

The Subarctic Forest–Tundra: The Structure of a Biome in a Changing Climate

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The *forest–tundra* (FT) is a term coined by Clements (1936) to describe the transition zone where the subalpine forest and alpine tundra communities meet. The term has been extended to include the high-latitude subarctic vegetation between the circumpolar boreal forest and the arctic tundra (Marr 1948, Hare 1959, Löve 1970, Hare and Ritchie 1972, Rowe 1972, Larsen 1980, Payette 1983). The vegetation mosaic of the FT is viewed as either an *ecotone*, a zonal subdivision, or a *biome*, depending on the scale of perception (Marr 1948, Hare 1959, Britton 1967, Rowe 1972, Nichols 1975, Payette 1983). The term *ecotone* is now gaining popularity, although the concept is an old one (Clements 1936), and it is now used to describe the structural and functional changes occurring at different spatial scales (Gosz 1993, Risser 1995).

In the subarctic FT, forest communities are often confined to wind-protected, well-watered, and seepage sites, whereas upland, exposed, well-drained sites are occupied by treeless communities. Across a south–north gradient, the FT extends from the *continuous-forest limit*, that is, the limit of the area where all well-drained sites are colonized by forest, to the *arctic tree line*, that is, the northernmost position of arboreal growth. The contrasted structure of the subarctic FT is the inverted mirror image of the agro-forested landscape, in which forests are typically located on the exposed sites and low-stature agricultural fields are found on the bottomlands and riparian soils. Much like the agro-forested landscape, the subarctic FT is heavily fragmented, with strong edaphic and elevational gradients at the local and regional scales. The subarctic FT in North America covers a large area, mostly on the acidic, nutrient-poor soils of the Precambrian shelf across northern Canada, east and west of Hudson Bay (Figure 1). With its patchy vegetation pattern, the subarctic FT is certainly one major bioclimatic zone that exemplifies the ecotone concept. The subarctic FT is composed of climate-sensitive forests and trees at their northernmost ranges, which may explain why it has been used extensively in paleoecological and ecological studies for the evaluation of the environmental impact of climatic change (Lamb 1985, Ritchie 1987, Gajewski et al. 1993, Spear 1993).

THE SHIFTING OF LOCAL SUBARCTIC TREE LINES THROUGHOUT THE FOREST–TUNDRA BIOME, WHICH IS LINKED TO ECOLOGICAL PROCESSES AT DIFFERENT SPATIOTEMPORAL SCALES, WILL REFLECT FUTURE GLOBAL CHANGES IN CLIMATE

Several biogeographical models were developed in the past two decades to predict the future development of the earth's major biomes, particularly the northern biota, in a high-CO₂, warmer world (COHMAP members 1988, Prentice et al. 1992, Starfield and Chapin 1996). Transient changes attributable to climate change have also been modeled at a local scale using several functional attributes of the vegetation cover and site characteristics (Pastor and Post 1988, Nobel 1993, Woodward 1993, Sirois et al. 1994, Clark and Ji 1995). The main interest of these more local-scale models is their greater potential for realistic predictions because they are based on both biotic and physical processes operating at shorter time scales (Huston et al. 1988, Clark and Ji 1995).

To evaluate and better understand the global response of the biome to past and future climate change, we will examine both the global and local structural components of the subarctic FT and their ability to be used as climate-sensitive markers. To do so, we have analyzed and published original

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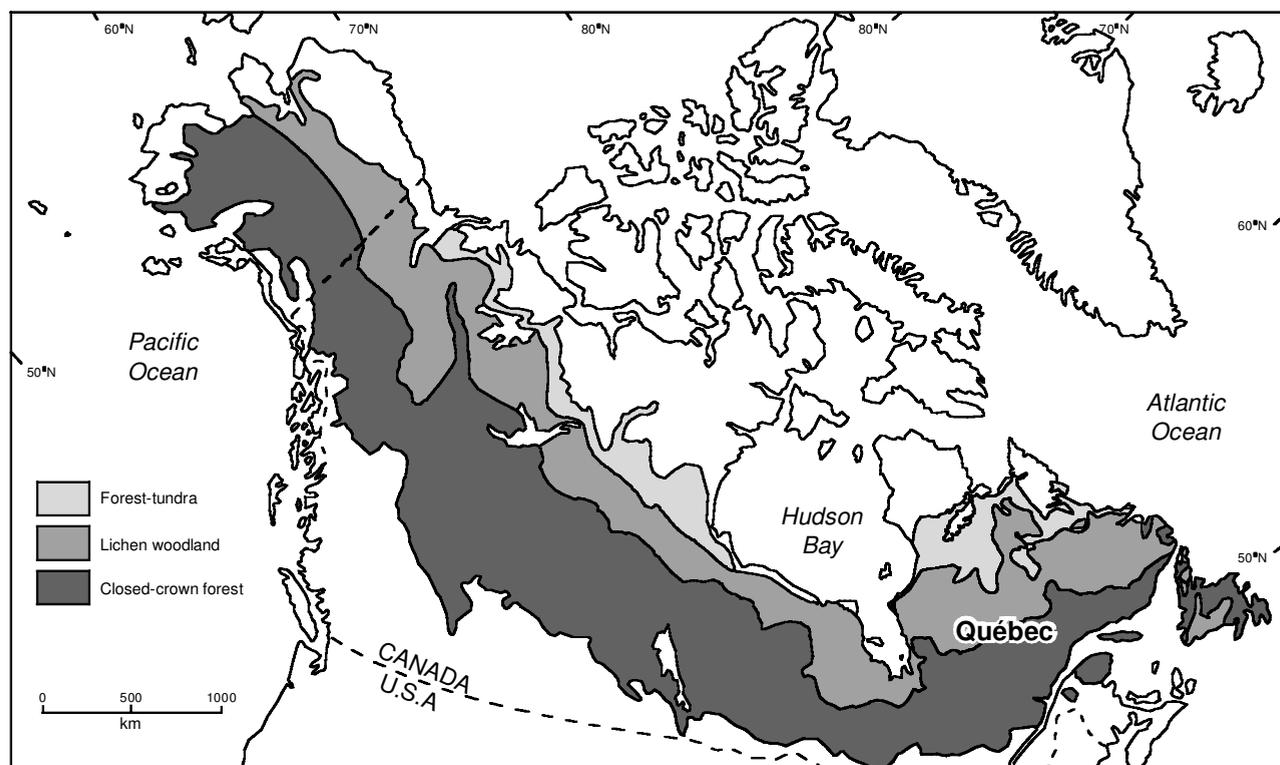


Figure 1. Major subdivisions of the North American boreal forest.

data for the subarctic FT of northern Québec, one of the widest FT areas of North America, linking the structure of the FT to ecosystem processes.

The forest:tundra ratio

The vegetation pattern of the FT is an archive of the long-enduring association of climate and fire during the late Holocene. From the continuous boreal forest to the arctic tundra, the spatial pattern of the FT (Timoney et al. 1993, Payette and Lavoie 1994) may be compared to a huge Swiss cheese (see Rapoport 1982), with “holes” made up of postfire, tundra-like lichen–shrub communities adjacent to the “filled” places occupied by postfire lichen–spruce stands. As in any comparison of this sort, however, the reality is more complex.

The overall Swiss-cheese pattern of the FT is quite apparent in the southern part, where the filled places are melded into an extensive forest carpet infrequently broken by small tundra gaps; in contrast, all the filled places are disconnected from each other in the northern part of the FT. Throughout the biome in northern Canada, the forest cover (including *krummholz*, i.e., stunted trees) occupying well-drained sites decreases systematically with increasing latitude (Rowe 1972, Payette 1983, Timoney et al. 1992). The FT is floristically poor, for instance, in eastern Canada, where only seven tree species are distributed locally in the southern part (aspen, *Populus tremuloides* Michx.; balsam poplar, *Populus balsamifera* L.; white birch, *Betula papyrifera* Marsh.; and jack pine, *Pinus banksiana* Lamb.) or throughout the biome (black spruce, *Picea mariana* [Mill.] BSP.; white spruce, *Picea glauca*

[Moench] Voss.; and tamarack, *Larix laricina* [DuRoi] K. Koch). Black spruce is by far the dominant species, and it is the reference species reported in this article.

In northern Québec, the forest:tundra ratio (FTR)—that is, forest cover (percentage) on well-drained sites versus total well-drained land cover (percentage) per unit area at a given latitude—fits a logarithmic trend, with larger forest loss in the region close to the boundary of continuous forest ($r^2 = 0.94$, $p < .0001$) (Figure 2a). This indicates that the region with the highest FTR is paradoxically the one most affected by deforestation per unit of latitude. Deforestation corresponds to forest-to-tundra shift at the site scale, caused by fire disturbance in climatically stressed forest stands. Indeed, deforested sites are all occupied by tundra vegetation growing on soils overlaid by charred tree remains. The sharp FTR gradient within the first 100-km stretch of land in the southern part of the FT, showing a 65% drop in the FTR, strongly contrasts with that of the last 100-km stretch of land in the northern part of the FT, with only a less than 5% drop in the FTR. From a structural point of view, and for a given time scale, postfire deforestation appears particularly active in the southern FT, whereas it is rather slow in the northern FT.

From 56°N to the tree line at 58°24'N, the decreasing forest cover with latitude is paralleled by a linear drop in the number ($r^2 = 0.73$, $p < .0001$) of individual forest patches. In the southernmost part of the FT, the forest cover is continuous, except for a small number of tundra patches located on the highest summits. Therefore, when the number of tundra patches (as opposed to forest patches at the tree line) from

55°09'N to 55°30'N is included, the global pattern of forest fragmentation exhibits a parabolic distribution, with the largest number of forest islands located in the middle of the FT (Figure 2b). Forest fragmentation is high at this point, very low near the continuous-forest border, and at its climax at the arctic tree line, where the dominant tundra communities occupy the sites of former forest communities. Similarly, the mean cover of forest patches decreases systematically from the mid-FT to the tree line, with smaller variations toward the tree line ($r^2 = 0.51$, $p < .0001$).

The FT as a constellation of subarctic tree lines

The spatial arrangement of the FTR is outlined by an assemblage of low, elongated hills typical of the Precambrian plateau, with thin soils and granite–gneiss outcrops interrupted by lakes and wetlands. This assemblage provides the initial topographic setting for fire spread. Fire ignition generally occurs on the well-drained parts of the vegetated hills. The basic “cellular” unit of the FT is a single, low-elevation, granitic hill exhibiting a striking, fire-induced vegetation toposequence: a cover of lichens and shrubs (with or without trees) at the top surrounded, often just a few meters below the summit, by dry to mesic lichen woodlands and wet spruce–moss stands downslope and near depressions (Figure 3a).

At several places, the toposequence corresponds to the extent of small fires (fewer than 100 ha), particularly in the northern FT and the shrub tundra (Payette et al. 1989). In areas affected by large fires (100,000–200,000 ha), for instance, in the southern FT, the cellular unit is reproduced seemingly infinitely. This creates a landscape of thousands of toposequences arranged in a geographical pattern that mimics the structural geometry of the bedrock and its superimposed, smoother glacial landforms. One can thus describe the FT as a constellation of subarctic tree lines, in far greater number in the middle and southern parts of the FT and steadily decreasing toward the ultimate arctic tree line (Figure 3b, right). Indeed, each vegetation toposequence corresponds to a neat tree-line situation (Stevens and Fox 1991), that is, a subarctic tree line. At any subarctic tree line, site factors (vegetational, edaphic, and topographic) appear as the proximal causes of tree exclusion from the lichen–shrub sites, particularly in the southern FT (Figure 3b). For hundreds of years after fire, nearby seed-bearing trees were generally unable to colonize the ground vegetation, even within a distance of tens or hundreds of meters from the forest edge, pointing to physical factors (soil moisture, lichen cover, temperature, and so on) as the ultimate causes of tree exclusion. Tree colonization of lichen tundra patches across the FT thus appears to be controlled by both local (site conditions) and regional (climate) factors.

As a result, although the arctic tree line is the northernmost, it is not necessarily the most climatically stressed of all FT tree lines. Some high-altitude subarctic tree lines south of the arctic tree line are often more climatically stressed. Accordingly, under a changing climate, the arctic tree line may not

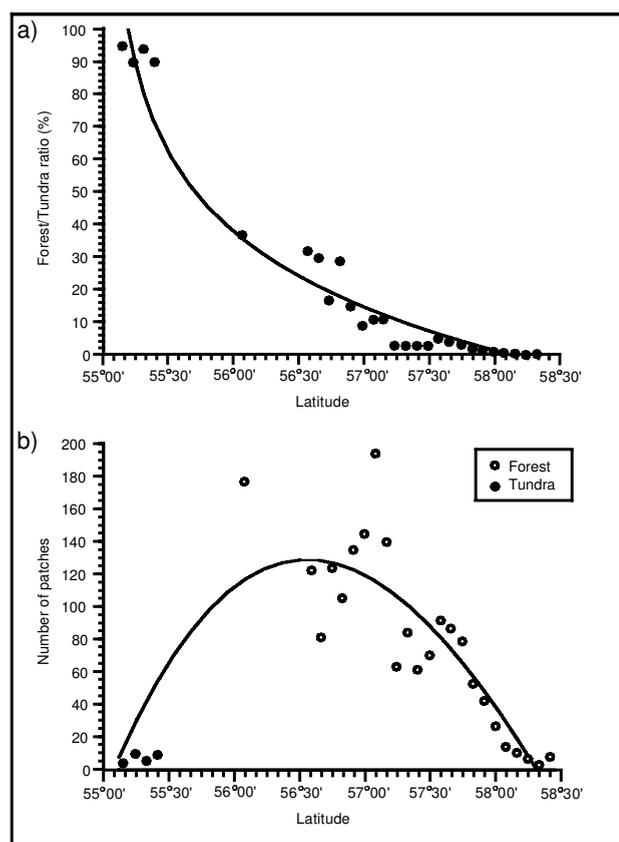


Figure 2. (a) Forest:tundra ratio (FTR) according to latitude, from the continuous boreal forest (55°N) to the arctic tundra (58°30'N) in northern Québec. FTR is the percentage of forest cover relative to the total vegetation cover (forest + tundra) in well-drained sites at each 5 minutes of latitude (or latitudinal slice) within a 1-km-wide transect between 74°W and 76°W. The first latitudinal slice was selected at random in the area of the continuous boreal forest, and the other slices were systematically positioned at each 5 minutes of latitude. The cover of forest and tundra was evaluated from panchromatic aerial photographs and checked by field surveys. The regions between 55°30'N and 56°N and between 56°05'N and 56°30'N were not surveyed because of extensive wildfires in 1954 at the time the aerial photographs were taken, which obscured both vegetation types. (b) Number of forest patches according to latitude, from 56°N to the tree line at 58°24'N, and number of tundra patches in the southernmost part of the forest–tundra around 55°09' to 55°30'N. The sampling design was the same as for Figure 2a.

be the first FT tree line to respond readily to climatic changes. Furthermore, the greater isolation of confined forest islands at the arctic tree line creates a situation of constrained fire spread because of the lack of wood fuel, thus reducing the probability of potentially damaging domino effects associated with large conflagrations, such as increased albedo, reduced snow depth in wind-exposed burned forests, and changed

snow patterns in nearby wetlands. The heavily reduced and scattered forest cover at the arctic tree line is a major positive factor increasing the probability of survival of tree line stands in the wake of future fire-mediated climatic changes.

Fire patterns at the biome scale

The current distribution and extent of forest islands and their associated subarctic tree lines across the FT (Figure 3)

are the direct consequences of fire patterns and repetitive failures of the postfire forest recovery process that are still visible and quite active today. For example, the patterns of forest fragmentation caused by fire can be fully appreciated when looking at the impact of a large fire, such as the 179,000-ha fire that occurred in 1954 at 56°N in the southern FT (Payette et al. 1989).

Within the fire perimeter, all the forest fragments correspond to the surviving vegetation that escaped the fire, and the other fragments correspond to the burned tundra and forest. In general, the percentage of surviving vegetation is likely to be higher with increasing fire size (Eberhart and Woodard 1987). For the 1954 fire in particular, we have estimated from air photographs that the surface of the unburned dry and mesic sites constitutes only 3.9% of the total burned area, including a meager 2.75% of surviving forest stands (Table 1). Residual vegetation within the perimeters of large fires is often located in wetter sites less prone to burn and may sometimes represent 15% of the total area covered by a fire (Gasaway and Dubois 1985). About 50% of the surfaces of all surviving lichen woodlands within the 1954 fire perimeter were bordered by natural firebreaks such as peatlands and lakes, and the remaining 50% escaped the fire under full dry to mesic soil conditions. If this type of fire event occurs during a period inimical to tree regeneration, which was verified in a re-

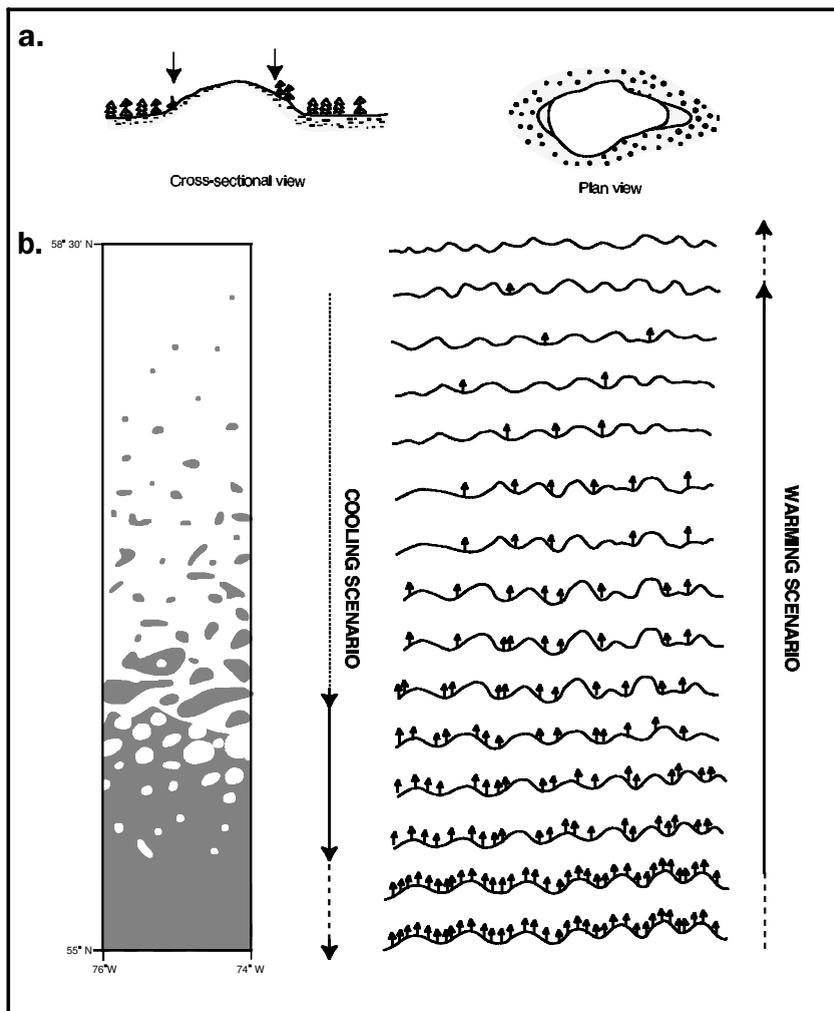


Figure 3. (a) Cross-sectional (left) and plan (right) views of the cellular unit of the forest-tundra, that is, a single granitic hill (outcrop or thin soil) supporting a fire-induced vegetational toposequence. Most trees are distributed along the slopes and depressions and form a subarctic tree line at the junction with the hilltop tundra-like vegetation. The arrows indicate the position of the subarctic tree line. The plan view shows the distribution of trees (open circles) and subarctic tree line (solid line) around the treeless hilltop. (b) Plan (left) and cross-sectional (right) views of the global FT. The plan view shows the patchy distribution of forest (grey) and tundra (white) according to latitude toward the ultimate arctic tree line (the distribution of forest and tundra match Figure 2a). The cross-sectional view shows the distribution of forest from the continuous-forest limit to the ultimate arctic tree line with intervening subarctic tree lines. Under a warming scenario, trees invade the treeless hilltops, thus decreasing the number of subarctic tree lines in the southern part of the biome and increasing the number of subarctic tree lines in the northern part (arrow with solid line). The northward displacement of the arctic tree line proceeds through the production of erect trees from stunted trees already present in the arctic tundra (arrow with broken line). Under a cooling scenario without fire disturbance, the forest cover remains somewhat stable throughout the biome. Under a cooling scenario with fire disturbance, trees are excluded from hilltops, thus increasing the number of subarctic tree lines in the southern part of the biome (arrow with solid line) and inducing the formation of subarctic tree lines south of the continuous-forest limit (arrow with broken line). The process of tree exclusion and the rate of decrease in the number of subarctic tree lines are far less significant in the northern part of the biome (arrow with dotted line). The position of the arctic tree line remains rather stable but may change sharply, assuming a larger magnitude of the fire-mediated climate disturbance.

cent demographic survey (Sirois and Payette 1991), then it is likely that the surviving lichen woodlands and nearby spruce–moss stands in wet depressions will constitute the only salient source areas for future tree expansion. Although the impact of the 1954 fire was negative for tree regeneration at a fairly large number of sites, several burned forests did regenerate, although at reduced levels.

To illustrate the fire-determined forest pattern of the northern FT, we compared the proportion of vegetation surviving the 1954 fire with the current forest vegetation about 100 km north, to check whether both forest distributions and covers were similar and probably associated with the fire factor. To do so, we delineated the occurrence of an identical hypothetical fire (179,000 ha) positioned at random at 1° of latitude north of the 56°N fire, using the same spatial distribution, that is, a fire having the same shape and the same surface as that of the 1954 fire. We evaluated the distribution and proportion of “surviving” lichen woodlands based on present spruce stands. The area occupied by the surviving well-drained stands, as well as their local distribution, was quite similar to those for the 1954 fire (Table 1). No significant differences (Kolmogorov-Smirnov test) between the situations were found in the size frequency of all remaining spruce islands (Figure 4). Also, forest islands at 57°N are all restricted to marginal sites. The locations of both surviving forests at 56°N and at 57°N are also roughly similar, with more than 70% of all stands surrounded by wetlands and lakes. Only 30% of all surviving stands were surrounded by fire-prone mesic and dry sites. It is noteworthy that 64% of all the northernmost surviving stands at the arctic tree line, between 58°04'N and 58°24'N, are also surrounded by wetlands and lakes, whereas the remaining stands are delineated by well-drained soils.

One may ask whether the postfire forest pattern at 57°N and throughout the northern FT is the result of a small or large number of catastrophic fires of various sizes during the late Holocene. The question is important on ecological grounds in light of the expected global change in the decades to come. At several forest and tundra sites in the northern FT, there is evidence for the occurrence of only one fire event in the last 2000 years that either promoted tree regeneration or completely destroyed the forest cover (Payette and Morneau 1993). This illustrates well the paradox of the northernmost forest ecosystems—that is, the relative stability of the tree line on the millennial time scale

Table 1. Percentage and distribution of forest islands surviving a large fire (179,000 ha).

Site	1954 Wildfire (56°N)	Hypothetical Wildfire (57°N)
Lichen islands	0.32	
Lichen islands with forests	1.18	
Forest islands	2.38	
Total unburned	3.88	
Islands	0.12	0.15
Peatlands	0.64	0.44
Peninsulas	0.42	0.17
Lakes	0.30	0.09
Subtotal	1.48	0.85
Terrestrial	1.27	1.15
Total forests unburned	2.75	2.00

(Lavoie and Payette 1996, Arseneault and Payette 1997b) and the lack of resilience of northern forests in the face of a rare, catastrophic fire event. Forest regeneration in this area showed variable postfire recruitment in the late Holocene, with a propensity for systematic deforestation during the last millennium (Arseneault and Payette 1997a).

Past fire occurrence across the FT was also recorded in paleosols from sandy deposits of fluvial and fluvio-glacial origin. During a fire, wind erosion is usually exacerbated by the complete combustion of the dry organic layers, causing soil erosion for some time (from months to years), and then soil stabilization through forest succession. Several postfire sequences of vegetation recovery were identified in dune deposits from the boreal forest to the arctic tundra during the last 4000 to 6000 ¹⁴C (radiocarbon) years, with at least 14 to 16 super-

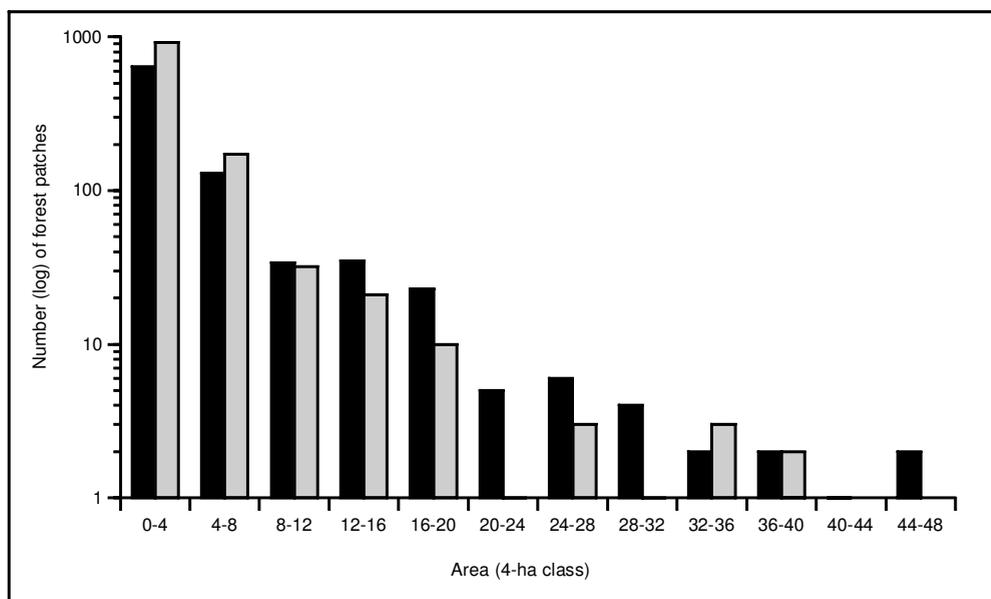


Figure 4. Number (log scale) of forest patches according to size (4-ha class) that survived a large 1954 wildfire (179,000 ha) at 56°N (black bars) and a similar hypothetical wildfire (179,000 ha) at 57°N (gray bars).

posed paleopodzols bearing spruce charcoal in the boreal forest but only one to three paleosols in the northern FT and at the tree line (Filion 1984, Filion et al. 1991). Of great significance is the decreasing number of spruce charcoal-bearing paleosols with latitude, an indirect indication of a low forest-fire frequency in dry sites of the northern FT during the late Holocene. Low rates of forest fire occurrence in the past (Filion 1984, Payette and Morneau 1993) and in this century (Payette et al. 1989) and scarcity and small size of forest islands suggest that deforestation of the northern FT—that is, all the tundra sites formerly forested as evidenced by charred tree remains at the soil surface—was likely the result of the action of one or very few fires.

Because the residual spruce islands are scattered in a huge matrix of tundra vegetation, the odds are for a decreasing occurrence of future large fires, assuming a fire regime similar to that of the 20th century, because of the lack of efficient combustibles. Between 1930 and 1984, fire frequency and the mean size of fires decreased from the continuous boreal forest to the arctic tree line–shrub tundra, that is, from 0.7 fire per year and 8000 ha to 0.4 fire per year and 80 ha, respectively (Payette et al. 1989). Accordingly, the probability of the long-term persistence of small forest islands is far greater near the arctic tree line. Between 1957 (as measured from aerial photographs) and 1985 (fire surveys from Payette et al. 1989), for instance, most burned forest islands were in the southern FT (burned areas in log: $r^2 = 0.59$, $p < .01$). As a result, the small number and size of spruce stands in the northern FT very likely induce a positive feedback at the biome scale, reducing the probability of occurrence of large fires and increasing the longevity of all forest islands. Paleoecological and ecological data on spruce stands of the northern FT point to their old-growth character, that is, one to several thousand years old and composed of populations of all ages, with some very old trees (Payette et al. 1985, Payette and Morneau 1993). In contrast, forests of the southern FT are postfire stands composed of populations of younger trees approximately the same age (Sirois and Payette 1991). As a result, the northern FT is an ecolog-

ical museum, and the southern FT is a vivid theater of the interplay between the forest biota and fire-climate forces.

The equilibrium line

Spruce populations across the FT and the shrub tundra are currently in nonequilibrium conditions. The *equilibrium line*, that is, the line where regeneration gain balances regeneration loss, is presently located in the upper boreal forest, at the line of contact between the continuous boreal forest and the southern FT. Does the current spruce distribution north of the continuous boreal forest indicate the position of former equilibrium lines? The general topographic profile across the FT and the arctic tundra takes the form of a large corridor pointing to the north, with a smooth decrease in both minimum and maximum ground altitudes per unit of latitude (Figure 5). Within this corridor, spruce stands in the FT and stunted spruce clones in the arctic tundra progressively reach the arctic tree line and the species limit at a negative rate of about 60–65 m per degree of latitude ($r^2 = 0.91$, $p < .0001$). The northernmost spruce stands at the arctic tree line are located around the 200-m (above mean sea level) cutoff line. Given the available low-elevation sites, a northward advance of trees or forests into the arctic tundra appears possible, provided suitable climatic conditions prevail. This makes spruce distribution along the 450-km transect, from the limit of continuous forest to the currently known species limit 100 km north of the tree line at 59°17'N, particularly inter-

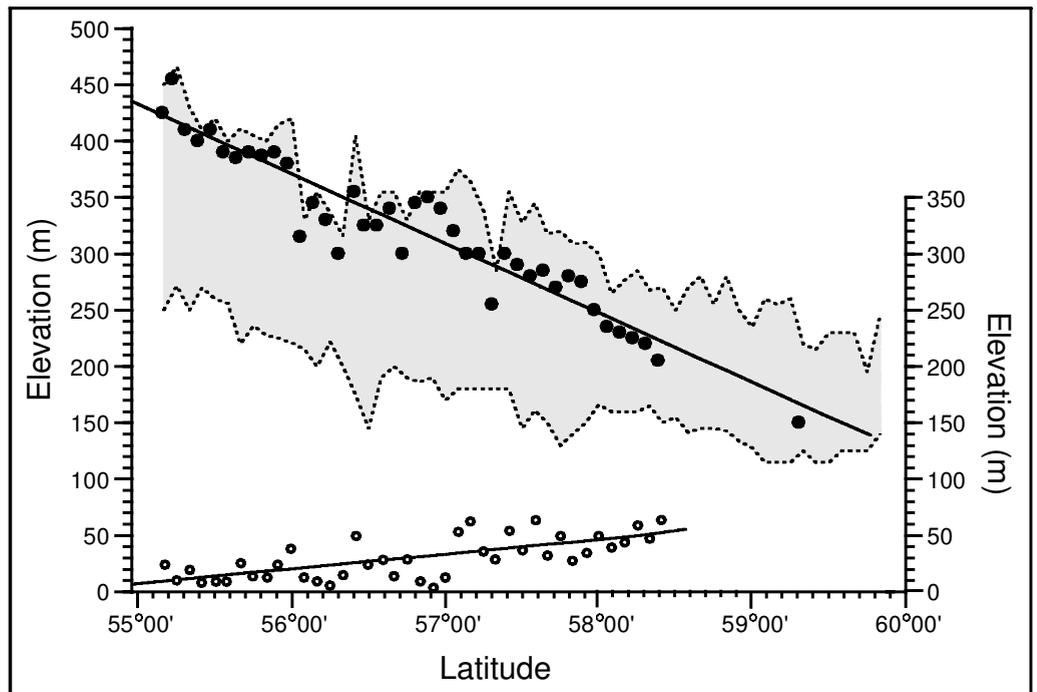


Figure 5. Maximum altitude of spruce stands (forest and krummholz [black circles]) according to latitude from the continuous-forest limit to the arctic tree line and the species limit in the arctic tundra. The amplitude of lowering of the subarctic treeline (open circles) is shown according to latitude. The shaded area between the dotted lines corresponds to the topographic corridor of maximum and minimum ground altitudes according to latitude from 55°N to 60°N. Data compilation was the same as for Figure 2a.

esting on biogeographical grounds, not only to interpret its dynamics during the Holocene but also to predict its future in a changing climate. This distribution raises some interesting points.

First, spruce distribution along the transect highlights a neat climatic control. No topographical barriers to the advance of any trees or forests north of the present arctic tree line have existed in the region since deglaciation. The current large-scale distribution argues strongly for a successful expansion of the species during the Holocene and suggests that an equilibrium in the global spruce population was reached at some point in the more or less distant past. A positive argument for a former equilibrium line is the low probability that spruce would reach a position north of the current species limit, at least under present conditions, given the absence of recent spruce establishment throughout the area. Indeed, present and past (based on macrofossils) distributions suggest that spruce may have reached its full potential range since the initial postglacial colonization. Based on the current negative rate of 60–65 m, the expected northernmost position of spruce in the arctic tundra lies between 59°45'N and 60°N.

However, looking only at the gross picture of spruce distribution may hide some failures of the hypothetical equilibrium line, such as the ups and downs of the maximum altitude of spruce stands from one latitudinal position to the next (Figure 5). Getting into the details of field conditions reveals the biogeographical background of spruce distribution along the latitudinal gradient: The general distribution is linear, while the local distribution from one latitudinal point to another is clearly sawtoothed. Spruce distribution is not controlled by climate alone, because regional and local factors, like fire and soil, also play a determining role. For instance, the northernmost forest islands stop at 58°24'N in a region where spruce stands would be able to occupy a thin elevational slice of 20–40 m, sites that are now colonized by tundra communities, between the “realized” altitudinal subarctic tree line and the lowermost well-drained ground surface (Figure 5).

The arctic tree line is also the northernmost area where all the unfilled sites below and above the current maximum altitude of spruce stands (Figure 5) were formerly occupied by spruce stands, as evidenced by spruce charcoal beneath the lichen mat. The current position of the arctic tree line most likely corresponds to the northernmost limit of spruce forests during the late Holocene (Lavoie and Payette 1996).

Therefore, the difference between maximum land elevation and maximum altitude of spruce stands at each of the 5-minute latitudinal slices south of the arctic tree line indicates a corresponding lowering of the subarctic tree line across the biome, averaging 50–60 m from the mid-FT to the present arctic tree line and 10–30 m from the mid-FT to the northern limit of continuous forest (at a rate of about 10–15 m per degree of latitude [$r^2 = 0.48, p < .0001$]; Figure 5). Thus, the current spruce distribution represents an incomplete imprint of a previous Holocene equilibrium line when the details of all the ups and downs of the altitudinal subarctic tree line are examined.

When spruce stands of the FT occupied all the well-drained sites, ranging from minimum to maximum altitudes at each latitudinal slice, the climatic gradient across the biome was somewhat smoother than at present, that is, about 50 m per degree of latitude ($r^2 = 0.89, p < .0001$). Three important conclusions can be drawn from the altitudinal patterns of spruce distribution: (1) The position of the modern forest limit, which roughly coincides with the current position of the arctic tree line and the northernmost distribution of spruce charcoal on the highest hilltops, has been relatively stable at least since the beginning of the deforestation period, well after 3000 years BP (Lavoie and Payette 1996). (2) The position of the modern forest limit likely corresponds to the northernmost position of forest during the Holocene, even at a time when the climatic gradient was smoother. (3) At the regional scale, forest expansion has been a continuous but lengthy process that stopped before 3000 BP, when the climate cooled to present conditions.

Several examples support the nonequilibrium state of the FT. During the 20th century, the northern limit of postfire regeneration of lichen–spruce woodlands was at least 130 km south of the present arctic tree line at 57°N (Payette et al. 1989), that is, in the middle of the FT. Most postfire lichen woodlands in the southern FT are younger than those of the northern FT, responding to a fire cycle of approximately 180 years (Payette et al. 1989, Sirois and Payette 1991). Furthermore, the known northern limit of seedling establishment is at the arctic tree line, in old-growth lichen woodlands (Payette et al. 1985, Lavoie and Payette 1994), about 100 km south of the current species limit. The position of the arctic tree line and forest limit coincides with the region where topographical contrasts (i.e., the range between maximum and minimum elevations at each 5-minute latitudinal slice) decrease strongly, possibly exacerbating wind-exposed conditions that reduce seedling establishment.

Tundra spruce were probably established by long-distance transport of FT seeds. The current species limit corresponds to a successful event of seedling establishment realized by long-distance transport long ago, as deduced from the size-derived (12-m diameter) age (roughly equivalent to 1000 years; clone age based on allometric relationships between clone size and time since last fire at a given site [Laberge et al. 2000]) of the northernmost spruce yet recorded (Payette and Delwaide 1994). Another argument against the equilibrium state is the size and age characteristics outlining the old-growth structure of tree line and tundra spruce populations. At the tree line, every lichen woodland is an old-growth stand, several hundred and often more than 1000 years old (Payette et al. 1985, Arseneault and Payette 1992, Payette and Morneau 1993), including living and dead spruce of all sizes.

Although occasional seed regeneration still prevails in the northernmost lichen woodlands, which may indicate local equilibrium, any conflagrations would cause their complete elimination, given the inability of the trees to produce a sufficiently large number of viable seeds to restore the stands to their prefire condition. To our knowledge, no young postfire

spruce stand has ever been reported across the arctic tree line in eastern Canada; all burned forests have been transformed into tundra during the last 100 years because of the failure of postfire regeneration.

New field data (Laberge et al. 2000) also point to the heterogeneous size structure of stunted spruce clones (ages are deduced from the diameters of clones genetically identified) at the arctic tree line and in the arctic tundra, corresponding to a population of all ages but with apparently no recent recruits; this point needs more attention, however, because seedlings and saplings, if present, are very difficult to locate because of their small size. Only medium- and large-size clones (greater than 3 m in diameter) have been reported to date in the arctic tundra, despite a search for smaller spruce. This apparent heterogeneous size distribution of tundra spruce needs more fieldwork before the ancient character of the northernmost spruce populations can be confirmed. However, the absence of any significant fire disturbances, due to the small size and low frequency of wildfires, has contributed so far to the maintenance of old-growth spruce vegetation in the northern FT and in the arctic tundra.

Directions of ecosystem development in a changing climate

All the forest islands of the subarctic FT are likely to face new threats from the impending climatic changes associated with greenhouse warming. In response to global warming, the new directions of vegetation change will probably take place at the site level. The vegetation cover at a particular site is the end product of past and present ecological conditions differentially expressed by each species because of their specific life-history traits and ranges of adaptations. Although they share the same environment, the constituent species may react to climate change in opposite ways. Some species are more sensitive to high-frequency climatic variability, whereas others respond over a longer period. Many long-lived tree species react more slowly and indirectly to a change than others having shorter reproduction schedules (Clark 1991, Zasada et al. 1992, Graumlich and Brubaker 1995, Lloyd and Graumlich 1997, Sirois 1997, Lloyd 1998).

The species-specific responses of tree line species to warming is particularly illuminating in this context. During the past 100–150 years, white spruce density increased in FT stands in western, central, and eastern Canada without any significant displacements of the arctic tree line (Payette and Filion 1985, Scott et al. 1987, Szeicz and MacDonald 1995); the same trend was observed in tamarack at the tree line in northern Québec (Morin and Payette 1984). Black spruce, which has a different strategy of seed dispersal associated with semi-serotinous cones, reacted to the warming by changing its growth form without any significant seedling recruitments (Lavoie and Payette 1994, Lescop-Sinclair and Payette 1995).

The structure and dynamics of the FT are the result of highly variable tree establishment at the local scale, which has a measurable and significant impact at larger spatial scales

when replicated throughout the biome. Indeed, trees play a central role in the functioning of the FT and in the ecosystem processes controlling soil–plant dynamics. The dynamic nature of the vegetation cover is caused to a large extent by climate (Woodward 1987). At least during the last 1000 years, subarctic forests have been eliminated by catastrophic wildfires during periods of climatically reduced tree regeneration. Thus, the process of vegetation change during the late Holocene was typically nonlinear, often because of the lack of time between fire incidence and climate change.

The exclusion of forests has consequences that are inherently local, particularly with the habitat degradation that tree removal creates (that is, causing a positive feedback inducing frost activity due to a thinner snowpack; Arseneault and Payette 1997a). Deforestation also increases the climatic differences between forest islands and nearby low-vegetated tundras to at least equal those between similar vegetation types located at both the southern and northern ends of the FT, several hundreds of kilometers away. Furthermore, the large-scale reduction of the forest cover induces positive feedback at the biome scale that exacerbates the climatic differences between the northern and the southern FT by increasing albedo (Hare and Ritchie 1972).

The most authoritative climatic scenarios developed for the expected warming predict more warmth in northern areas relative to temperate and tropical areas (Houghton et al. 1996). Warmth will be distributed asymmetrically throughout the year, with diminished seasonal contrasts because of greater warming in winter. Warming will take place progressively during several decades, and the northern and southern FT, just a few hundred kilometers apart, will experience rather similar heat gains. Any substantial short-term vegetation changes will probably be mediated by fire disturbances, which are more likely in the southern FT (Figure 3). Although the expected warming may be accompanied by increased soil wetness, the probability of fire ignition should rise in the days and weeks following the snowmelt period, that is, during the “fire window” in spring and early summer, the period most propitious for fire ignition and spread (Johnson 1992). This does not rule out the likelihood of tree invasion into the nearby lichen–heath tundra from seed bearers located in the adjoining subarctic tree lines if wetter soil conditions predominate.

The patterns of reforestation of the FT in a warmer and humid climate will probably be modeled on those of the present distribution and abundance of forest islands (Figure 2). As a result, the colonization may take the form of advancing local subarctic tree lines in each toposequence. This may occur more rapidly in the southern FT than in the northern FT because of the larger number of seed-bearing trees and greater warmth. Under colder conditions, fire disturbance and its correlative deforestation damage will be most effective in the southern FT. The current logarithmic depletion of the forest cover in the southern FT (Figure 2a) may be an indication of the overwhelming influence of a recent and rapid deforestation process on spruce stands, possibly during the last major

climatic excursion associated with post-Medieval warmth and Little Ice Age cooling.

Forest-to-tundra shifts in a colder fire-prone climate will thus proceed more rapidly than the tundra-to-forest shifts in a warmer fire-prone climate. The reason for this difference is the regeneration strategy of black spruce trees, which is fire dependent. More specifically, depending on size, fire in a colder climate will "instantaneously" eliminate relatively large tracts of forest if they are composed of trees unable to produce viable seeds, whereas it will take a longer time to colonize new sites with successful seed-bearing trees because of short-distance seed dispersal and vagaries in timing between forest development and fire. Like several other natural phenomena, the construction of a forest takes more time than its destruction, whatever the causes of the destruction.

Conclusion

It is likely that the Holocene equilibrium line before 3000 BP corresponded to the position of the modern forest limit and arctic tree line, at the line of contact between the northern FT and shrub tundra. The Holocene equilibrium line climaxed during a period of forest maximum, when all the tundra sites currently above the local subarctic tree lines were occupied by forest stands. Based on present evidence, tundra spruce trees north of the arctic tree line are outliers of all ages, established from seeds transported from more or less remote areas associated with the changing positions of the equilibrium line, the forest limit, and the arctic tree line.

We suggest that the subarctic FT is a complex vegetation mosaic derived from a once-larger Holocene forest later disrupted by nonlinear, regressive fire-climate processes. These processes have induced a constellation of local subarctic tree lines, including the northernmost tree line at the arctic border. Accordingly, any evaluation of the global response of the biota to climate change will best be achieved by looking at the reaction of tree species from the boreal forest to the arctic tundra, in particular the subarctic tree lines across the entire biome.

The basic ecological pattern of the FT is the result of dramatic local vegetation shifts from forest to tundra communities, caused by fire disturbance and producing as many tree line sites as there are such forest-to-tundra reversions. The cumulative spatial extension of local forest-to-tundra shifts across the biome during the late Holocene has created the present vegetation pattern of the subarctic FT, which is today a fragmented forest assemblage because of abrupt, cumulative deforestation events at the site scale. Similarly, the future development of the FT in a warming climate will most likely proceed from the same spatial arrangement, with tundra-to-forest shifts operating at a larger scale, with more or less synchronous tree filling of local tundra sites.

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