

forest ecology

Competitive Advantage of Black Spruce Over Balsam Fir in Coniferous Boreal Forests of Eastern North America Revealed by Site Index

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The boreal zone of northeastern North America is characterized by mixedwood forests dominated by balsam fir (*Abies balsamea* (L.) Mill.) in the south and by coniferous forests dominated by black spruce (*Picea mariana* (Mill) B.S.P.) in the north. Site index values of balsam fir and black spruce were compared in 364 sites spread across the boreal zone of northwestern Quebec to determine if the northward dominance shift from balsam fir to black spruce could be explained by a difference in height growth. Site index of both species decreased along a south–north gradient, although the trend was only significant for balsam fir on clay deposits. Site index values shifted from being significantly higher for balsam fir in the boreal mixedwood forest, to being slightly (but not significantly) higher for black spruce in the coniferous forest. Mean annual temperature had a significant positive effect on site index for both species, and precipitation of the growing season had a significant negative effect only for balsam fir. The competitive advantage of black spruce over balsam fir in coniferous forests is due to a greater tolerance to cooler temperatures and water-logged soils.

Keywords: boreal zone, mixedwood forests, coniferous forests, site index, surface deposit, climate, *Abies balsamea*, *Picea mariana*

Distributions of tree species and vegetation zones can be influenced by climate (Woodward 1987), disturbances (Asselin et al. 2003, Flannigan and Bergeron 1998, Lozon and MacIsaac 1997, Rupp et al. 2000), physical barriers (Davis et al. 1986, Rupp et al. 2001), soil type (Lafleur et al. 2010), nutrient availability for seedlings (Davis et al. 1999, Jarvis and Linder 2000), interspecies competition (Davis et al. 1998), or combinations of those factors.

In northeastern North America, the boreal zone can be divided into two bioclimatic domains differentiated by their dominant late-successional species (Saucier et al. 1998). Balsam fir (*Abies balsamea* (L.) Mill.) dominates in the southern part of the zone, hereafter called boreal mixedwood forest because paper birch (*Betula papyrifera* Marsh.) is the main companion species. Black spruce (*Picea mariana* (Mill) B.S.P.) dominates in the northern part of the zone, hereafter called coniferous forest. Moving north from boreal mixedwood to coniferous forests, balsam fir is increasingly less abundant and its populations become more scattered (Messaoud et al. 2007b). Balsam fir stands and individuals in the coniferous forest are often relics resulting from fire-induced fragmentation of formerly larger populations (Ali et al. 2008). The transition between boreal mixed-

wood and coniferous forests is still under fire control, as fires are larger and more severe in coniferous than in boreal mixedwood forests (Bergeron et al. 2004). Large and severe fires are detrimental to balsam fir regeneration because most seeds fall short distances from seed trees (Asselin et al. 2001). Furthermore, balsam fir seeds are not stored in soil seed banks, as are those of black spruce (Albani et al. 2005).

Notwithstanding the importance of fire in explaining the transition between boreal mixedwood and coniferous forests, other factors might affect remnant seed trees, reducing the ability of balsam fir to recolonize burned sites. Reduced balsam fir seed production and seedling survival in coniferous compared to boreal mixedwood forests has already been linked to cooler temperatures and shorter growing seasons (Messaoud et al. 2007a). Competition between balsam fir and black spruce could also play a role, black spruce being more tolerant of cool temperatures and spruce budworm infestations than balsam fir. In addition, small or suppressed trees produce less seeds than large or dominant trees (Greene et al. 2002, Messaoud et al. 2007a), contributing to a decrease in potential reproduction. We hypothesize that the transition between boreal mixedwood and coniferous forests might be partly explained by

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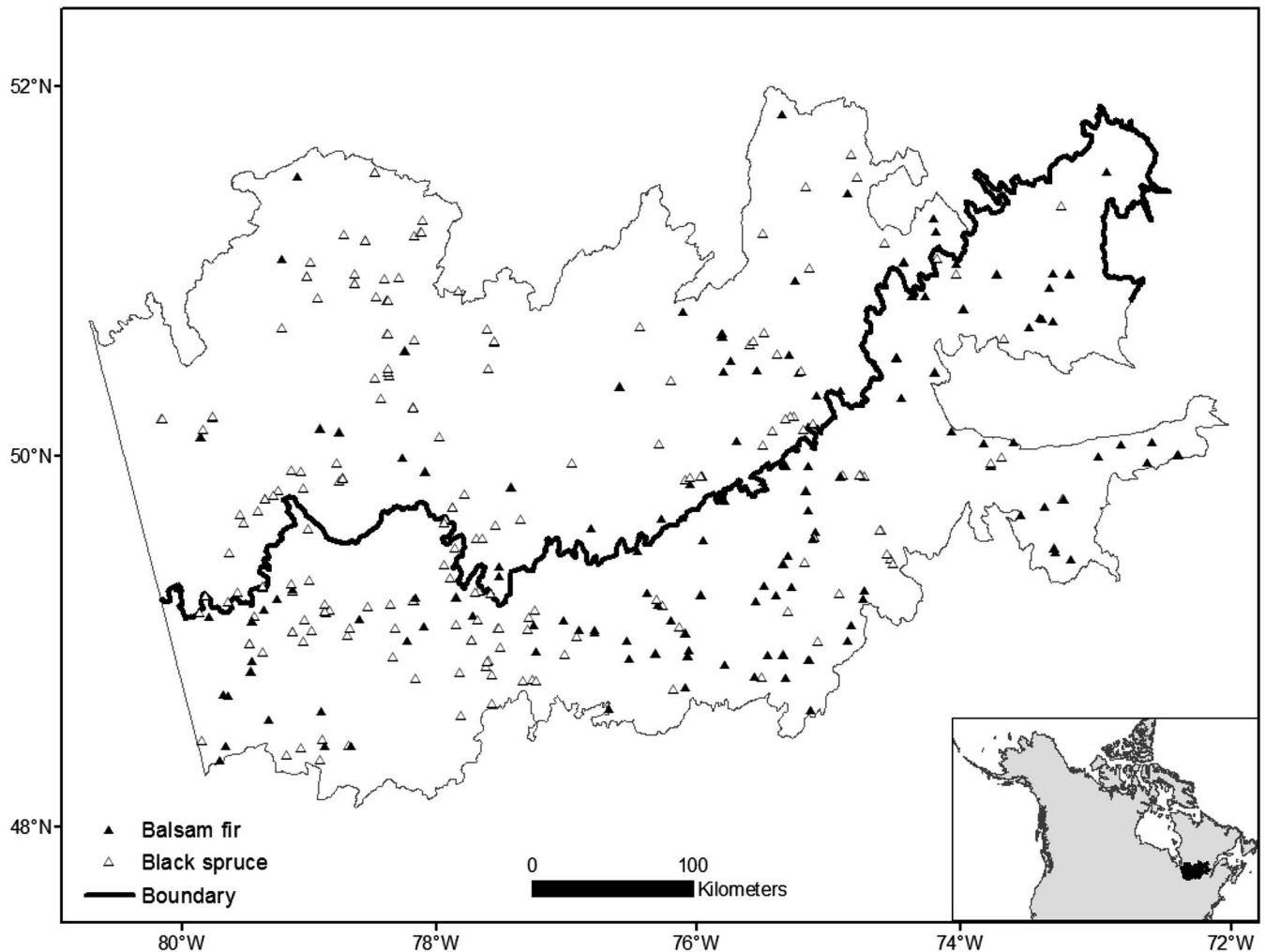


Figure 1. Study area and distribution of the sample plots for the two studied species. The thick black line indicates the boundary between boreal mixedwood (south) and coniferous (north) forests. Black and white triangles indicate stands dominated by balsam fir and black spruce, respectively.

black spruce outcompeting balsam fir in terms of height growth in coniferous forests (Arris and Eagleson 1989, Larsen 1980).

To test our hypothesis, we compared site index values for balsam fir and black spruce in 364 sites spread across the boreal zone of northwestern Quebec. The site index is a measure of the height of dominant and codominant trees at a reference age, usually 50 years as in the stands examined here (Carmean 1954, Chen et al. 1998a, 1998b, Nigh et al. 2002). Site index and height growth are strongly influenced by climate conditions and site quality (Béland and Bergeron 1996, Chen et al. 2002, Nigh et al. 2004, Wang et al. 2004, Wang and Huang 2000). Therefore, higher site index values indicate better growth conditions during the first 50 years (Wang and Huang 2000). Site index values usually decrease with increasing latitude or elevation, and species reaching their distribution limit usually perform less well than the dominant species in the area (Klinka et al. 1996, Wang et al. 2004). Thus, we expected site index values to be lower in coniferous than in boreal mixedwood forests for both balsam fir and black spruce. We also expected the northward decline in site index values to be steeper for balsam fir, thus indicating a competitive advantage to black spruce in coniferous forests.

Methods

Study Area

The study area is located in Quebec (eastern Canada), between 47°23' N and 51°13' N and between 70°41' W and 79°28' W (Figure 1), with elevation ranging between 135 and 642 m above sea level (a.s.l.). Boreal mixedwood forests are represented by the western balsam fir–white birch bioclimatic subdomain, whereas coniferous forests correspond to the western black spruce–moss bioclimatic subdomain (Saucier et al. 1998). Trembling aspen (*Populus tremuloides* Michx.), paper birch, and jack pine (*Pinus banksiana* Lamb.) occur immediately after fire in boreal mixedwood and coniferous forests. Topography is more accentuated in boreal mixedwood than in coniferous forests, and in the eastern rather than in the western part of the study area (Messaoud et al. 2007b).

Within the boreal mixedwood forests of the study area, mean annual temperature varies between 0–1° C, length of the growing season ($\geq 5^{\circ}$ C) between 150 and 160 days, mean annual precipitation between 800 and 1,200 mm, and percentage of precipitation falling as snow between 40 and 45%. In coniferous forests, mean annual temperature varies between –2.5 and 0° C, length of the growing season ($\geq 5^{\circ}$ C) between 120 and 155 days, mean annual precipitation

Table 1. Age (years), dbh (cm), height (m), and site index (m) of balsam fir and black spruce trees sampled in boreal mixedwood and coniferous forests.

Species	Variables	Mixedwood	Coniferous
Balsam fir <i>N</i> = 143	Age	74.79 ^{Aa} (14.86)	85.87 ^{Ba} (17.57)
	dbh (cm)	19.96 ^{Ab} (3.92)	18.51 ^{Aa} (4.17)
	Height (m)	15.69 ^{Aa} (2.90)	15.07 ^{Aa} (3.45)
	Site index (m)	11.81 ^{Ab} (2.89)	9.71 ^{Ba} (2.45)
Black spruce <i>N</i> = 221	Age	79.20 ^{Ab} (16.14)	81.76 ^{Aa} (16.98)
	dbh (cm)	18.14 ^{Aa} (4.23)	17.75 ^{Aa} (3.88)
	Height (m)	15.64 ^{Aa} (3.03)	15.21 ^{Aa} (3.15)
	Site index (m)	10.95 ^{Aa} (2.26)	10.33 ^{Aa} (2.40)

Numbers in parentheses indicate standard deviation from the mean. The letters at right of each number indicate similar (same letter) or different (different letters) values for the different species (lower case letters) and forest types (capital letters).

Table 2. General linear models of site index as a function of forest type, surface deposit, slope, and aspect for balsam fir and for black spruce.

Species	Source	<i>F</i>	<i>P</i>
Balsam fir	Model <i>R</i> ² = 0.515		
	Age	67.35	<0.0001
	Forest type	10.94	0.0012
	Surface deposit	1.40	0.2392
	Slope	1.31	0.2547
	Aspect	0.21	0.9587
	Forest type*surface deposit	8.15	0.0050
Black spruce	Model <i>R</i> ² = 0.341		
	Age	94.07	<0.0001
	Forest type	1.73	0.1902
	Surface deposit	1.04	0.3081
	Aspect	0.81	0.5435
	Slope	0.10	0.7516
	Forest type*surface deposit	0.11	0.7370

Significant relationships are shown in bold.

between 700 and 1,000 mm, and percentage of precipitation falling as snow between 25 and 50% (Saucier et al. 1998).

Sampling

We used 364 permanent and temporary sample plots of the Quebec Ministry of Natural Resources (QMNR; circular plots; radius = 11.28 m; area = 400 m²; Figure 1). The selected plots were in the two studied bioclimatic subdomains, on clay and till soils, and in homogenous stands, older than 50 years and younger than 120 years, with a tree density over 25%, and with tree height over 7 m. Data included site coordinates (latitude, longitude, elevation), slope, aspect, and surface deposit (clay or till). Plots from the QMNR network are randomly located and are, thus, representative of the conditions encountered in the studied bioclimatic subdomains.

In addition, age, total height, and crown class (dominant, codominant, intermediate, or suppressed) for each species and for each plot were obtained from the QMNR. From these data, 3–4 dominant or codominant trees from the two studied species in each plot were selected with no visible damage, straight single trunks, and that were at least 50 years (preferably 70 years) at 1-m height. Selected trees were cored at 1 m above the root collar. In the laboratory, the cores were sanded and annual growth rings were counted. Average height and age were calculated for each plot and for each species, and site index was estimated from the fitted equation relating height and age (Pothier and Savard 1998)

$$SI = b_1 * H_d^{b_2} * (1 - e^{-b_3 A_c})^{b_4 H_d^{b_5}}$$

where *SI* is the site index, *H_d* is total height, *A_c* is the age at 1 m above root collar, and *b*₁ to *b*₅ are parameters provided by Pothier and Savard (1998) for each studied species.

Climate Variables

Latitude, longitude, elevation, slope, and aspect of each plot were used to derive climate variables using the BIOSIM9 modeling software (Régnière and Saint-Amant 2008). Climate variables included mean annual temperature (MAT, °C), mean temperature of the growing season (May to September, MT_GS, °C), sum of growing degree-days > 5° C (GDD), total annual precipitation (PP, mm), and total precipitation during the growing season (PP_GS, mm).

Statistical Analyses

We compared *SI* values between forest types, between surface deposits, and between species using analyses of covariance (ANCOVA) and Tukey–Cramer multiple comparison tests taking into account different sample size. We used a general linear model to link site index values of each species to slope, aspect, surface deposit, and forest type. Age of the trees was included as a covariate because trees were older in the coniferous forest than in the boreal mixedwood forest. An interaction term between forest type and surface deposit was included to account for the fact that clay soils are slightly more abundant in coniferous than in boreal mixedwood forests (Veillette 1994). The choice of the variables was driven by data availability from the QMNR dataset.

We also related site index values for both species to climate variables (MAT, MT_GS, GDD, PP, PP_GS) using stepwise multiple linear regression (threshold for inclusion in the model: *P* < 0.05). This analysis was warranted by the fact that the two forest types are located along a south–north gradient coincident with a climate gradient and also because we have shown previously that other parts of balsam fir's life cycle are affected by climate variations (Messaoud et al. 2007a). All analyses were conducted using the SAS software (Cody and Smith 1991).

Results

Site Index Comparisons Between Forest Types and Species

Site index (*SI*) values were different between boreal mixedwood and coniferous forests for balsam fir and for black spruce with lower values in the latter forest type, but the difference was only significant for balsam fir (Table 1). Balsam fir trees sampled in coniferous forests were significantly older than trees sampled in boreal mixedwood forests, while dbh and height were not different between forest types. Black spruce trees sampled in both forest types did not significantly differ in age, dbh, or height.

Table 3. Unstandardized coefficients, standard errors, and *P*-values from the stepwise multiple linear regression relating site index (dependent variable) to climatic variables.

	Balsam fir			Black spruce		
	(Model $R^2 = 0.2569$)			(Model $R^2 = 0.0795$)		
	Unstandardized coefficient	Standard error	<i>P</i>	Unstandardized coefficient	Standard error	<i>P</i>
MAT	2.47599	0.35632	<0.0001	1.06671	0.24525	<0.0001
MT_GS	–	–	–	–	–	–
GDD	–	–	–	–	–	–
PP	–	–	–	–	–	–
PP_GS	–0.02133	0.00624	<0.0008	–	–	–

Mean annual temperature, MAT; mean temperature of the growing season, MT_GS; sum of growing degree-days > 5° C, GDD; total annual precipitation, PP; precipitation during the growing season, PP_GS.

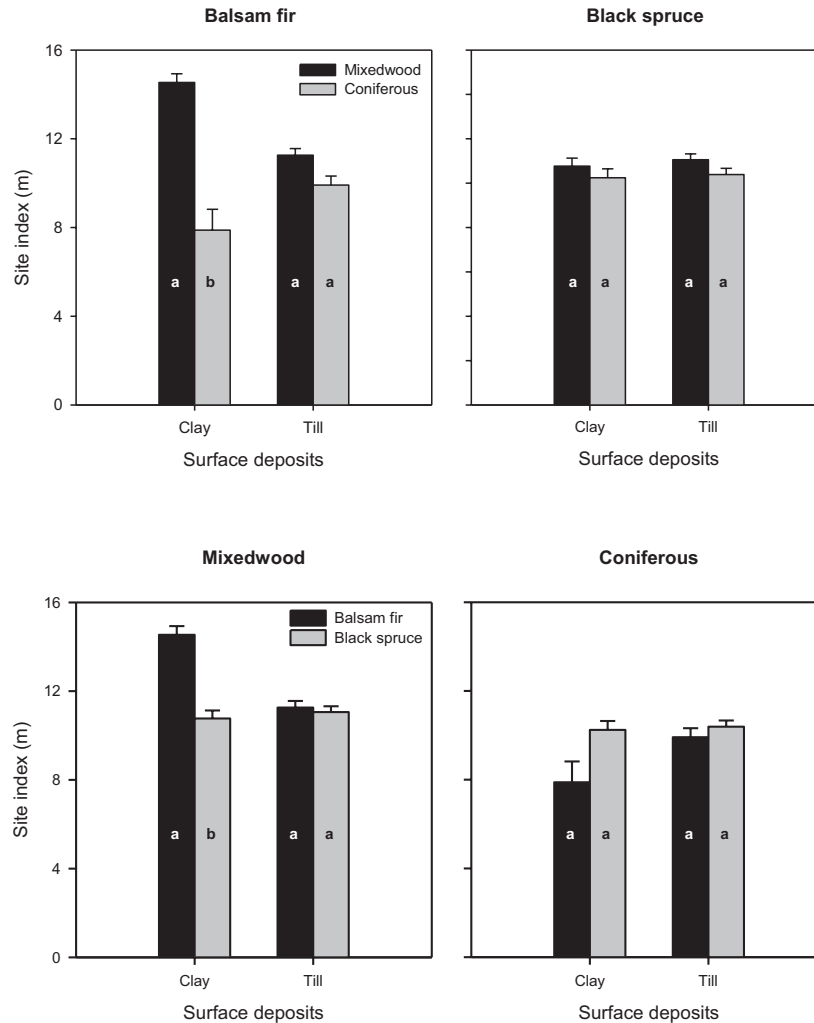


Figure 2. Site index values of balsam fir and black spruce in relation to surface deposit (clay versus till) and forest type (boreal mixedwood versus coniferous) (average \pm standard error). Upper panels: comparisons between forest types on each surface deposit for balsam fir (left) and black spruce (right). Lower panels: comparisons between species on each surface deposit for boreal mixedwood (left) and coniferous (right) forests. The letters inside each bar indicate similar (same letter) or different (different letters) site index values.

SI values were different between species in both forest types, although the difference was only significant in boreal mixedwood forests (Table 1). SI values were higher and lower for balsam fir in boreal mixedwood and coniferous forests, respectively. In boreal mixedwood forests, sampled balsam fir trees were younger, had greater dbh, and similar height compared to black spruce. In coniferous

forests, sampled balsam fir and black spruce trees had similar age, dbh, and height (Table 1).

Controlling for tree age (the covariate in the ANOVA, which had a significant effect on SI values for both species), SI values for balsam fir were significantly related to forest type and to the interaction between forest type and surface deposit (Table 2). For black

spruce, SI values were not significantly related to any other variable (Table 2).

Species Performance and Environmental Conditions

Stepwise multiple linear regression showed that SI values of balsam fir and black spruce were positively related to mean annual temperature (Table 3). In addition, there was a significant negative effect of precipitation of the growing season on SI for balsam fir, but not for black spruce (Table 3).

Balsam fir had significantly lower SI values in coniferous than in boreal mixedwood forests on clay deposits (Figure 2). For black spruce, SI values did not significantly differ between forest types or surface deposits. In boreal mixedwood forests, SI values were significantly higher for balsam fir than for black spruce on clay but did not significantly differ on till. In coniferous forests, no significant difference was observed between either species' SI values, whether on clay or on till (Figure 2).

Discussion

SI values were lower in coniferous forests for both species, as expected in response to the northward trend toward cooler climate and shorter growing season (Klinka and Chen 2003, Monserud et al. 2006, Nigh 2006, Ung et al. 2001), although the difference was significant only for balsam fir (Table 1). The larger difference in SI values between forest types for balsam fir could be explained by the fact that the species is less adapted to cooler climates than black spruce (Bakuzis and Hansen 1965). This difference in climate sensitivity caused a shift from SI values being higher for balsam fir in boreal mixedwood forests to being marginally higher for black spruce in coniferous forests. A similar trend was observed in other studies. For instance, Klinka et al. (1996) reported that SI values for subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) and Engelmann spruce (*Picea engelmannii* (Parry ex Engelmann)) in British Columbia decreased with elevation, but the decline was more pronounced for Engelmann spruce because this species is less cold tolerant than subalpine fir. Sirois (1997) studied the dynamics of balsam fir at the species' northern distribution limit in James Bay (north of our study area) and found that balsam fir was always codominant in a canopy dominated by black spruce.

In addition to temperature, precipitation and surface deposit also play an important role in the northward transition from balsam fir to black spruce dominance. Indeed, the significant difference in SI values between balsam fir and black spruce in boreal mixedwood forests is only apparent on clay soils. In the coniferous forest, although SI values are not significantly different between species, the difference was larger on clay soils (and, this time, to the advantage of black spruce). Clay soils are more efficient at holding water, which is an advantage in boreal mixedwood forests, where summer temperatures are higher and where moisture stress is more likely than in coniferous forests. However, higher water content also means that cold penetrates faster and lasts longer in clay than in till, thus hampering balsam fir height growth in coniferous forests (Fowells 1965), as only balsam fir SI was negatively affected by precipitation of the growing season. Messaoud et al. (2007b), in the same study area, reported a detrimental effect of low soil temperatures on balsam fir. Furthermore, black spruce dominance, coupled with low soil temperatures and high water content promotes *Sphagnum* growth and paludification in coniferous forests (Fenton et al. 2005, Simard et al. 2007), thus creating site conditions unfavorable to balsam fir growth.

Conclusion

A northward decrease of balsam fir height growth due to direct and indirect (through surface deposit) climatic effects appears to be partly responsible for the dominance shift from balsam fir in mixedwood forests to black spruce in coniferous forests of the boreal zone of northeastern North America. This adds to the other factors already identified as contributors to the northward decline of balsam fir, i.e., reduced seed production and seedling survival (Messaoud et al. 2007a) and poor adaptation to a regime of large and frequent fires (Ali et al. 2008).

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