacity were the main factors constraining plant colonization and species migration.

2.2 *Impacts of recent global warming on boreal and temperate tree species*

Ecotones, i.e., transition areas between two adjacent ecological communities, are sensitive to climate variations (Loehle, 2000; Goldblum and Rigg, 2005). In these areas, the projected climate change is susceptible to cause detectable shifts in species composition, whereas in the middle of a broad forest zone such changes might not occur. Because northern treeline ecosystems (i.e., the transition zone between the boreal forest and the tundra) are sensitive to changes in climatic conditions, several authors have used these ecosystems as proxies of biotic changes in response to global warming (e.g. Kullman, 1998, 2001, 2002b; Gamache and Payette, 2004). Thus, several studies have shown that at the end of the Little Ice Age (ca. 1850), northern treelines of North America and Eurasia began migrating poleward in response to warmer temperatures. In Canada, Payette and Filion (1985) and Caccianiga and Payette (2006) showed that the white spruce treeline along the east coast of Hudson Bay expanded significantly during the last 100 years in response to recent climatic warming. Lloyd and Fastie (2003) found similar results for white spruce in Alaska, concluding that the recent shift in the location of the forest-tundra border was a response to recent warming. In northern Quebec, Gamache and Payette (2005) showed along elevational transects that black spruce treelines from the southern forest-tundra moved northward through the establishment of seed-origin spruce, while those from the northern forest-tundra rose through height growth of stunted spruce. Similarly, Johnstone and Chapin (2003) recently found that the lodgepole pine (*P. contorta*) was still expanding northward in central Yukon, demonstrating that this species is not in equilibrium with current climate. In Eurasia, Kharuk et al. (2005) showed that the Siberian pine (*P. sibirica*) and birches (*Betula* spp.) were penetrating into a zone traditionally occupied by two larch species (*L. gmelinii* and *L. sibirica*) in response to climatic change during the past three decades. Similarly, Kullman (1998, 2001, 2002b) showed that treelines in the Swedish Scandes responded positively to recent global warming with upward and northward tree species invasion into the tundra. Finally, several other authors have linked the recent warming with increased tree density or tree growth at the treeline (Morin and Payette, 1984; MacDonald et al., 1998; Gamache et Payette, 2004).

While several studies have focused on the transition at the treeline, surprisingly few specifically addressed the effects of recent climate change on the transition zones between forested areas, e.g. between boreal coniferous and mixedwood forests or between boreal mixedwood and temperate deciduous forests. Reasons that might explain the lack of studies in these areas include (*i*) the slow and gradual changes in climatic conditions, (*ii*) the difficulty to observe range shift because of the complex structure of forested ecosystems compared to treeline ecosystems, (*iii*) slow demographic rates and limited dispersal, (*iv*) natural disturbances and succession that could mask range shifts due to climatic variations, and (*v*) the complexity of inter- and intraspecific interactions that could hide the effects of recent climate change on species range. However, montane ecosystems provide an ideal environment for observing shifts in forest distribution in response to climate change because of steep climatic gradients across elevation, which in many respects are comparable to latitudinal climatic gradients, but with clear boundaries between forest types that may facilitate detection of range shifts (Diaz et al., 2003). In that respect, in 2004 Beckage et al. (2008) resurveyed plots established in 1964 along elevation transects in the Green Mountains of Vermont, U.S., to examine whether a shift had occurred in the location of the transition zone between the northern hardwood and boreal forests. They found an increase in dominance of hardwood species and a concomitant decrease in boreal species within the transition zone. Using aerial photographs and satellite imagery, they found an estimated 91- to 119-m upslope shift in the upper limits of the northern hardwood-boreal transition zone from 1962 to 2005. This shift was consistent with a 1.1°C increase in annual temperature, along with a 34% increase in precipitation. They concluded that the upslope shift they observed was the result of climate-driven shifts in competitive balance between hardwood and boreal species in the transition zone in conjunction with increased canopy turnover.

As one may argue, the above-cited observations do not exclude that these recent range expansions may only represent the most recent phase of Holocene tree migration. However, these observations of recent, directional shifts at the northern treelines are consistent with expectations of species migration in response to climatic warming, and offer further support to the idea that tree species will in all likelihood migrate poleward in response to projected climate change.

2.3 *Projected impacts of global warming on boreal and temperate tree species*

Computer model simulation has been extensively used in the recent years to forecast migration rates of tree species and to predict future forest composition. These simulations indicate that, in response to climatic warming and changes in water balance, plant species and communities from the boreal and temperate forests are likely to experience longer growing seasons (Chuine et al., 2000; Goldblum and Rigg, 2005) and modified disturbance regime (Flannigan et al., 1998; Stocks et al., 1998; Flannigan et al., 2001; Bergeron et al., 2004). In response to global warming, simulations also anticipate significant shifts in plant species ranges (Overpeck et al., 1991; Iverson and Prasad, 1998; McKenney et al., 2007). However, the rate at which current climate change is occurring is deemed unprecedented (IPCC, 2007). For this reason, there is concern that the extent of the range shifts will surpass the dispersal capacity of many species, especially when considering habitat fragmentation (Schwartz, 1993; Dyer, 1994).

Using general circulation models (GCM), Overpeck et al. (1991) predicted that climate change could lead to significant vegetation change. The array of the genera they simulated were likely to be displaced northward by at least 100 km, and in some cases (e.g. *Picea* spp.), by as much as 1000 km. Their results suggest that spruce and northern pine (i.e. *P. strobus*, *P. banksiana* and *P. resinosa*) populations in the eastern U.S. could decline in abundance because of a northward shift of their southern range limit. In parallel, southern oaks (*Quercus* spp.) and pine populations are expected to move northward by as much as 500 km because of local drying, while the area of greatest abundance of birches could change significantly. Thus, in eastern U.S., areas now dominated by mixed conifer-hardwood forests could become increasingly deciduous. Such range shifts would also change the composition of the eastern Canadian boreal forest which would become more pine-rich than at present. Furthermore, Overpeck et al.'s (1991) simulation indicates that the area now occupied by tundra vegetation would decrease where simulated warming favors the expansion of tree populations. Therefore, according to Overpeck et al. (1991) in the absence of altered forest disturbance rates, barriers to seed dispersal, or soil limitations, vegetation change is likely to reach the simulated doubled CO_2 patterns within 300 to 500 years. These results support paleoecological observations that biome compositions will not remain constant as plant taxa respond individualistically to future climate change.

Similarly, assessing the sensitivity of Canadian biomes to climatic change, Rizzo and Wiken (1992) showed that climate change under a 2 X CO_2 scenario resulted in major shifts in boundaries between biomes. For instance, the temperate forest expanded in the eastern boreal forest, while the arctic tundra was displaced by the subarctic tundra in the west but not in northern Quebec. Instead, the subarctic tundra in northern Quebec was replaced by the boreal forest which shifted northward. Rizzo and Wiken (1992) also indicated that beyond climatic factors, ecological assemblages are dependent upon site factors such as soil texture and fertility, water availability, slope, aspect, and elevation.

They concluded that it cannot be assumed that climatic change would result in extensive shift of species to new suitable areas because (*i*) a lag would likely occur before vegetation and soils mirror the new prevailing climate, and (*ii*) adjacent geomorphology and physiography may not be favorable for the establishment of migrating species. Therefore, according to Rizzo and Wiken (1992), transformation of the current biomes should not be instantaneous because soils will remain relatively unchanged for a long period of time, which would limit the establishment and growth of species following dispersal.

Likewise, in a series of studies predicting the distribution of over 70 tree species following climate change in the eastern United States, Iverson and Prasad (1998, 2002) concluded that several species now occurring in the temperate or boreal forests would show range expansion and/or shifts (Table 1). For example, balsam fir, sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) were expected to migrate north, showing an important range decline in the eastern U.S. Other species (e.g. *Ulmus americanus*, *Acer rubrum*, and *Acer saccharinum*), however, are expected to show little change in their current range. Moreover, their results suggest that some species (e.g. *Carya tomentosa*, *Celtis laevigata*, *Cercis canadensis* and *Diospyros virginiana*) currently absent in Canada or present only in southernmost Ontario could become established in eastern Canada in a near future. They concluded, however, that historic rates of migration (~10-50km/100 years) will not likely occur with current fragmented habitat.

Table 1. Predicted species potential area change in the U.S. -: area decrease, 0: no change, +: area increase (after Iverson and Prasad, 1998)

Species	Area
Abies balsamea[1]	-
Acer rubrum	0
Acer saccharinum	0
Acer saccharum[1]	-
Betula alleghaniensis[1]	-
Betula papyrifera[1]	-
Caprinus carolina	+
Carya cordiformis	-
Carya ovata	0
Fagus grandifolia	-
Fraxinus americana	-
Pinus resinosa[1]	-
Pinus strobus	+
Populus deltoids	+
Populus grandidentata[1]	-
Populus tremuloides[1]	-
Quercus rubra	-
Thuja occidentalis	-
Tilia americana	-
Tsuga canadensis	-
Ulmus americana	0

[1] species projected to become absent from the United States.

Finally, McKenney et al. (2007) used GCMs and species current climatic envelopes (CE) - which related species boundaries to macroscale climatic variables such as temperature and precipitation (Hampe and Petit, 2005) - to predict the potential impacts of climate change on the distribution of North American trees. They concluded that the mean centers of future CEs were predicted to shift northward between 3.0 and 6.4 degrees latitude (i.e., 330 and 700 km) on average (Table 2). Their simulation predicted that by the end of the 21st century the CE of most of species modeled would shift into northern Ontario and Quebec. For example, the sugar maple CE is projected to shift north between 3.3 and 8.7 degrees, and that of the yellow birch between 3.9 and 8.2 degrees (Table 2). As found by Iverson and Prasad (1998; 2002), several of the species modeled (e.g. *Q. palustris*, *B. nigra*, and *Liriodendron tulipifera*) are projected to expand their range into southern Canada by the end of the 21st century.

Table 2. The 20 North American tree species with the largest projected shifts in latitude (after McKenney et al., 2007).

Species	Northward shift in climate envelope latitude (degrees)
Alnus rhombifolia	9.7
Tilia americana	9.2
Salix nigra	9.0
Acer saccharum	8.9
Ostrya virginiana	8.7
Acer saccharinum	8.7
Quercus rubra	8.7
Prunus serotina	8.5
Ulmus rubra	8.4
Fraxinus americana	8.4
Quercus alba	8.4
Betula alleghaniensis	8.2
Pinus strobus	8.2
Populus deltoids	8.2
Juglans nigra	8.2
Juglans cinerea	8.1
Celtis occidentalis	8.0
Quercus palustris	7.9
Quercus macrocarpa	7.9
Betula nigra	7.8

Furthermore, there is concern about the effects of habitat fragmentation on species dispersal in response to climate change. Indeed, fragmented habitats could give rise to many remote areas which may become climatically suitable but beyond the dispersal capacity of many species, consequently reducing potential colonization of those remote habitats. Several other authors (e.g. Schwartz, 1993; Iverson et al., 1999; Schwartz et al., 2001) suggested migration rates of 1-10 km per century to be the maximum future rates in highly fragmented habitats. This is alarming, especially if long-distance dispersal events have significantly lesser effects on the projections of future migration into highly fragmented forests compared to migration rates in fully forested situations. According to Walther et al. (2002), increased extinction risks due to future global warming and accelerated by habitat loss and fragmentation are expected.

In the studies cited above, assessments of future distribution change are based on the climate envelope approach that relates species distribution to some *a priori* selection of climatic variables that are intended as indicators of the true underlying physiological or biophysical limits on species distribution. Although, non-climatic factors such as dispersal, competition, and disturbance regime could also influence species migration, these factors are systematically omitted in models simulating the impact of climate change on plant distribution. In addition, despite the fact that soil factors are of utmost importance to plant establishment and growth, and that modelers recognize their potential to influence the success of plant migration and establishment (e.g. McKenney et al., 2007), soil factors are almost systematically omitted in models simulating the effects of climate change on plant migration. Hence, the following sections will focus on the effects of climate change on soil biochemical properties and root systems, and then on the potential response of North American temperate and boreal tree species to changes in soil properties as mediated by climate change. But first, I will briefly review how soil factors and processes currently limit plant distribution.

3.0 Soil limits to plant growth and distribution

The type of vegetation covering a region depends on several environmental factors, among which soil is of utmost importance. Indeed, soil provides plants with a medium for growth and supplies them with nutrients (Aber and Melillo, 1991). Hence, the nutrient status of an ecosystem's soil (in combination with pH, moisture and aeration) limits plant growth and has the potential to influence species distribution and community composition (Shaver and Chapin, 1980; Roberts and Wuest, 1999; Shaver et al., 2001). But what is soil? What constitutes it and how is it formed?

3.1 Soil pedogenesis

Soil is the unconsolidated mineral or organic material lying at the surface of the earth that serves as a natural medium for the growth of land plants, and that has been subjected to the effects environmental factors (SSSA, 2001). Indeed, during pedogenesis, i.e. soil development, soil physico-chemical properties are influenced by several environmental factors. These factors, also known as “state factors”, include climate; living organisms; parent material; topography; and time (Figure 1; Jenny, 1994).

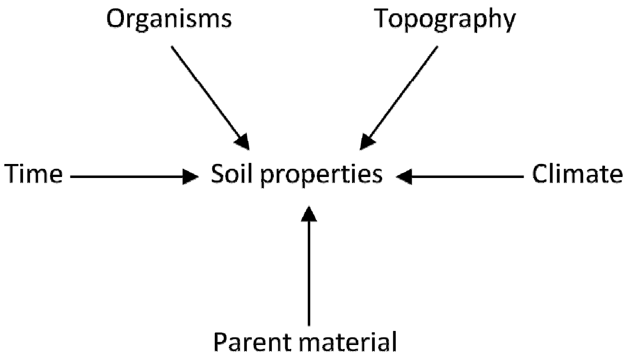

Figure 1: Factors influencing soil development (adapted from Jenny, 1994).

Climate plays a very important role in the genesis of a soil. On the global scale, there is a correlation between major soil types and climatic variables (Aber and Melillo, 1991; Brady and Weil, 2004), i.e. with temperature and precipitation regime. While temperature has a direct influence on the weathering of bedrock to produce mineral particles, moisture availability promotes the weathering of bedrock and sediments, and chemical reactions (Pidwirny, 2006). The availability of moisture also has an influence on soil pH and the decomposition of organic matter (Knoepp and Vose, 2007; Voroney, 2007). At regional and local scales, climate becomes less important in soil formation (Pidwirny, 2006). Instead, pedogenesis is more influenced by factors like living organisms, parent material, topography, and time.

Living organisms have a role in a number of processes involved in pedogenesis including organic matter accumulation, profile mixing, and biogeochemical nutrient cycling (Coleman and Wall, 2007; Plante, 2007). Under equilibrium conditions, vegetation and soil are closely linked with each other through nutrient cycling. The cycling of nitrogen and carbon in soils is almost completely controlled by the presence of animals and plants (Coleman and Wall, 2007). Through litterfall and the process of decomposition, organisms add humus and nutrients to the soil which influences soil structure and fertility.

Parent material refers to the rock and mineral materials from which the soils develop. These materials can be derived from residual sediment due to the weathering of bedrock or from sediment transported into an area by way of erosion (Jenny, 1994). The influence of parent material on pedogenesis is usually related to soil texture, soil chemistry, and nutrient cycling. Hence, some parent materials lead to the development of soils that possess unique characteristics that may be favorable or detrimental for some plant species. For instance, some species, such as the eastern white cedar (*Thuja occidentalis*), are associated with lime-rich soil (Burns and Honkala, 1990). Likewise, some species are closely associated with serpentine outcrops. Plant inhabiting these habitats experience drought, heavy metal (such as Cr, Co, and Ni) exposure, and nutrient stress (Kruckeberg, 1984). Important nutrients lacking in serpentine include calcium, potassium, and phosphorous (Kruckeberg, 1984), which are rapidly lost through weathering and leaching. Nitrogen is also scarce due to limited plant growth. Hence, serpentine soils often support fewer species than non serpentine soils (Kruckeberg, 1954). Nonetheless, some plant species, such as *Adiantum viridimontanum* and *Aspidotis densa*, are adapted to thrive on these soils.

Topography generally modifies the development of soil on a local or regional scale. Pedogenesis is primarily influenced by topography's effect on microclimate and drainage. Soils developing on moderate to gentle slopes are often better drained than soils found at the bottom of valleys (Pidwirny, 2006). Good drainage enhances a number of pedogenic processes that are responsible for the development of soil horizons, such as podzolization (Thorn et al., 2001). Steep topographic gradients inhibit the development of soils through the continued removal of surface sediments, i.e. erosion (Jenny, 1994). Furthermore, in the Northern Hemisphere, south-facing slopes tend to be warmer and drier than north-facing slopes (Small and McCarthy, 2002). These differences result in the soils of the two areas being different in terms of depth, texture, biological activity, and soil profile development.

Time influences the temporal consequences of all of the factors described above. Many soil processes become steady state overtime when a soil reaches maturity (Jenny, 1994). Pedogenic processes in young soils are usually under active modification through negative and positive feedback mechanisms in attempt to achieve equilibrium.

These “state factors” interact to influence the pedogenic processes that lead to the formation of the different types of soils found in northeastern North America, such as podzols, brunisols, and gleysols. These types of soils possess distinctive physico-chemical properties that, in combination with other environmental and habitat factors, influence plant growth, species distribution, and community composition (Lomolino et al., 2006).

In eastern North America podzols are typical of cool and moist climates (Pidwirny, 2006). In such climates plant growth may be substantial, but the low temperatures inhibit microbial activity so organic matter accumulates (Clymo et al., 1998; Charman, 2002). As the humus decays organic acids are released and leached through the soil profile by percolating water. The hydrogen ions of these acids tend to replace cations that are important for plant growth, such as calcium, potassium, magnesium and sodium (Brady and Weil, 2004). This process leaves behind a silica-rich soil containing oxidized iron and aluminum compounds, but few cations. Although coniferous forests are typical of podzolic soils, mixedwood and hardwood forests can also be found on podzols (Bérard and Côté, 1996).

Brunisols, which tend to develop in warmer climates that podzols, occur commonly in southern Quebec and Ontario. Compared to podzols, they are generally less acidic, more rich in base cations (Bérard and Côté, 1996), and are found under vegetation types that produce readily decomposable litter, such as maple forests. Thus, brunisols can support plant communities that are more nutrient-demanding than those found on podzols (Aber and Melillo, 1991).

Gleysols, which are typical of clay deposits, are found in ecosystems that are frequently flooded or permanently waterlogged (Pidwirny, 2006). These conditions tend to slow the decomposition of organic matter, which results in low soil fertility. In turn waterlogged conditions and low soil fertility reduce plant growth and the productivity of ecosystems (Charman, 2002). In northeastern North America gleysols are typical of the Clay Belt of northeastern Ontario and northwestern Quebec, and of the St. Lawrence lowlands.

3.2 Humus forms

Another important soil characteristic that may influence the productivity of an ecosystems and species distribution is humus form. Humus form integrates information on soil biological activity, pH, moisture, and nutrient availability (Wilson et al., 2001), all of which are known to influence plant composition and the productivity of ecosystems.

Three forms of humus are generally recognized: mor, moder and mull. Mor humus is primarily found on coarse textured soils under cool and humid climate, or where acidifying vegetation predominates (Brady and Weil, 2004). It is formed of undecomposed or partially decomposed organic matter that is not incorporated into the mineral soil (MNDNR, 2003). It is recalcitrant to decomposition and pedofauna is rare or absent (Table 3). Hence, decomposition is slow and is accomplished primarily by fungi. In mor humus, because calcium is rare, fulvic acids are abundant and are responsible of podzolization. Thus, the pH of mor humus is usually low (<5.0), and the C:N ratio is generally high (>20) (Berg and McClaugherty, 2007). Consequently, these soils are generally of low fertility, and trees rely mainly of organic forms of N for nutrient supply (Schimel and Bennett, 2004). This form of humus is typical of podzols. In northeastern North America, although mor humus is typical of coniferous forests, such as fir or spruce forests, it is also common under hardwood forests, such as beech-maple stands, which produce relatively recalcitrant litter because of high lignin content (Melillo et al., 1982).

Table 3. Biological and physico-chemical properties of humus forms (adapted from Berg and McClaugherty, 2007).

Humus form	pH	C:N	Fauna	Flora	Organic matter decomposition	Mineralization
Mull	±5.0	10-15	Earthworms	Bacteria	Rapid	Rapid
Moder	4.0-5.0	15-25	Arthropods	Bacteria/Fungi	Moderate	Slow
Mor	3.5-4.5	>25	Collembola/Acari	Fungi	Slow	Very slow

Moder humus is characteristic of mesic hardwood forests lacking earthworms. It is formed of undecomposed and partially decomposed remains of broad-leaved deciduous forest litter that is shallowly incorporated into the mineral soil (MNDNR, 2003).

Decomposition is moderately slow and is accomplished by bacteria and invertebrates (Table 3). It is characterized by the presence of litter (L), fermentation (F), and humus (H) layers. The humus layer gradually grades into the mineral topsoil. The pH is usually low (4.0-5.0) and the C:N ratio typically varies between 15-25 (Berg and McClaugherty, 2007). In eastern North America, this form of humus is typical of brunisols found under yellow birch-sugar maple stands.

Mull humus is formed of well-decomposed organic matter that is mixed deeply into the mineral soil. It is characterized by the presence of a thin litter (L) layer comprised only of remnants from the previous fall and a thick topsoil layer (MNDNR, 2003). Mull is typical of hardwood forest with earthworms, such as sugar maple stands (MNDNR, 2003). In these stands, earthworms are responsible for mixing leaves and humus into the topsoil. Decomposition and mineralization are typically rapid in mull humus. The pH is usually higher (±5.0) than that of moder and mor, and the C:N ratio varies between 10-15 (Berg and McClaugherty, 2007). This form of humus is generally rich in nutrients, and can support nutrient-demanding plant communities (Walker, 1998). This form of humus is also typical of brunisols.

Thus, we saw that several environmental factors are responsible for soil development, humus formation and soil nutrient status. Soil factors, in combination with climate variables, interact to influence plant growth and community composition, and hence to produce the wide arrays of forest stands found in northeastern North America. Thus, in response to projected climate change, migrating tree species will have to cope with soil properties inherited from slow pedogenic processes that started soon after the retreat of the glaciers at the end of the last ice age, and that are still in progress today. Hence, soil formation is considered to be irreversible, which means that a soil never returns completely to its initial state during its development (Targulian and Krasilnikov, 2007). Only deep erosion (such as may result from glaciations), down to unaltered parent material returns a soil back to the initial stage of its development. However, although the results of soil development are deemed irreversible, climate change has the potential to alter biochemical processes and modify soil properties, at least in the upper part of the solum, which in turn has the potential to influence ecosystem productivity and species distribution. The following section reviews the possible effects of climate change on soil biochemical factors and processes.

4.0 Responses of soil factors and processes to projected climatic change

It is widely accepted that projected global warming is susceptible to impact soil factors and processes (Goulden et al., 1998; Davidson and Janssens, 2006). For example, in northern latitudes, longer growing seasons are expected to reduce the length and extent of the snow cover period, therefore increasing soil temperature (IPCC, 2007), a factor known to influence the rate of chemical reactions, and impact soil carbon (C) reservoir. In turn, this altered soil C reservoir may result in a positive feedback to the atmosphere, exacerbating the global warming (Cox et al., 2000; Knorr et al., 2005; Davidson and Janssens, 2006).

The relationship between temperature and the rate of chemical reactions was first proposed by Arrhenius in the 1880’s (Voroney, 2007). This relationship states that the rates of chemical reaction increase with rising temperature, due to increased molecular interactions. Therefore, soil temperature, along with water availability, is of great biological significance because it controls many terrestrial biogeochemical processes such as soil respiration (i.e., CO_2 emission; Raich and Schlesinger, 1992), litter decomposition (Hobbie, 1996), N mineralization and nitrification (MacDonald et al., 1995), denitrification (Malhi et al., 1990), CH_4 emission (Crill et al., 1988; Crill, 1991; Johnson et al., 1996), fine root dynamics (Gill and Jackson, 2000; Pregitzer et al., 2000; Sullivan et al., 2007), and plant nutrient uptake (BassiriRad et al., 2000; Schmidt et al., 2002). In northern latitudes, these processes may ultimately influence plant growth and alter plant communities (Chapin et al., 1995; Sturm et al., 2001; Sullivan et al., 2007).

Over the last 10 to 15 years, the need for information on the response of ecosystems to altered climate has been addressed by a growing number of temperature-manipulation experiments. These experiments have shown that rates of soil respiration generally increase with warmer temperature (Figure 2; PeterJohn, et al., 1993, 1994; McHale et al., 1998; Rustad and Fernandez, 1998; Lavigne et al., 2003; Hartley et al., 2007). Soil respiration is the sum of microbial respiration by decomposition of organic matter and root respiration. In the boreal and temperate forest, a large part of soil organic matter is stored in the forest floor as organic matter that is physically unprotected from microbial decomposition. Thus, an increase in soil temperature generally results in greater rates of microbial activity, which in turn results in increased rates of litter decomposition and nutrient mineralization (Domisch et al., 2006; Rinnan et al., 2007). For example, after 2 years of decomposition in a northern hardwood forest, mass remaining of American beech leaf litter was respectively approximately 60, 50 and 42% for ambient, ambient+5°C, and ambient+7.5°C soil temperature treatment (McHale et al., 1998). Interestingly, the decomposition of sugar maple litter was unaffected by the soil temperature treatment. Similarly, after 30 months of decay in soil heated approximately 5 °C above ambient temperature in a spruce-fir forest, mass loss of red spruce litter increased 19% but that of red maple (*A. rubrum*) was unaffected (Rustad and Fernandez, 1998). In a mixed deciduous forest, PeterJohn et al. (1994) observed that heating the soil by 5°C doubled

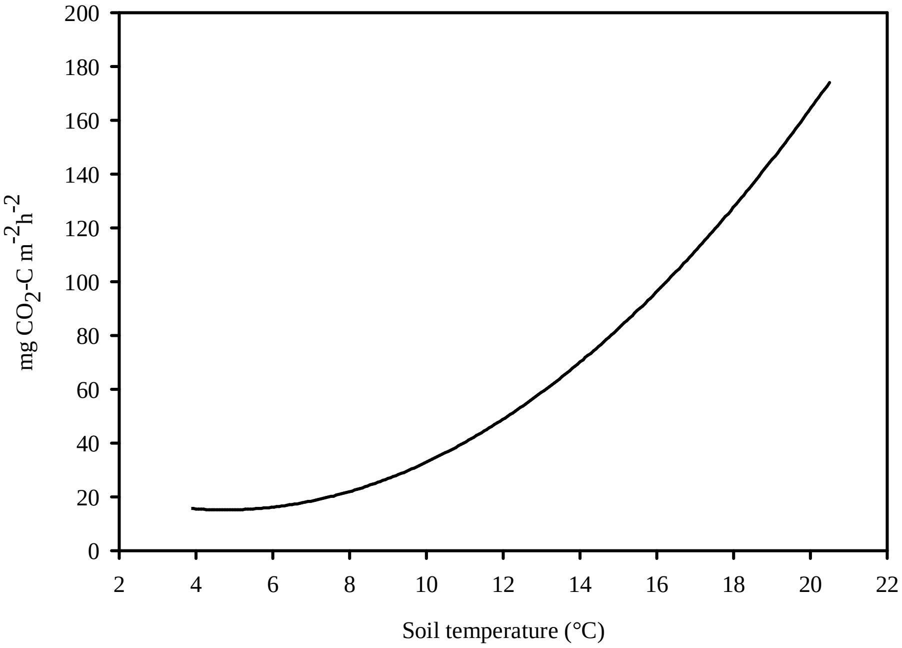

Figure 2. Relationship between mean daily CO_2 flux from soil and soil temperature (adapted from Boone et al., 1998).

daily rates of net N mineralization in both mineral soil and forest floor. In an experiment using buried heating cables, Van Cleve et al. (1990) showed that soil heating of black spruce stands significantly increased decomposition of the forest floor which resulted in greater extractable N and P concentrations in the forest floor, higher N concentrations in the soil solution, and elevated spruce needle N, P, and K concentrations. They attributed higher foliar N content to greater nutrient availability from higher rates of decomposition. Similarly, Wickland and Neff (2008) showed that in black spruce stands soil respiration was greater at 20°C than at 10 °C. Thus, as shown above, increased soil temperature can be responsible for higher soil respiration and nutrient mineralization in hardwood, mixedwood, and coniferous forest. Since productivity in temperate (Vitousek et al., 1982; Melillo et al., 1993; Reich et al., 1997; Joshi et al., 2003) and boreal (Van Cleve and Zasada, 1976; Chapin et al., 1986) forest is often limited by the plant N supply, an increase in N availability to plants should increase NPP. Thus, it can be hypothesized that increased soil temperature due to global warming will increase soil nutrient supply. In the boreal forest, increased nutrient availability may therefore promote the growth of nutrient-demanding species already present, or it may facilitate the establishment of more nutrient-demanding hardwood species, such as sugar maple and yellow birch, and promote the conversion of boreal forest communities, dominated by coniferous species, to mixedwood communities.

However, Giardina and Ryan (2000) showed that increasing temperature does not consistently result in increased rates of decomposition in forest soils. Instead, they found that rates of decomposition were constant across a global-scale gradient in mean annual temperature. Hence, their results suggest that rates of decomposition in forest soils are not controlled solely by temperature limitations to microbial activity. Low soil organic matter quality could also be responsible for the limited substrate availability for the microbial biomass, and may limit microbial respiration (Wickland and Neff, 2008). Indeed, forest-derived C consists of lignin-dominated remains and precipitated by-products of plant and microbial residue that are poor carbon sources for microbes. Thus, rates of nutrient mineralization could be slowed down, consequently decreasing the amount of nutrient available for plant growth, and limiting species migration.

Water is another important soil factor regulating biogeochemical processes. It affects the moisture available to organisms as well as soil aeration status, the nature and amount of soluble materials, the osmotic pressure, and the pH of the soil solution (Voroney, 2007). In addition, water ensures the transport of nutrients by mass flow and diffusion. Microbial activity is also strongly dependent upon water availability: too much or too little water reduces microbial respiration (Davidson et al., 1998; Savage and Davidson, 2001; Martin and Bolstad, 2005; Wickland and Neff, 2008), and hence nutrient mineralization (Figure 3; Wang et al., 2004; Knoepp and Vose, 2007). When plant residues are submerged in water for extended periods of the year and availability of oxygen is limited, microbial activity is reduced, which results in slowed biological decay and accumulation of organic matter (Clymo et al., 1998). Where water is nonlimiting, biological activity may depend mainly on temperature, and standard Arrhenius theory can be used to predict temperature effects. But as soils dry, moisture exerts more control upon biological processes than temperature (Martin and Bolstad, 2005; Wickland and Neff, 2008).

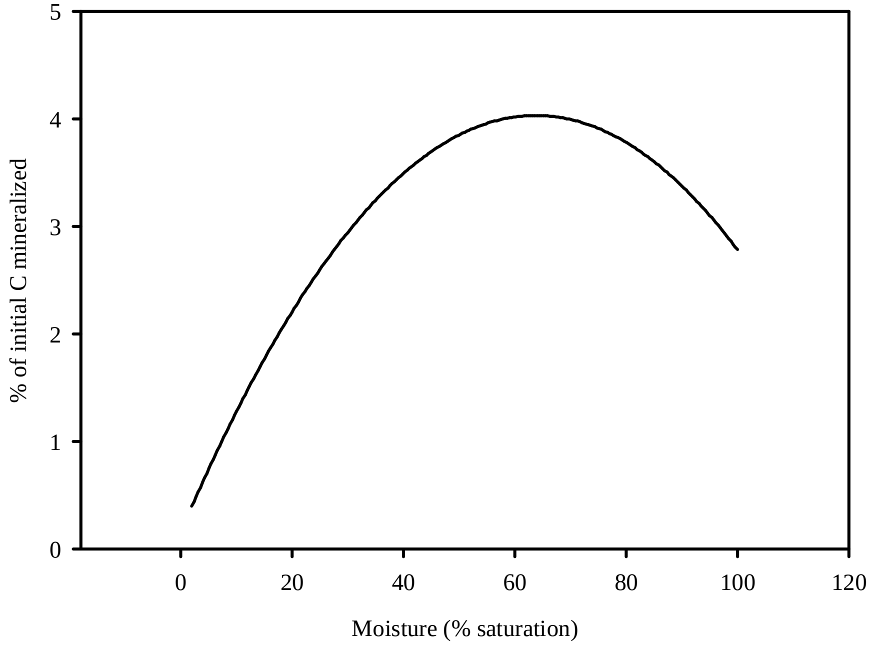

Figure 3. Mean % of initial C mineralized versus soil moisture content (adapted from Wickland and Neff, 2008).

Precipitation regimes under the projected climate change differ greatly according to different regions of the world. Where evapotranspiration is expected to exceed precipitation, drought conditions could occur and could result in reduced microbial activity and nutrient mineralization. Similarly, in regions where precipitations are expected to exceed evapotranspiration, reduced soil microbial activity and mineralization rates could result from newly created waterlogged conditions. In turn, nutrient limitation resulting from both drought or waterlogged conditions can impact on forest productivity (Johnston and Williamson, 2005; Simard et al., 2007).

Furthermore, soil water reacts with soil CO_2 to produce carbonic acid, a major weathering agent (Berner, 1992; Drever, 1994). This acid, together with other acids such as sulfuric and nitric acids, are consumed in both cation exchange and mineral dissolution reactions, which acidifies soil (Reuss et al., 1987; Kohler and Hildebrand, 2003; Oh and Richter, 2004). Rainfall can also affect soil pH through the leaching of nutrients such as calcium (Ca) and magnesium (Mg), which are replaced by acidic elements such as aluminum (Al) and iron (Fe) (Voroney, 2007). Thus, with the projected increase in global temperature - which has the potential to increase soil temperature and hence soil respiration - and increase in precipitation over eastern North America, it can be speculated that soil acidity will increase, increasing losses of nutrients (especially Ca and P), and causing a reduction in the availability of nutrients (Likens et al., 1996; Friedland and Miller, 1999; Ouimet et al., 2001). In eastern North America, this reduction in nutrient availability is suspected to contribute to the slower growth of sugar maples (Ouimet and Camiré, 1995; Duchesne et al., 2002; Juice et al., 2006). Similarly, low soil pH has been cited as a hypothesis to explain the location of the boundary between the mixedwood and coniferous forest. Indeed, low soil pH could prevent the establishment of the balsam fir in the coniferous zone, as this species is intolerant of low pH (Béland and Bergeron, 1993; Paré and Bergeron, 1996). However, despite the fact that several authors have reported negative effects of soil acidification on the growth of sugar maple, Fisher and Binkley (2000) consider that pH is seldom a problem for tree nutrition and growth, except on dry sites where high pH and high salt concentrations combine to impair tree growth. In fact, it is recognized that most tree species do well across a wide range of pH values. Thus, for most tree species soil pH may not represent a major challenge for establishment.

Moreover, although predicted changes in atmospheric CO_2 are small compared to the relatively high CO_2 concentrations in the pore space of soils, increased atmospheric CO_2 is susceptible to influence nutrient availability through altered mineralization (Lipson et al., 2005). Indeed, effects of elevated atmospheric CO_2 on soil microbial organisms could be mediated by plant root production and exudation (Zak et al., 2000). In response to elevated CO_2, microbial biomass and activity have thus been observed to decrease (Diaz et al., 1993), increase (Williams et al., 2000), or remain unchanged (Randlett et al., 1996). In turn, these modifications in microbial biomass and activity are susceptible to influence the decomposition of soil organic matter and N mineralization/immobilization, and consequently the amount of nutrient available for plant growth (Figure 4). Thus, long-term primary production response to elevated CO_2 depends on soil nitrogen (N) mineralization. Despite much effort, it is still uncertain how elevated CO_2 affects long-term soil N dynamics.

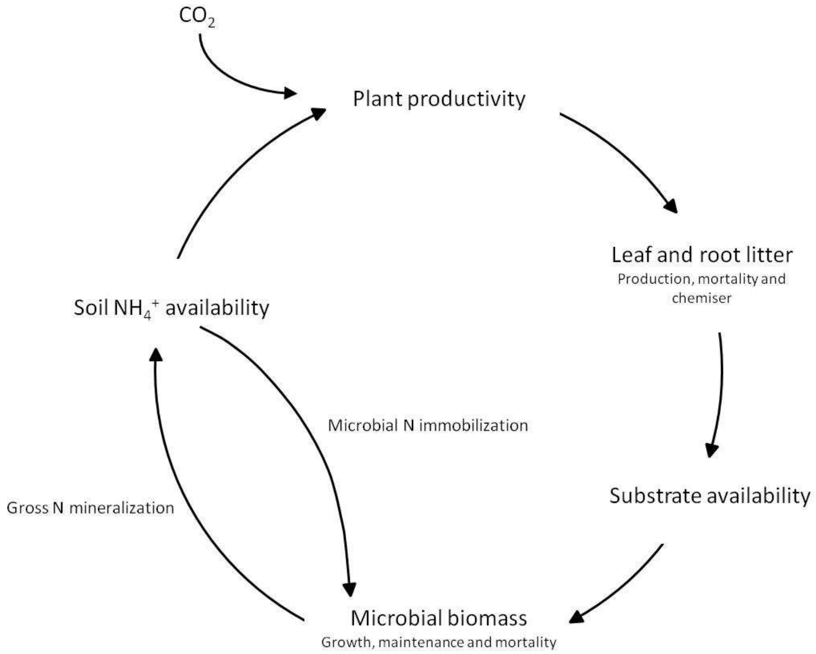

Figure 4. Illustration of the relationships between plant and microbial activity in terrestrial ecosystems, and the potential for these relationships to be altered by elevated atmospheric CO_2. Plant production is often limited by N made available by the decomposition of organic matter in soil. At the same time, the growth and maintenance of soil microorganisms is controlled by the amount and type of organic compounds entering soil via plant litter production. If elevated CO_2 alters the amount of energy available for microbial growth in soil, it also has the potential to alter the microbial demand for N (i.e. microbial immobilization) and decrease the amount of inorganic N available for plant uptake (after Zak et al., 2000).

Along with biological effects on microbial respiration and nutrient mineralization, soil temperature and water availability influence nutrient uptake through direct effects on the growth and physiology of plant root system (McMichael and Burke, 1998; Joslin et al., 2000; Pregitzer et al., 2000; Pregitzer and King, 2005). Usually, root growth begins at low, limiting temperature, and growth rate increases with rising temperature to an optimum (Figure 5). Then, root growth declines with further increasing temperature. Root responses to increasing soil temperature are common for tree species, such as white oak (*Q. alba*) (Teskey and Hinckley, 1981), trembling aspen (*P. tremuloides*), jack pine (*P. banksiana*) and black spruce (Steele et al., 1997). Possible mechanisms for enhanced root growth in warmer soils include: source-sink relationships between above- and belowground plant parts (Day et al., 1991; Landhaüsser et al., 1996; Schwarz et al., 1997), greater production of growth hormones (Atkin et al, 1973; Bowen, 1991; Kramer and Boyer, 1995), and increased rates of enzymatic reactions and cell divisions (Larcher, 1995; Taiz and Zeiger, 2006). Root vertical distribution is also influenced by soil temperature due to direct effect on growth, and to indirect effects on the availability of nutrient and water (Pregitzer and King, 2005). This is particularly important in harsh environments such as tundra where the depth to which root can grow is limited by permafrost. Finally, it is well known that roots proliferate where resource availability is high (Pregitzer et al., 1993). Thus, when water is not limiting, roots proliferate near the surface of the soil where higher temperatures do not limit growth and accelerate rates of nutrient mineralization. It can therefore be hypothesized that increased soil temperature due to global warming has the potential to increase root growth rates which could in turn facilitate the establishment of migrating tree species.

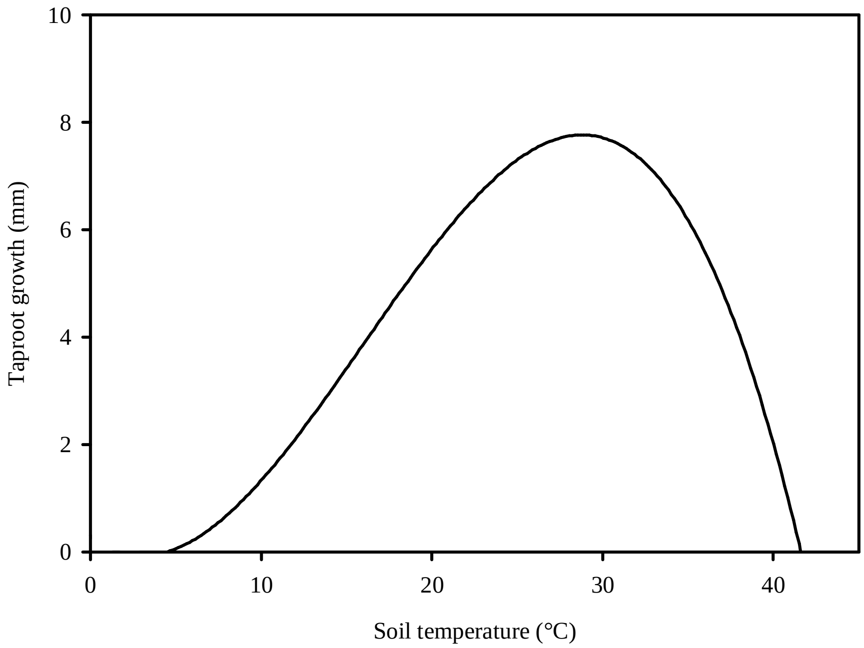

Figure 5. Root growth response to soil temperature (adapted from Kaspar and Bland, 1992).

Root nutrient uptake is also influenced by the control that soil temperature and water exert on root physiology. Indeed, several studies have suggested that rates of nutrient uptake increase with increasing temperature (Chapin, 1974a,b; BassiriRad, 2000). However, the mechanisms explaining this relation are not well understood. Nevertheless, it is known that root respiration increases with rising soil temperature in part because enhanced photosynthesis provides more energy for active transport (Atkin et al., 2000). Higher rates of root respiration result in higher concentrations of CO_2 in soil solution, which favors ion exchange at the surface of soil particles, releasing nutrients which can be taken up by plant roots (Larcher, 1995). However, increased soil respiration results in increased carbonic acid in the soil solution which can decrease soil pH. In turn, this increase in soil acidity has the potential to affect the availability and uptake of nutrients (Marschner, 1995). Properties of the cell membranes also change with soil temperature, affecting nutrient uptake. At low soil temperature, there is a decrease in water uptake caused by higher viscosity of water and reduced permeability of cell membranes, which increase resistance to water movement within the root (Figure 6; Kramer and Boyer, 1995; Wan et al., 2001). Therefore, it can be speculated that increased soil temperature has the potential to increase cell membrane permeability and enhance water and nutrient uptake.

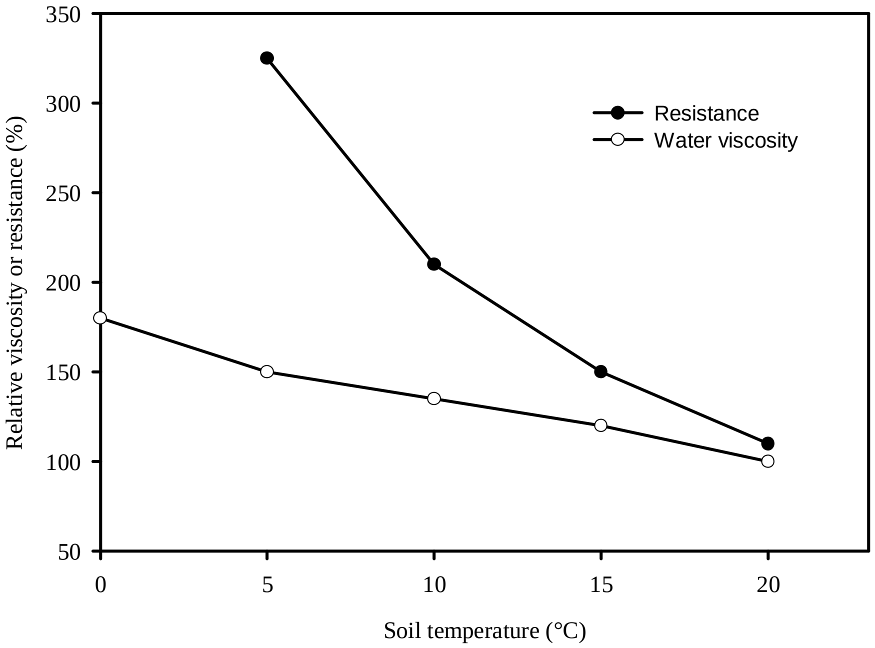

Figure 6. Relative viscosity of water and relative resistance for water flow through roots at low soil temperatures (adapted from Wan et al., 2001).

The above considerations emphasize the complexity of the influence that soil temperature and water availability exert on soil factors and processes, such as nutrient availability and plant growth, and illustrate the difficulty to generalize about the multiple, interacting processes occurring in the soil. For instance, although the projected global warming may increase nutrient mineralization (and potentially nutrient availability) through increased microbial activity, increased precipitation and soil CO_2, could enhance nutrient losses through leaching and cation exchange. Nevertheless, it remains clear that the projected climate change has the potential to alter soil temperature and water regime, and hence soil processes and plant growth. At least for northeastern North America, it seems that the possible modifications to soil physico- and biochemical properties and processes due to projected climate change has the potential to be beneficial for tree growth and the establishment of migrating species. Because tree species respond individually to environmental factors, it can then be speculated that altered soil factors will influence different species in different ways. Ultimately, these differences could be translated in different colonization abilities and migration rates, which will likely alter current tree communities.

5.0 Response of tree species to altered soil factors as mediated by climate change

As one considers the wide distribution range of temperate and boreal tree species, it appears evident that not only are these species adapted to a wide range of climatic conditions, but also, as soil factors are partly controlled by climate, to a wide range of soil conditions. However, it should be kept in mind that it is the local adaptations of its different populations that give a species its ability to thrive under various climate regimes and soil conditions. Therefore, in response to climate change and altered soil factors, it seems likely that southern populations of a given species could respond differently to the modification of soil factors or could respond to a different set of soil factors than northern populations. Thus, a species' response to altered soil conditions as mediated by climate change are likely to be various and complex. This section will give an insight of possible responses of some temperate and boreal tree species to altered soil conditions and climate.

It is reasonable to believe that at the end of the last ice age, soon after the retreat of the ice sheath, plants established onto uncolonized glacial deposits. Slowly, soils began to develop in response to climate, topography, and biological factors (i.e., plants and soil microorganisms), and so did plant communities. In contrast, unless massive forest die-off, species that will migrate in the boreal and temperate forests in response to climate change will have to establish on sites that are already colonized by plants, and thus will have to cope with competition for habitat resources. In addition, these migrating species will have to cope with soils that are already developed and that possess properties that may not be suitable for their establishment. For instance, podzols of boreal forests are generally low in nutrient content compared to hardwood forest brunisols (Aber and Melillo, 1991; Bérard and Côté, 1996). Thus, nutrient-demanding species typical of hardwood forests may not be able to thrive in podzols following their establishment. Moreover, some parent materials may lead to the development of soils, such as serpentine, which support unique type of vegetation. Therefore, the colonization of a new habitat by a plant species could be constrained by factors related to soil and biotic interactions.

As shown by numerous authors, soil properties have the potential to influence plants in many ways, especially during their establishment phase. Indeed, the nature of the microsite (e.g. mineral *vs*. organic soil), and its physico-chemical properties such as temperature, water and nutrient availability, and pH are important soil factors influencing seed germination and seedling establishment (Grossnickle, 2000; Spittlehouse and Stathers, 1990). For example, the establishment of a species into a new habitat can be constrained by the inability of its seeds to germinate because of inadequate soil moisture (Ammer et al., 2002) or allelopathic interactions (Zackrisson and Nilsson, 1992). In addition, soil temperature is a primary factor limiting growth during the early part of a plant's establishment phase (Grossnickle, 2000; Danby and Hik, 2007). As shown above, soil temperature places stress on plants by affecting their water movement capability, gas exchange, and subsequent root growth. This in turn affects seedling growth and survival. In some cold climates, a dense canopy may keep soil temperature so low that it delays germination and slows up seedling development (Stathers and Spittlehouse, 1990; Groot et al., 1997). However, removal of the forest cover may result in increases in soil temperature to lethal levels for germination and seedling growth (Fisher and Binkley, 2000). Finally, once established, seedlings must find sufficient amounts of nutrients in order to survive, grow, and reproduce (Grossnickle, 2000). Therefore, several soil factors have the potential to influence species' migration success in response to climate change.

5.1 Migration from the boreal forest to the tundra

Species migration from the boreal forest into the tundra may first be limited by the lack of soil and humus. For instance, on rocky outcrops where soil is absent, the establishment of trees is deemed impossible. Similarly, in areas where waterlogged conditions and low soil temperature combine to slow down the development of soils and to reduce humification rates, the establishment of tree species unadapted to these conditions may be hindered (Anderson, 1991).

Furthermore, with the projected climate warming the permafrost is expected to thaw at certain locations, enhancing the decomposition of soil organic matter and increasing the availability of nutrients (Euskirchen et al., 2006). These modifications could facilitate the establishment of trees north of the treeline, causing a northern range extension of the boreal forest. Alternatively, deeper permafrost could restrict the drainage of melted water at the surface creating waterlogged conditions that may limit soil organic matter decomposition and nutrient availability, therefore preventing the establishment of species unadapted to these conditions. Thus, in areas where there is significant peat accumulation and underlying permafrost, only a few species such as eastern larch and black spruce could establish and thrive.

Nevertheless, where soil exists and permafrost is absent, the expected rise in summer temperatures at the transition zone between the tundra and the boreal forest could improve soil conditions which in turn could enhance seed germination and seedling growth, ultimately causing a rise in treeline. For example, in an Alaskan shrub tundra, Hobbie and Chapin (1998) found that the seed germination of 3 treeline species (*Betula papyrifera*, *P. glauca* and *P. tremuloides*) increased as a result of simulated global warming. Although the success of seed germination was attributed to an increase in air temperature, seedling growth was dependent on soil conditions, i.e., it was reduced in nutrient-poor or cold and wet soils, such as tussock or heath tundra.

However, contrary to Hobbie and Chapin (1998) who found that the growth of white spruce seedlings increased in response to simulated warming, Barber et al. (2000) and Lloyd and Fastie (2002) found a reduction in mature white spruce growth rate in response to warming. In these studies, the authors attributed this growth reduction to drought stress. Therefore, these different responses to warming between early and late life stages of white spruce emphasize that the response of a tree to any given environmental factors may vary throughout its life cycle and that this could have repercussions on its establishment, survival, and reproduction success. Thus, in the tundra and at the transition zone with the boreal forest, soil factors will likely play an important role throughout the development of trees following their establishment in new habitats. The distribution range of a species could therefore be constrained by a specific limiting phase of its life cycle.

In response to climate warming, tree species now occurring in the boreal forest are therefore susceptible to migrate northward where soil conditions allow, i.e., at or slightly north of the transition zone between the tundra and the boreal forest. However, as one moves further to the north, the lack of mineral soil and organic matter will prevent the establishment of trees and the development of forests, except along river banks and in depressions where soils may be well developed. Therefore, in eastern North America the area now occupied by the tundra will likely decrease because of the northward expansion of the transition zone between the tundra and the boreal forest.

5.2 Migration from the temperate to the boreal forests

In the boreal forest, high soil moisture and low temperature are the major factors controlling nutrient cycling and forest productivity (Van Cleve et al., 1983a,b). Locally, permafrost may exacerbate the effects of high soil moisture and low temperature on nutrient cycling and forest productivity. In response to global warming, a combination of warmer soils and increased evapotranspiration may therefore enhance nutrient cycling and potentially increase forest productivity, and hence allow the establishment of more productive, southern tree species that requires higher supply of soil nutrients. However, in the northern part of the boreal forest, where discontinuous permafrost exists, deeper permafrost may restrict drainage of melted water at the surface, creating waterlogged conditions that may limit the establishment of species unadapted to these conditions. As a result, black spruce and larch stands will likely persist where waterlogged conditions prevail.

In response to altered climate, tree species not currently present in the boreal forest could establish on sites where soil conditions are favorable. Hence, the northern distribution limit of several temperate forest tree species could move north. For instance, the northern red oak (*Q. rubra*) is known to be relatively tolerant to drought conditions (Fekedulgen et al., 2003; Hartman et al., 2005). In northeastern North America, despite projected higher precipitation, soil moisture could decrease because of increased evapotranspiration. Hence, some parts of the boreal forest could become more favorable for the establishment of red oaks.

Studying the growth of sugar maples located at the deciduous–boreal forest ecotone, Barras and Kellman (1998) found that sugar maple seedlings were of broad tolerance and were present in all micro-habitats. The broad tolerance of the sugar maple to soil conditions was confirmed by Kellman (2004) in a transplantation experiment where the species' establishment in the boreal forests was successful, at least at the germination and seedling growth stage. Furthermore, according to Goldblum and Rigg (2005) the sugar maple had a great potential for increased growth rates at the transition zone between the deciduous and boreal forests under the predicted climate change. Thus, it seems that soil conditions found in the boreal forest will not constrain sugar maple germination and seedling establishment. Therefore, provided sufficient seed availability, projected increase in temperature and precipitation in northeastern North America could enhance the future status of the sugar maple at its northern limit and facilitate its range expansion northward in response to climatic change.

As shown with the northern red oak and the sugar maple, in response to climate change, improved soil conditions or broad tolerance to soil conditions may facilitate the migration and establishment in the boreal forest of tree species now typically occurring in the temperate forest. Other tree species, such as the red maple and the yellow birch, which distribution limits occur at or near the transition zone between the temperate and the boreal forest, could establish in the boreal forest in response to climate change. Therefore, the migration of temperate tree species within the area currently occupied by the boreal forest is locally probable. However, as shown above podzols of coniferous forest could hinder the establishment of nutrient-demanding species, such as sugar maple, or species associated with lime-rich soil, such as the eastern white cedar. Thus, while climate change has the potential to improve soil conditions for plant growth, plants will also have cope with soil properties inherited from slow pedogenic processes. These antagonistic forces are likely to slow down potential tree migration in response to climate change.

5.3 Differential migratory response between northern and southern populations

As shown above, soil factors and processes are likely to be modified by climate change, and could facilitate the establishment of migrating tree species in the different forest biomes of northeastern North American. However, not only could climate change and subsequent soil modifications promote the northward expansion of tree species' distribution limits, but they may also allow the persistence of a species within the current limit of its distribution range. Indeed, as stated earlier, because of local adaptations southern and northern populations of a given species may respond differently to modification of soil factors or could respond to a different set of soil factors. Thus, local adaptations may be critical for allowing the establishment or the replacement of populations of a given species within the current limit of its distribution range.

Hence, provided climate and genetic adaptations allow, for a given species it can be hypothesized that, at the continental or regional scales, soil factors should not represent major constraints for the northward expansion of its populations located at the southern limit or at the center of its distribution range. Because over its range the species is locally present or abundant, one can assume that soils, at least locally, are suitable for the establishment of migrating populations. Similarly, for populations located at the northern limit of the species' distribution range, short-distance (e.g. <10 km) migration should be possible as soil factors do not vary much over these distances. However, long-distance (e.g. >100 km) migration could be hampered by soil factors that would prevent seed germination and seedling development. For example, despite probable favorable climate envelopes, it is unlikely that the sugar maple or the yellow birch will establish in the James Bay lowlands because of deep peat accumulation that creates waterlogged conditions unfavorable for the growth of these species. Similarly, the tundra, characterized by shallow or non-existing soils, is unlikely to be rapidly colonized by the tap-rooted jack pine despite more favorable climatic conditions. Thus, because occurrence of soil is a prerequisite for the establishment of trees, the relative importance of soil factors for successful migration should be high in the tundra. In contrast, in the boreal and temperate forests, as soils are already developed, the relative importance of soil factors for tree establishment could be lower. However, inherited soil characteristics such as low nutrient availability in podzols, and exposure to heavy metals in serpentine soils could locally restrict or slow down migration. In the boreal and temperate forests, other factors such as competition and disturbance regime could be as important as soil properties for tree establishment.

Climate change and altered soil factors and processes are thus highly susceptible to interact to influence the projected migration and establishment of tree species. However, although the importance of these factors in the distribution of plants species is widely accepted, elevated atmospheric CO_2 and other biotic and abiotic factors could interact with climate and soil factors to further influence tree migration and establishment. Some of these factors could even prove more important than climate and soil for the migration and establishment of trees. The next section will give an insight of some of these factors and how they are susceptible to influence tree migration and establishment.

6.0 Differential responses of tree species to elevated CO_2 and tree migration as influenced by other biotic and abiotic factors

As shown in the previous section, soil factors could be determinant, at least locally, for the establishment and growth of several tree species during their northward migration. However, plants do not rely solely on climatic variables and soil resources for their growth. Atmospheric CO_2 constitutes another essential substrate for plant growth and to which they respond differently according to species. Hence, projected increases in atmospheric CO_2 could trigger different responses according to species, which could alter interspecific interactions and ultimately community composition.

As shown by several authors, plant growth responses to elevated CO_2 vary depending on species (Spinnler et al., 2002; Körner, 2006). Indeed, in response to elevated CO_2, growth rates can increase, decrease or remain unchanged (Karnosky et al., 2003; Poorter and Navas, 2003; Nowak et al., 2004; King et al., 2005). Differences in genotypes (McDonald et al., 2002), competitive ability (McDonald et al., 2002), and environmental conditions - particularly nutrient (de Graaff et al., 2006) and water availability (Nowak et al., 2004) - can be responsible to this variation. Furthermore, in addition to changes in growth rates, changes in the physiology and biochemistry of individual species under elevated atmospheric CO_2 and altered climate is likely to affect biotic interactions, such as competition (Poorter and Navas, 2003), herbivory (Holton et al., 2003), pollination (Erhardt et al., 2005) and root–rhizosphere dynamics (Pregitzer et al., 2007). This can lead to shifts in the dominance of species, affecting their influence on ecosystem properties (Kröner, 2004; Whitham et al., 2006). As species exhibit wide variation in their individual responses to altered environmental conditions, competitive interactions are likely to change (Roumet, 2002; Mohan et al., 2004; Ward and Kelly, 2004). Hence, given the different species responses to CO_2, the direct effects of elevated CO_2 will likely contribute to the species shifts already resulting from climate change (Parmesan, 2006). These species shifts have potentially larger consequences, because the responses of dominant forest species to elevated CO_2 can cascade through the entire ecosystem, affecting soil microbial communities (Phillips et al., 2002; Chung et al., 2006), soil nutrient status, and the carbon stocking capacity of ecosystems.

Moreover, other biotic and abiotic factors could prove important to restrict tree establishment and species migration. First, specific local adaption may prevent the expected northward migration of tree species or populations caused by climate warming. At the continental scale, two of the most important local adaptations are that to cold and photoperiod that helps prevent frost damage (Heide, 1985; Skre, 2002). In northern latitudes, a long-day photoperiod ensures that growth will begin and terminate when frost vulnerability is low. Thus, northward migration of species or populations adapted to warmer temperatures and shorter photoperiods may be constrained because the short photoperiod required to break dormancy occurs when frost hazard in higher latitude is high. Therefore, despite improved climatic and soil conditions, the southern populations of a given species may not be able to migrate successfully.

Second, altered disturbance regime may also be important to promote or restrict the future distribution range of tree species. Disturbances, whether fires, insect outbreaks or windstorms, are acknowledged to temporarily alter ecosystem composition and functions, and to initiate ecological succession. Therefore, disturbances can favor or exclude a particular species from an ecosystem. Hence, in conjunction with climate warming, altered disturbance regime could lead to the establishment of ecosystems in which composition and structure are radically different from ecosystems occurring prior to the alteration of the disturbance regime.

Third, habitat fragmentation and land use could also represent major constraints to tree migration and establishment. Indeed, in natural ecosystems cleared for human activities such as agriculture or urbanization, the remaining intact habitat fragments tend to be isolated from each other, increasing the distance a species must travel in order to find new suitable habitat and decreasing the probability of successful migration.

Fourth, in the absence of disturbance, competition for habitat resources such as light, water and nutrients could also constrain tree species migration and colonization of new habitat. Recent experimental and manipulation studies on the effect of raised temperatures (Hänninen, 1996; Epstein et al., 2004) or changed nutrient levels (Karlsson and Nordell, 1996; Shaver et al., 2001) have revealed the importance of the response of individual trees species to altered climate rather than wholesale community shifts. In this context, predicted climate change scenarios are expected to have profound effects on the competition between species and on their relative distribution across the landscape.

Fifth, suitable habitat for tree species will fluctuate greatly with climate change. Such large changes would also have significant effects on other users of the forest, such as pollinators and seed-dispersers. The inability of these associated organisms to cope with the projected climate change could jeopardize the plants species that rely on them for their pollination or their dispersal. Furthermore, altered climate could favor the establishment or population expansion of detrimental insect pest, such as the mountain pine beetle (*Dendroctonus ponderosae*) (Carroll et al., 2006), that could cause important damage to forest and limit future tree reproduction and migration in response to climate change.

Finally, the ease with which plants migrate northward as climate changes will depend, in part, whether immigrants find the mycorrhizal fungi and rhizosphere bacteria that they require (Perry et al., 1990). As mycorrhizae are known to enhance plant nutrient and water uptake (Eissenstat and Volder, 2005), it could be hypothesized that immigration of a given plant species onto a new site will be facilitated if it is accompanied with its associated mycorrhizal species. Some fungal species may migrate with their hosts, but many may not, for example, those species fruiting belowground and spreading slowly.

Therefore, it seems clear that the future northward migration of trees will not respond to a single biotic or abiotic factor. Rather, trees are likely to respond to complex interactions between climate variables - including increased atmospheric CO_2, soil factors and processes, genetic adaptations, disturbance regime, competition, associated pollinators and dispersers, and associated soil microorganisms.

7.0 Conclusion

As plant species distribution is partly controlled by climatic variables such as annual average temperature and precipitation regime, the projected climate change is expected to modify the distribution range of tree species. Because tree species are likely to respond individually to altered climate, tree communities are also expected to be modified. Furthermore, as soil factors and processes are partly determined by climate variables, climate change is expected to alter soil properties. In turn, these soil modifications are likely to interact with altered climate variables to influence tree species distribution and community composition. Hence, tree species' response to the projected climate change is likely to be complex and nonlinear. According to Midgley et al. (2007), tree species responses to global warming may fall into one of four broad categories: local extinction, *in situ* persistence, *in situ* adaptation over generation, and migration. Thanks to long lifespan or broad environmental tolerance, *in situ* persistence may allow some tree species to remain present in the landscape long after suitable climatic or environmental conditions have changed. Although genetic adaptation may influence tree species response to altered environmental conditions (Davis and Shaw, 2001), rapid adaptation will be possible only for short-lived tree species that reproduce early in their life cycle. If tree community composition is to change in response to global warming and altered environmental conditions, two pathways are possible: *in situ* conversion, i.e., the replacement of dominant species by subdominant species, or migration. *In situ* conversion is likely to begin before immigrants establish and start to play a significant functional role. Yet, if the climate changes rapidly, and especially if climate change is accompanied by widespread disturbance, some species and their functions may be lost before those functions can be replaced. Currently it is not possible to tell what proportion of local, regional or global floras may persist or adapt to climate change in situ, but *in situ* conversion and migration will be necessary to maintain the functions of ecosystems.

At the continental or regional scales, if one does not consider other biotic or abiotic factors, soil factors should not represent major constraints for the northward shift of populations located at the southern limit or at the center of their distribution range. Because populations are already in place, one can assume that soils, at least locally, are suitable for the establishment of migrating populations. At some locations, however, unfavorable soil properties, such as waterlogged conditions, or soil characteristics inherited from pedogenic processes, such as podzolization, could preclude the establishment of migrating species not adapted to these conditions. For populations located at the northern limit of their distribution range, short-distance (e.g. <100 km) migration should be possible as soil factors do not vary much over these distances, while long-distance (e.g. >100 km) migration, however, could be constrained by soil factors that preclude seed germination and seedling establishment. However, for both short- and long-dispersal other factors such as disturbance regime and the concurrent migration of associated pollinators and dispersers, and associated soil microorganisms will also influence the migration and establishment of tree species in new habitats.

Because the presence of soil is a prerequisite for the establishment of trees, the absence of soil or its low development may be the most important factor constraining the establishment of trees in the tundra, along with climate variables and genetic adaptation. The relative importance of soil factors should thus be high in the tundra. In contrast, in the boreal and temperate forests where soils are already developed, soil relative importance for tree establishment should be lower. Other factors, such as competition and disturbance regime should be as important for tree establishment. However, local soil conditions, such as low pH and waterlogged conditions, or pedogenic processes, such as podzolization, could also be important to restrict species migration and establishment in the boreal forest. Likewise, soil characteristics developed during pedogenic processes, such as podzolization, could hinder the establishment species. Thus, while climate change has the potential to improve soil conditions for plant growth, this forcing will have cope with irreversible soil properties inherited from pedogenic processes. These opposing forces are likely to hinder tree migration in response to climate change.

In conclusion, the migration of tree species is thus highly probable within the area currently occupied by the boreal and temperate forest, but will be restricted to the more favorable sites in the tundra because of the absence of extended soils. While the area covered by the boreal forest biome will in all likelihood decrease because of the northward expansion of the temperate forest biome and the constraints imposed by the tundra environment, the area covered by the temperate forest biome could remain the same, but show a poleward shift. However, in both biomes the fate of individual species remains uncertain and is dependent upon their response to complex interactions between climate variables, soil factors and processes, genetic adaptations, disturbance regime, competition, associated pollinators and dispersers, and associated soil microorganisms. Therefore, species are more likely to respond to climate change than whole biome. Moreover, some species, such as yellow-poplar (*Liriodendron tulipifera*) and pin oak (*Q. palustris*), which are currently occurring in the eastern US only, may migrate to southeastern Canada in response to global warming. Thus, new plant species assemblages are likely to emerge from climate change. However, questions remain to be answered, such as will the soils of the boreal forest be fertile enough to support the growth of more productive hardwood species? Reliable predictions of the fate of tree species communities, and thereby the policy and management choices of the future, will require a clear understanding of tree responses to a wide range of biotic and abiotic factors. Furthermore, human assistance may be needed if tree species are to realize their newly expanded, potential natural ranges.

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Appendix I

How to discriminate between the effects of climatic variables from those of soil factors on the establishment and growth of trees in response to climate change.

Greenhouse study

In order to discriminate between the possible influence of climatic warming from that of soil properties on the migration and establishment of trees, I propose to set up a greenhouse study in which seeds and seedlings of different tree species typical of the temperate and boreal forests are sowed or planted individually in pots containing soils representative of the different biomes found along a latitudinal gradient in eastern North America. For example, soils could be collected at regular intervals (e.g. every 5° of latitude) from the southern limit of the temperate deciduous forest (ca. 35°N) to the northern limit of the boreal forest (ca. 58°N). Then, the pots could be placed in several greenhouses in order to recreate different climatic regimes (i.e., warm and moist, warm and dry, cold and moist and cold and dry). If the pots stay long enough in the greenhouse, it should be possible to discriminate between the effects of climate from that of soil on the germination success and growth of the selected species in response to climate change.

Field study

A field-based study could also be set up to discriminate between the influence of climatic warming and soil properties on tree establishment and growth. For example, for a given species typical of the temperate forest, seeds and seedlings of different provenance (e.g. from the southern and the northern limit of its distribution) could be sowed and planted along two or three latitudinal transects. Sowing and planting locations could be located at the center of the species' distribution range, at the northern limit of its range, and then at 1 km, 5 km, 10 km, 50 km, 100 km, 200 km, and 500 km north of its actual range. Using sugar maple as a model, the transects would span from the deciduous to the coniferous forests, via mixed hardwood-softwood forest. Thus, it should be possible to discriminate between the possible effects of climatic variables from that of soil properties on the germination success and growth of the selected species in response to climate change.