

Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration?

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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 the local and regional scales vegetation patterns are more strongly related to edaphic and topographic factors. The projected global warming and alteration of the precipitation regime will influence tree physiology and phenology, and is likely to promote northward migration of tree species. However the influence of soil characteristics on tree species migration is not as well understood. Considering the broad tolerance of most tree species to variations in soil factors, soils should not represent a major constraint for the northward shift of tree species. However, locally or regionally, soil properties may constrain species migration. Thus, while climate change has the potential to induce a northward migration of tree species, local or regional soil properties may hinder their migratory response. These antagonistic forces are likely to slow down potential tree migration in response to climate change. Because tree species respond individually to climate variables and soil properties, new tree communities are likely to emerge from climate change.

Key words: climate change, tree migration, soil properties, temperate forest, boreal forest.

Résumé : La distribution des espèces et la composition des communautés végétales varient le long de gradients environnementaux. À l'échelle continentale, le climat joue un rôle primordial dans la distribution des espèces végétales, alors qu'aux échelles locale et régionale la distribution des espèces est surtout influencée par les variables édaphiques et la topographie. Le réchauffement climatique projeté et l'altération du régime des précipitations sont susceptibles d'influencer la physiologie et la phénologie des arbres, et d'entraîner leur migration vers le nord. Toutefois, l'influence des caractéristiques des sols sur le potentiel migratoire des arbres est peu connue. Puisque la plupart des espèces d'arbres possèdent une grande tolérance aux variations édaphiques, les sols ne devraient pas constituer un obstacle majeur à leur migration vers le nord. Toutefois, localement ou régionalement, les sols pourraient posséder des propriétés qui pourraient restreindre la migration des espèces. Alors que les changements climatiques ont le potentiel de provoquer la migration des espèces vers le nord, localement ou régionalement les propriétés des sols pourraient limiter leur capacité migratoire. Ces forces en opposition pourraient restreindre le potentiel migratoire des arbres en réponse aux changements climatiques. Parce que les espèces d'arbres répondent de manière individuelle aux variables climatiques et aux propriétés des sols, de nouvelles communautés d'arbres pourraient résulter des changements climatiques.

Mots-clés : changements climatiques, migration des arbres, propriétés des sols, forêt tempérée, forêt boréale.

Introduction

Plant species distribution and plant community composition vary along environmental gradients (Allen and Hoekstra 1990; Levin 1992), and several community and landscape studies have linked species responses to environmental gra-

dients at different spatial scales (Mäkipää 1999; Hollingsworth et al. 2006). For instance, at the continental scale climate plays the most important role in determining plant distribution and community composition (Woodward 1987; Neilson 1995), while at the local and regional scales vegetation patterns are more strongly related to edaphic and topographic factors (Ertsen et al. 1995; Iverson et al. 1997). Across all scales, temperature and the balance between precipitation and evapotranspiration are particularly important, as they largely control the rates of biological reactions, for instance microbial activity (Hobbie 1996; Moore et al. 1999) and net primary productivity (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 greenhouse gases (i.e., carbon dioxide [CO₂], methane [CH₄], and nitrous oxide [N₂O]) have in-

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creased markedly as a result of human activities and now exceed pre-industrial values (IPCC 2007). Due to the radiative forcing of these greenhouse gases, world surface temperatures 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). In northeastern North America, warming is projected to be somewhere between 3 and 4 °C and precipitation is projected to increase by 10%–20% by the end of the 21st century (IPCC 2007).

This increase in atmospheric CO₂ concentration and the concomitant warming and modification of water regimes will, in all likelihood, influence plant physiology (Keeling et al. 1996; Myneni et al. 1997), phenology (Raulier and Bernier 2000; Delbart et al. 2008), growth (Huang et al. 2007; Brassard et al. 2009), and thus modify the future range and dynamics of many plant species and ecosystems (Overpeck et al. 1991; Hansen et al. 2001; Neilson et al. 2005; 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 feedback to local abundance and community composition. Recent analyses of long-term data sets indicate that some North American tree species are already responding to recent anthropogenic climate change, particularly at the northern treeline of the boreal forest (Lloyd and Fastie 2003; Gamache and Payette 2005; Caccianiga and Payette 2006). Current responses include in situ species conversion (i.e., the replacement of dominant species by subdominant species [Midgley et al. 2007]) and species migration.

Because forest ecologists have been studying successional patterns since the pioneering works of Clements (1916) and Gleason (1926), the processes driving in situ conversion are relatively well understood. However, because it is a much slower process, migration is not as well understood. Nevertheless, to understand species migration in response to climate change, ecologists rely (i) on paleoecological studies that relate past species migration to past changing climate, and (ii) on studies of invasive exotic species. While paleoecological studies reveal that at the end of the last glaciation plant species followed a poleward migration behind the retreating glacier (e.g., Davis 1983; Jackson et al. 1997), studies of invasive exotic species reveal that species invasion (migration) rate is determined both by dispersal rate and population growth rate at the invasion (migration) front (Hastings et al. 2005).

Although temperature and precipitation are often considered the major factors determining plant species and ecosystem distribution, other factors such as dispersal ability, competition, predation, disturbance regime, and rate of genetic adaptation are also important. Although these factors 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, probably due to the difficulties of implementing these processes in simulation models. 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 plant species, soils are often omitted in models simulating plant species migration. Iverson and colleagues

(Iverson and Prasad 1998, 2002; Iverson et al. 2008a, 2008b) recently published results from models simulating the range shift response of several North American tree species to climate change which included soil variables. Although soil variables were important predictors of species range shift in response to climate change, the authors did not offer any explanation as to how soil variables could facilitate or constrain tree species migration in response to projected climate change.

Considering that (i) projected climate change is expected to promote poleward migration of forest tree species, (ii) upon migration, species are likely to encounter soil conditions different from their original locations, and (iii) soil factors influence tree species through effects on seed germination, seedling establishment, growth and reproduction, our objective is to demonstrate how soil factors could influence the migration of tree species in response to climate change 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). First, we briefly review tree migration in response to past, recent, and projected climate change. Second, we review how soil factors currently limit tree establishment and growth, and species distribution. Finally, we review the potential responses of tree species to climate change, and how this response could be influenced by soil factors. Although this work focuses on the migration of trees in response to climate change in northeastern North America, results from studies carried out elsewhere in North America, in Europe, and in Asia are used to support our hypotheses for responses in northeastern North America.

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

Response of boreal and temperate tree species to past global warming

Based on pollen and plant macrofossils (e.g., seeds, fruits, leaves, twigs, and wood) preserved in sediments in wetlands, peatlands, and lakes, several authors reported evidence of past migration of trees following the end of the last ice age about 12 000 years ago.

As early as 15 000 years ago, changes in biome and plant community composition began in what is now the southeastern US, where boreal species were replaced by hardwood species (Webb 1988). As shown by several authors (e.g., Jackson et al. 1997; Williams et al. 2004), most of the tree species now found in the northeastern North American boreal and temperate forests were able to track the warming trend of the Holocene. While *Picea* spp. reached their current northern range limit about 3 000 to 5 000 years ago (Jackson et al. 1997; Williams et al. 2004), *Abies balsamea*, *Quercus* spp., and *Fagus grandifolia* reached southern Quebec around 10 000 BP, 7 000 BP, and 6 000 BP, respectively (Muller and Richard 2001; Williams et al. 2004). According to these records, tree species migrated at different rates, reinforcing Gleason's (1926) idea of an individualistic view of plant succession and resulting chance combinations of species assemblages.

Although none of the paleoecological studies cited above mention soil factors or processes as having influenced tree establishment behind the retreating ice sheet, soil factors

and processes most likely constrained seed germination and seedling establishment; this is supported by studies on both primary succession in areas where glaciers are currently retreating, such as Glacier Bay, Alaska (Chapin et al. 1994), and in areas devastated by recent volcanic eruptions, such as Mount St. Helens (del Moral and Wood 1993). Both Chapin et al. (1994) and del Moral and Wood (1993) identified nutrient limitation to plant growth as a factor limiting colonization in early primary succession. As Walker and Syers (1976) pointed out, most newly deposited substrates, such as glacier deposits, are devoid of N, which is required for plant growth. In these “young” soils, N must therefore be obtained from the atmosphere by biological N fixation or atmospheric deposition. Thus, N-fixing species such as *Alnus* spp. and *Dryas* spp. may have been among the first plant species to colonize the newly available sites following the retreat of the North American ice sheet (Reiners et al. 1971), and their presence may have enhanced growth of associated species (Chapin et al. 1994). Therefore, tree establishment may well have followed that of N-fixing plant species by a few decades. However, studying the causes of primary succession at Glacier Bay, Alaska, Fastie (1995) showed that tree species were not necessarily preceded by N-fixing plants. Nevertheless, over time, N fixation and atmospheric deposition have increased the availability of N in the soil in sufficient amounts to allow the establishment of more N-demanding species (Stevens and Walker 1970; Gorham et al. 1979).

Studying the influence of landscape structure and climate variability on the late Holocene migration of *Juniperus osteosperma* in the western US, Lyford et al. (2003) showed that species migration was in part constrained by the distribution of suitable substrate. For *Juniperus*, suitable substrates consisted of coarse-textured soils, particularly in regions of resistant sandstones and coarse shales, and highly suitable surface materials consisted of rock outcrops and colluvial deposits.

Hence, these studies strongly suggest that soil factors and processes restricted tree migration through constraints on seedling establishment following the gradual retreat of the North American ice sheet during the Holocene.

Impacts of recent global warming on boreal and temperate tree species

At the continental and subcontinental scales, the transition zones between adjacent biomes and vegetation communities are sensitive to climate variation (Goldblum and Rigg 2005). In these zones, projected climate change could cause detectable shifts in species composition, whereas in the middle of broad forest zones such changes might not take place. 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 change in response to global warming (e.g., Kullman 2001, 2002; Gamache and Payette 2004). Several studies showed that at the end of the Little Ice Age (ca. 1850), the northern treelines of North America and Eurasia began migrating poleward in response to warmer temperatures. In Canada, Payette and co-workers showed that the *Picea glauca* (Payette and Fillion 1985; Caccianiga and Payette 2006) and *Picea mariana* treelines

(Gamache and Payette 2005) expanded significantly northward during the last 100 years in response to recent climate warming. In Alaska, Lloyd and Fastie (2003) found similar results for *Picea glauca*, concluding that the recent shift in the location of the forest–tundra border was a response to recent warming. In Eurasia, Kharuk et al. (2005) showed that *Pinus sibirica* and *Betula* spp. were penetrating into a zone traditionally occupied by two larch species (*Larix gmelinii* and *Larix sibirica*) in response to climate change during the past three decades. Similarly, Kullman (2001, 2002) showed that treelines in the Swedish Scandes have responded to recent global warming with altitudinal and northward tree species invasion into the tundra.

While these latter studies focused on the transition at the treeline, few have 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. Montane ecosystems provide an ideal environment for observing shifts in forest distribution in response to climate change because of steep climatic gradients across elevation. In many respects, these ecosystems 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 2004, Beckage et al. (2008) re-surveyed plots established in 1964 along elevation transects in the Green Mountains of Vermont, US, 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 91–119 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, and 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.

These observations of recent, directional shifts at the northern treelines are consistent with expectations of species migration in response to climate warming, and offer further support to the idea that tree species will in all likelihood migrate poleward in response to projected climate change. Once again, while it is known that soil factors influence plant development, and hence the likelihood of species range shift, soil factors are rarely explicitly discussed when explaining species recent range shifts. Nevertheless, Gamache and Payette (2005) suggested that at the microsite scale, the suitability of seedbed and seedling establishment substrate are important for successful range shift, and that suitable seedbeds and establishment substrates may vary from region to region. However, as suggested by Beckage et al. (2008), at a broader scale, soil factors may not represent major constraints for tree species range shift.

Projected impacts of global warming on boreal and temperate tree species

Simulation models have been utilized extensively in recent years to forecast migration rates of tree species and to

predict future forest composition. These models are most often based on the climate envelope (CE) approach that relates species distribution to an a priori selection of climatic variables that are indicators of underlying physiological or biophysical limits on species distribution. These simulations indicate that, in response to climate warming and changes in water balance, plant species and communities in the boreal and temperate forests are likely to experience longer growing seasons (Chuine et al. 2000; Goldblum and Rigg 2005) and modified disturbance regimes (Flannigan et al. 2009; Jiang et al. 2009).

Further, simulations also anticipate significant shifts in plant species ranges in response to global warming. For instance, 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 *Picea* spp. and northern pine (i.e., *Pinus strobus*, *Pinus banksiana*, and *Pinus resinosa*) populations in the eastern US could decline in abundance because of a northward shift of their southern range limit. In parallel, southern oak (*Quercus* spp.) and pine species are expected to move northward by as much as 500 km because of local drying. Thus, in the eastern US, areas now dominated by mixed conifer–hardwood forests could become increasingly deciduous. In addition, Overpeck et al.'s (1991) simulation indicates that the area now occupied by tundra vegetation would decrease where simulated warming favours the expansion of tree populations. These results support paleoecological observations that biome compositions will not remain constant as plant taxa respond individually to future climate change.

Similarly, McKenney et al. (2007) used GCMs and species current climatic envelopes to predict the potential impacts of climate change on the distribution of North American trees. They concluded that the mean centres of future climatic envelopes were predicted to shift northward by several degrees of latitude. Their simulation predicted that by the end of the 21st century the CE of most of the species modeled would shift into northern Ontario and Quebec. For example, *Acer saccharum* CE is projected to shift north by about 1000 km, and that of *Betula alleghaniensis* by about 900 km. Further, several of the species modeled (e.g., *Quercus palustris* and *Betula nigra*) are projected to expand their range into southern Canada by the end of the 21st century.

In the above-cited studies, assessments of future distribution change are based on the climate envelope approach. Although soil factors are of utmost importance to plant establishment and growth, and modelers recognize their potential to influence the success of plant migration and establishment, soil factors are often omitted from models simulating the effects of climate change on plant migration. Nevertheless, in a series of studies Iverson and Prasad (1998, 2002) and Iverson et al. (2008a, 2008b) used a set of soil variables (e.g., water-holding capacity, pH, permeability, texture, organic matter content) along with climate variables to predict the distribution of several tree species following climate change in the eastern US. Their results showed that several species now occurring in the temperate or boreal forests would show range expansion and (or)

shifts. For example, *Abies balsamea*, *Acer saccharum*, and *Betula alleghaniensis* were expected to migrate north, showing an important range decline in the eastern US, while 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 the near future. Their simulations showed that soil factors were important for species to achieve successful range shift; those most important were soil permeability rate (cm h^{-1}), organic matter content, pH, cation exchange capacity, percent clay, and bulk density.

Although we recognize important methodological differences between the studies of Iverson and Prasad (1998) and McKenney et al. (2007), a thorough examination and comparison of both studies reveals the importance of soil constraints on the migratory potential of several species common to these studies. For instance, while the unconstrained migration scenario of McKenney et al. (2007) predicts that by the end of the 21st century the centre of the climatic envelope of *Carya cordiformis* will be located at 44.5°N and that of *Quercus rubra* at 48.7°N, the soil-constrained scenario of Iverson and Prasad (1998) predicts that the latitudinal optimum of *Carya cordiformis* will be located at 39.4°N, and that of *Quercus rubra* at 40.4°N. The differences in migratory potential between these two studies may reflect the constraints that soil conditions exert on species establishment, growth, and reproduction.

Soil limitations to plant growth and tree species distribution

The type of vegetation that characterizes a region depends on several environmental factors, among which soil is of the utmost importance. Soil can indeed influence plant community composition through differential effects on individual plant species. Texture, porosity, aeration, temperature, moisture and nutrient content are among the soil variables that can independently and (or) in interaction influence plant development (Aber and Melillo 1991; Marschner 1995). Their relative importance may or may not vary throughout the life cycle of an individual plant, i.e., during the plant's germination, establishment, growth, and reproduction phases. In Germany for instance, Ammer et al. (2002) showed that the establishment of *Fagus sylvatica* in *Picea abies* stands was constrained by seed germination that is limited by inadequate soil moisture. Soil temperature is also a primary factor limiting growth during early establishment. In Ontario and the Yukon, respectively, Grossnickle (1988) and Danby and Hik (2007) showed that soil temperature places stress on *Picea glauca* seedlings by affecting soil water movement, gas exchange, and subsequent root growth. Once established, seedlings must acquire sufficient nutrients to survive, grow, and reproduce. For instance, in Ontario and Saskatchewan, Fogal et al. (1999) showed that seed production of *Pinus banksiana* in seed orchards was positively influenced by the addition of fertilizer, while in Sweden, Karlsson and Örlander (2002) showed that nutrient status of *Pinus sylvestris* influenced cone and seed production. Therefore, several soil factors have the potential to influence plant

growth and species' migration success in response to climate change, and therefore plant community composition.

Several authors studying exotic plant invasion showed that soil property modifications by invasive species influence their own invasion rate (Levine et al. 2006; Gómez-Aparicio and Canham 2008). Indeed, forest species, by producing organic compounds, can influence soil weathering rates and nutrient availability (Binkley and Giardina 1998; Nezat et al. 2004). For instance, in British Columbia, Tuason and Arocena (2009) found that the rhizosphere of *Picea glauca* and *Abies lasiocarpa* had lower pH and higher exchangeable Ca^{2+} and K^{+} content than adjacent soils, and suggested that organic acids exuded by the tree's root system might have played a role in the modification of the properties of their rhizosphere. Therefore, because of their ability to modify soil properties, some tree species may with time create soil conditions favourable to their establishment and persistence, and detrimental to other tree species (i.e., already established or migrating species).

Because it is beyond the scope of this synthesis, we will not provide any further details on the generally accepted influence of soil properties on plant growth. Rather, we refer the readers to Aber and Melillo (1991) and Marschner (1995) for a thorough discussion on this topic.

Tree species responses to soil factors during climate change-induced migration

At the end of the last ice age, plant species migrating behind the retreating glacier established on uncolonized glacial deposits in a reorganizing environment. Over time, soils began to develop in response to climate, topography, and biological factors (i.e., plants and soil microorganisms), as did plant communities. Early in the colonization process, competition for habitat resources such as water and nutrients was probably negligible because of the scattered distribution of individual plants. With time, however, competitive interactions became more prominent, possibly having an important influence on species migration rate and community composition (Ravazzi 2002).

In contrast, unless massive forest dieback occurs, 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 may thus compete for habitat resources upon their establishment. These migrating species will also colonize soils that are already developed, and that may locally possess properties that delay or constrain their establishment. Consequently, in these recipient habitats, competitive interactions and soil properties may interact to influence the population growth of migrating species. Because it is beyond the scope of this synthesis, we will not provide details on the possible influence of competitive interactions on plant migration and establishment. We refer the readers to Scheller and Mladenoff (2008) for a discussion on this topic.

Migration from the boreal forest to the tundra

As shown in a previous section, in both Eurasia and North America several tree species located at the treeline moved north in response to recent climate change. These recent invasions of the tundra may be indicative of the relatively

high tolerance of boreal forest tree species to soil conditions found in the tundra, or that soil conditions in the tundra are closely similar to those found in the boreal forest. Nevertheless, locally species migration may be limited because of particular soil conditions.

First, species migration from the boreal forest to the tundra may be limited by waterlogged conditions and a small soil or humus volume for root exploitation. In areas where waterlogged conditions and low soil temperatures combine to slow soil development and reduce decomposition rates, the establishment of tree species unadapted to these conditions may be hindered (Anderson 1991). Similarly, on rocky outcrops where soil is absent, the establishment of trees is unlikely.

Likewise, species migration could be limited by permafrost, which would prevent seedling establishment by limiting root development and penetration into the soil. Projected temperature increases, however, will likely lead to permafrost degradation, especially in regions where discontinuous permafrost prevails. In northern Canada, for instance, a warming of 4–5 °C could reduce the area underlain by discontinuous permafrost by up to 50% (Woo et al. 1992). As shown by Waelbroeck et al. (1997), the warming and melting of the permafrost are associated with an increase in N mineralization rates, and, as pointed out by Woo et al. (1992), the melting of the permafrost can create areas of improved drainage as a result of improved vertical movement of water through the soil. Consequently, plant species that are unable to establish on cold, poorly drained soils underlain by permafrost could expand as permafrost melts. Permafrost warming and melting have, therefore, the potential to facilitate plant species migration and to affect plant community composition.

For instance, at the arctic treeline in northwestern Alaska, Lloyd et al. (2003) showed that well-drained soils on steep banks sustain plant communities different from those found on adjacent level tundra underlain by permafrost. They also found that thaw-pond banks sustained a higher density of trees and shrub species, and that shrubs were taller on banks. Thaw-pond banks likely provided better microsites for growth than the tussock tundra that covered the more level terrain. According to Lloyd et al. (2003), it is therefore likely that the establishment of shrubs and trees in the tundra is constrained by a set of environmental factors, including both above ground and below ground conditions. In the tundra, the response of trees to climate warming could therefore be conditional upon the formation of well-drained microsites. Such microsites are likely to be restricted in extent, at least during the first stages of permafrost degradation, and thus the establishment of migrating tree species is likely to be delayed (Lloyd et al. 2003). Nevertheless, over time, as permafrost melts and soil conditions improve, the establishment of tree species could be facilitated and their migration accelerated.

Furthermore, where permafrost is non-existent or where the soil active layer is thick, the expected rise in summer temperatures at the transition zone between the tundra and the boreal forest could improve soil conditions, enhancing seed germination and seedling growth, ultimately causing a northward shift of treeline species. For example, in an Alaskan shrub tundra, Hobbie and Chapin (1998) found that the

seed germination of three treeline species (*Betula papyrifera*, *Picea glauca*, and *Populus tremuloides*) increased as a result of simulated global warming. Although the success of seed germination was attributed to increased air temperature, subsequent seedling growth depended on soil conditions, i.e., growth was reduced on nutrient-poor or cold and wet microsites, such as tussock or heath tundra.

Contrary to Hobbie and Chapin (1998), Barber et al. (2000) and Lloyd and Fastie (2002) observed a reduction in the growth rate of mature *Picea glauca* in response to warming. The latter authors attributed this growth reduction to drought stress. Although the planted seedlings of Barber et al. (2000) and Lloyd and Fastie (2002) were located further south, and were consequently more liable to drought than those planted by Hobbie and Chapin (1998), the contrasting responses to warming between early and late life stages of *Picea glauca* emphasize that the response of a tree to any given environmental factor may vary throughout its life cycle. This variable response could have repercussions on establishment, survival, and reproduction success. Thus, in the tundra and in the transition zone between the boreal forest and the tundra, soil factors will likely play an important role during tree development, following establishment in new habitats. The distribution range of a species could therefore potentially be constrained during a specific phase of its life cycle.

The preceding paragraphs show that in response to climate warming, current boreal tree species are likely to be capable 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 north, thin (or the absence of) mineral soil and organic matter, permafrost, and waterlogged conditions could prevent or delay the establishment of trees and the development of forests. Those species showing broad tolerance to soil conditions may not see their migration constrained by soil, and may therefore migrate poleward, following the warming trend. However, species having narrower tolerance to soil conditions could see their migration constrained by soil conditions during the first stages of global warming; constraints may subsequently diminish as soil properties change (in response to climate and biotic variables) and become favourable for their establishment and growth.

Migration from the temperate to the boreal forest

In the boreal forest, high soil moisture, low temperature, and fire are the major factors controlling nutrient cycling and forest productivity (Van Cleve et al. 1983; Bonan and Shugart 1989). In response to global warming, a combination of warmer soils and increased evapotranspiration may therefore enhance nutrient cycling and potentially increase forest productivity, allowing the establishment of more productive and nutrient-demanding southern tree species (e.g., *Acer saccharum*, *Fagus grandifolia*, *Quercus rubra*, and *Tilia americana*). However, locally or regionally deep peat soils such as those found in the James Bay Lowlands (Quebec and Ontario) may not be as responsive to global warming as other types of soils, primarily because of their chemical composition and high water content. These deep organic soils may persist for a long time, despite otherwise favourable climate conditions for decomposition. Excluding

regions where deep peat accumulation occurs, in response to altered climate, the establishment of tree species not currently present in the boreal forest should be possible where soil conditions are favourable, and the northern distribution limit of several temperate forest tree species could therefore move north.

For instance, in Ontario, studying sugar maple growth at the deciduous–boreal forest ecotone, Barras and Kellman (1998) found that *Acer saccharum* seedlings were of broad tolerance to forest floor depth and moss cover, and were able to establish in the boreal forest. The broad tolerance of *Acer saccharum* 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. According to Goldblum and Rigg (2005), *Acer saccharum* has good potential for increased growth rates at the transition zone between the deciduous and boreal forests under predicted climate change. Thus, it appears that soil conditions found in the boreal forest will not constrain *Acer saccharum* 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 *Acer saccharum* at its northern limit and facilitate its range expansion northward.

Further, several studies conducted in northeastern Canada have shown that broadleaf species such as *Populus tremuloides* can rapidly establish following harvesting in stands previously dominated by *Picea mariana* (Chen et al. 2009; Laquerre et al. 2009). The presence of *Populus tremuloides* in *Picea mariana* stands has been shown to induce changes in the soil macrofaunal community and to accelerate the rate of soil processes by having either direct or indirect influence on microbial activity (Légaré et al. 2005; Laganière et al. 2009, 2010). In turn, these modified soil conditions have the potential to favour the establishment of new species and consequently modify plant community composition (Légaré et al. 2001; Chávez and Macdonald 2010), and allow for the persistence of a species within the current limit of its distribution range.

Therefore, the migration of temperate tree species within the area currently occupied by the boreal forest is probable where soil conditions allow. As shown for *Acer saccharum*, 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 *Acer rubrum* and *Betula alleghaniensis*, for which distribution limits occur at or near the transition zone between the temperate and the boreal forest, could potentially become established in the boreal forest (Tremblay et al. 2002). Locally, however, properties of coniferous forest soils could hinder the establishment of species associated with base-rich soils, such as basswood (Burns and Honkala 1990), or unable to withstand waterlogged conditions such as those found in the peaty soils of the James Bay Lowlands. Under these latter conditions, tree species migration is likely to be restricted or delayed. Because species respond differently to soil conditions, species showing broad tolerance to soil conditions could migrate poleward with the warming trend, whereas species showing narrower tolerance

to soil conditions could see their migration delayed, at least during first stages of global warming. Nevertheless, as soil properties change (in response to climate and biotic variables) and become favourable for their establishment and growth, the migration of these species could proceed. We acknowledge that while some soil properties may change within a few years or a few decades (e.g., nutrient availability and surficial melting of the permafrost), other properties may change only over the course of centuries or millennia (e.g., soil texture and thickness of the organic layer).

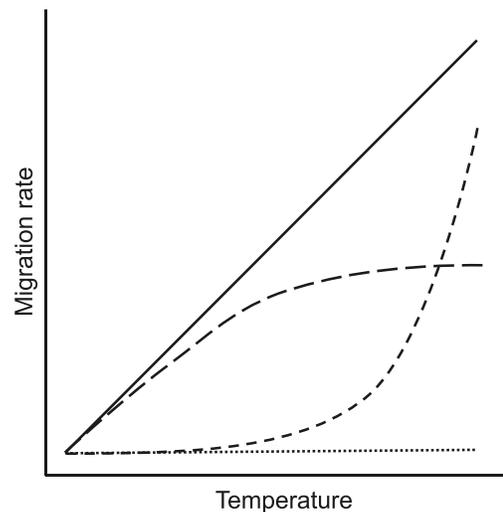
Synthesis

Since plant species distribution is under partial control of climate variables such as annual average temperature and precipitation regime, the projected climate change is expected to modify the distribution range of tree species. Furthermore, as soil factors and processes are partly determined by climate variables, climate change is also expected to alter soil properties. Because plant species are influenced by soil factors and processes, soil modifications in turn are likely to interact with altered climate variables to influence tree species migrational response. Hence, tree species' response to the projected climate change is likely to be complex.

We suggest that the migrational response of trees species to climate change, especially to global warming and to soil conditions, could fall into one of four broad categories (Fig. 1). First, tree species migration could be fully constrained by unfavourable soil properties. Second, migration could be constrained by soil properties during the early stage of the projected temperature increase, and then be relieved later on as soil properties change (in response to climate change and biotic effects) and become favourable for seedling establishment and tree growth. Third, migration could proceed without soil constraints during the early stage of the temperature increase, and then be constrained subsequently as soil properties change (in response to climate change and biotic effects) and become detrimental to seedling establishment and tree growth. Fourth, migration could proceed without soil constraints for the full duration of the temperature increase. Because tree species are likely to respond individually to altered climate and soil conditions, the composition of tree communities is therefore expected to be modified.

Provided climate and genetic adaptations permit, for a given species soil factors should not represent a major constraint for the northward shift of populations located at the southern limit or at the centre of their distribution range. Because populations are already present, one can assume that the soils, at least locally, are suitable for the establishment of migrating populations. At some locations, however, unfavourable soil properties such as waterlogged conditions could preclude or slow down the establishment of migrating species that are poorly adapted to these conditions. For example, despite probable favourable climate envelopes, it is unlikely that *Acer saccharum* or *Betula alleghaniensis* will establish in the James Bay Lowlands, due to deep peat accumulation that creates waterlogged conditions unfavourable for their growth (Table 1). Similarly, the tundra, characterized by shallow or waterlogged soils and rocky outcrops, is unlikely to be rapidly colonized by deep tap-rooted species

Fig. 1. Because tree species respond differently to climate variables and to soil properties, the migrational response of trees to climate change and soil properties could fall into one of four broad categories; (i) tree species migration could be fully constrained by soil properties (dotted line); (ii) migration could be constrained by soil properties during the early stage of the projected global warming, and then relieved later on as soil properties change (in response to climate change and biotic effects) and become favourable for seedling establishment and tree growth (short dashed line); (iii) migration could proceed without soil constraints during the early stage of the global warming, and then be constrained later on as soil properties change (in response to climate change and biotic effects) and become detrimental to seedling establishment and tree growth (long dashed line); (iv) migration could proceed without soil constraints during the full length of the global warming (solid line).



such as *Pinus banksiana*, despite more favourable climate conditions (Table 1). Table 1 illustrates potential soil constraints to the migration of selected species. For both short distances and long range dispersal, however, other factors such as disturbance regime, concurrent migration of associated pollinators and dispersers, and associated mycorrhizal fungi (e.g., in the boreal forest ericoid and ectomycorrhizal fungi have biochemical and physiological attributes that make them highly efficient at scavenging for organic N and P) and competition will also influence the migration and establishment of tree species in new habitats. Nevertheless, marginal populations could favour a rapid response to climate change.

Because the presence of soil is a prerequisite for tree establishment, the limited development of the soil profile may be an important factor constraining the establishment of trees in areas of the tundra where soils are poorly developed. As well, in some locations waterlogged conditions and permafrost may constrain tree establishment and therefore species migration. The importance of soil factors should thus be locally high in the tundra relative to other factors such as disturbance regime and competition. In contrast, in the boreal and temperate forests where soil profiles are well-developed, the importance of soil conditions for tree establishment should be lower relative to disturbance regime, competition, and concurrent migration of associated pollinators and dispersers. Local soil conditions, such as

Table 1. Selected North American tree species and potential soil constraints on their migrational response to climate change.

Species	Potential soil constraints
<i>Abies balsamea</i>	Low soil pH
<i>Acer saccharum</i>	Waterlogged conditions, low nutrient availability
<i>Betula alleghaniensis</i>	Waterlogged conditions, low nutrient availability
<i>Betula papyrifera</i>	Waterlogged conditions
<i>Carya cordiformis</i>	Low nutrient availability
<i>Carya ovata</i>	Low nutrient availability
<i>Fagus grandifolia</i>	Waterlogged conditions, low nutrient availability
<i>Faxinus americana</i>	Low nutrient availability (especially N and Ca)
<i>Fraxinus nigra</i>	Dry soils, low nutrient availability
<i>Picea glauca</i>	Waterlogged conditions, permafrost
<i>Pinus banksiana</i>	Waterlogged conditions, alkaline soils, soil depth
<i>Pinus resinosa</i>	Waterlogged conditions, alkaline soils
<i>Pinus strobus</i>	Waterlogged conditions
<i>Populus balsamifera</i>	Waterlogged conditions, low nutrient availability (especially Ca and Mg)
<i>Populus tremuloides</i>	Waterlogged conditions
<i>Tilia americana</i>	Low soil pH, low nutrient availability
<i>Ulmus americana</i>	Low nutrient availability

waterlogged conditions, could also restrict species migration and establishment in the boreal forest.

Therefore, the migration of tree species is highly probable within the area currently occupied by the boreal and temperate forest, but will be restricted to the more favourable sites in the tundra (Gamache and Payette 2005; Lloyd 2005; Caccianiga and Payette 2006; Lloyd et al. 2007). 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 constraints imposed by the tundra environment, the area covered by the temperate forest biome could remain the same, but show a poleward shift. In both biomes, the fate of individual species remains uncertain and is dependent upon their response to complex interactions among climate variables, soil factors and processes, genetic adaptations, modification of disturbance regime, competition, associated pollinators and dispersers, and associated soil microorganisms (e.g., mycorrhizae). Therefore, individual species are more likely to respond to climate change than an entire biome. Further, some species, such as *Betula nigra* and *Quercus palustris*, which currently occur in the eastern US only, may migrate to southeastern Canada in response to global warming. New plant species assemblages are therefore likely to emerge from climate change, which may pose new challenges to forest managers.

In conclusion, while climate change has the potential to improve soil conditions for plant growth, plants will also have to cope with soil properties that may hinder their establishment. These antagonistic forces could slow down the migration of some species in response to climate change. Despite the difficulties to reliably predict the fate of tree species communities in response to climate change, policy and management choices of the future will require an understanding of possible species responses to biotic and abiotic factors, including soil factors. Human assistance may also be needed if tree species are to realize their newly expanded, potential natural ranges.

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