



Effect of increased *Populus* cover on *Abies* regeneration in the *Picea*–feathermoss boreal forest

Marie-Lyne Arbour & Yves Bergeron

Keywords

Abies balsamea; Coniferous boreal forest; Facilitation; Mixed stands; *Populus tremuloides*; Regeneration.

Nomenclature

Marie-Victorin (1995).

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Arbour, M.-L. (corresponding author, mariearbour@gmail.com) & **Bergeron, Y.** (yves.bergeron@uqat.ca): NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Université du Québec à Montréal, C.P. 8888, Succursale Centre-Ville, Montréal, Québec, Canada H3C 3P8.

Abstract

Question: Does the increase in *Populus tremuloides* cover within the *Picea mariana*–feathermoss domain enhance establishment and growth conditions for *Abies balsamea* regeneration?

Location: Boreal forest of northwest Quebec, Canada.

Method: To document the effect of *Populus tremuloides* on *A. balsamea* regeneration, mixed stands with a heterogeneous presence of *P. tremuloides* adjacent to *Picea mariana*-dominated stands were selected. *Abies balsamea* regeneration, understorey environment and canopy composition were characterized from 531 sampling units distributed along transects covering the mixed–coniferous gradient. Abundance of understorey *A. balsamea* regeneration was described using three height groups: seedling (< 30 cm), small sapling (30 to < 100 cm) and tall sapling (100 to 300 cm). Growth characteristics were measured from 251 selected individuals of *A. balsamea* (< 3 m).

Results: Results showed that *A. balsamea* regeneration was generally more abundant when *P. tremuloides* was present in the canopy. Differences between seedling and sapling abundance along the mixed–coniferous gradient suggest that while establishment probably occurs over a wide range of substrates, the better growth conditions found under mixed stands ensure a higher survival rate for *A. balsamea* seedlings.

Conclusions: The abundant *A. balsamea* regeneration observed within mixed stands of the *Picea mariana*–feathermoss domain suggests that the increase in *P. tremuloides* cover, favoured by intensive management practices and climatic change, could contribute to acceleration of the northward expansion of the *A. balsamea*–*Betula papyrifera* domain into the northern boreal forest dominated by *Picea mariana*.

Introduction

Ecological boundaries of forest ecosystems are likely to experience major shifts with ongoing global warming (Emanuel et al. 1985; Prentice et al. 1992; Malcolm et al. 2002; Bonan 2008). In boreal regions, sensitivity to climate change is expected to be high as climatic factors limit growth, reproduction and establishment of many species (Rizzo & Wiken 1992; Grace et al. 2002; Chapin et al. 2004). However, predictions suggesting the predominant control of climate on species distribution may greatly underestimate the role of local processes and biotic interactions in species migration dynamics (Brooker et al.

2007; Caplat et al. 2008; Lafleur et al. 2010). In fact, the ability of a species to increase its abundance may be highly influenced by the presence or absence of other species and facilitation could play a key role in regulating community composition (Brooker et al. 2008).

In northwest Québec, the continuous boreal forest is divided into two bioclimatic domains: the southern *Abies balsamea*–*Betula papyrifera* domain and the northern coniferous *Picea mariana*–feathermoss domain (Saucier et al. 1998). All major species are present in both domains and the transition from *A. balsamea* to *P. mariana* dominance is partly explained by a combination of disturbance regime characteristics and landscape configuration (Gauthier

et al. 2000). The abundance of broad-leaved species within the *A. balsamea*–*B. papyrifera* domain and the numerous lakes that can act as firebreaks both induce smaller and less severe fires, which favours fire-intolerant species such as *A. balsamea*. On the other hand, the flat topography of the northern *P. mariana*–feathermoss domain favours increased fire size and severity, to the advantage of fire-tolerant species, such as *P. mariana* (Bergeron et al. 2004). While fire regime is the main factor determining the successional pathways, a climate-related decrease in reproductive potential of species dominating the *A. balsamea*–*B. papyrifera* domain (*A. balsamea* and *Picea glauca*) has also been observed along the latitudinal gradient of their natural ranges (Messaoud et al. 2007a).

Succession patterns in the *A. balsamea*–*B. papyrifera* domain are characterized first by an abundance of shade-intolerant broad-leaved species, *Populus tremuloides* and *B. papyrifera*, which are replaced by the dominant coniferous species *A. balsamea* and *Picea glauca* (Bergeron & Dubuc 1989; Bergeron 2000; Gauthier et al. 2000). In the coniferous domain *P. mariana* is the main post-fire invader and eventually dominates the canopy of all stand types (Lecomte & Bergeron 2005). These stands are prone to paludification (i.e. an accumulation of organic matter and expansion of *Sphagnum* spp. cover, creating waterlogged conditions that reduce soil temperatures, decomposition rates, microbial activity and nutrient availability), which can promote *P. mariana* regeneration at the expense of late successional species, such as *A. balsamea* (Turetsky 2003; Fenton et al. 2005; Lavoie et al. 2005; Lecomte & Bergeron 2005; Fenton & Bergeron 2006). In northwest Quebec, *P. mariana* stands situated on fine textured soils and containing *P. tremuloides* as a minor component are particularly sensitive to broadleaf encroachment following logging (Grondin et al. 2003; Laquerre et al. 2009). At these northern latitudes, *P. tremuloides* could also benefit from warmer temperatures in the coming decades (Huang et al. 2010). Interest in understanding the dynamics of *P. mariana* and *P. tremuloides* stands has grown over the last few years. Recent studies conducted in this region suggest that the presence of *P. tremuloides* in the coniferous domain could halt the paludification process because their easily decomposable litter accelerates nutrient cycling and inhibits moss and *Sphagnum* spp. growth (Van Cleve & Noonan 1975; Fenton et al. 2005; Légaré et al. 2005; Laganière et al. 2009).

An increased abundance of *P. tremuloides* on a landscape presently dominated by *P. mariana* could favour the displacement of *P. mariana* to the benefit of *A. balsamea*. In fact, the presence of *A. balsamea* regeneration in mixed stands of the coniferous domain, suggests a positive interaction between *P. tremuloides* and *A. balsamea*.

Facilitation occurs when a species enhances the survival, growth or fitness of another species (Callaway 1997). *Populus tremuloides* may facilitate *A. balsamea* in the southern part of the coniferous domain by creating favourable conditions for the establishment and growth of *A. balsamea* individuals. In general, success of natural regeneration relies mainly on seed supply, seedbed suitability and the environmental conditions for germination and seedling growth (Daniel et al. 1979; Caspersen & Sapruff 2005). The cold, acidic conditions that develop under *P. mariana* are detrimental to *A. balsamea*, a species usually associated with mesic sites in this part of the boreal forest (Bergeron & Dubuc 1989; Messaoud et al. 2007b). An increase in *Populus* cover within the *P. mariana*–feathermoss domain, coupled with a warmer climate, could offer more suitable conditions for *A. balsamea* regeneration, thus potentially leading to a northward expansion of the *A. balsamea*–*B. papyrifera* domain. The objective of this study is to observe whether *A. balsamea* regeneration within the *P. mariana*–feathermoss domain of northwest Quebec is positively associated with the presence of *P. tremuloides* in the canopy. We hypothesize that understorey *A. balsamea* are more abundant in the coniferous domain when under *P. tremuloides* cover because the mixed stands provide both suitable sites for establishment and better growth conditions.

Methods

Study area

The study area is part of the *P. mariana*–feathermoss forest of western Quebec (Saucier et al. 1998), located at the border of the Abitibi-Témiscamingue and Nord du Québec regions (49°09'N to 49°15'N, 78°44'W to 78°51'W). This region is part of the Northern Clay Belt of Quebec and Ontario (Vincent & Hardy 1977). The disturbance regime is characterized by large fires that kill most above-ground vegetation (Heinselman 1981; Payette 1992). The fire cycle length has increased from 101 years before 1850, to 398 years since 1920; the mean stand age is 148 years (Bergeron et al. 2004).

The Lake Matagami Lowland corresponds to the southwestern part of the *P. mariana*–feathermoss forest. The topography is generally flat with a nearly continuous forest cover (Bergeron et al. 1998). The landscape is dominated primarily by *P. mariana* with a significant component of broad-leaved or mixed stands originating from clearcuts or fire (Bergeron et al. 1998). The closest meteorological station is located at La Sarre, with a mean annual temperature of 0.8 °C and mean annual precipitation of 856.8 mm for the 1961–1990 period (Environnement Canada 1993). The length of the growing season is about 155 days (Robitaille & Saucier 1998).

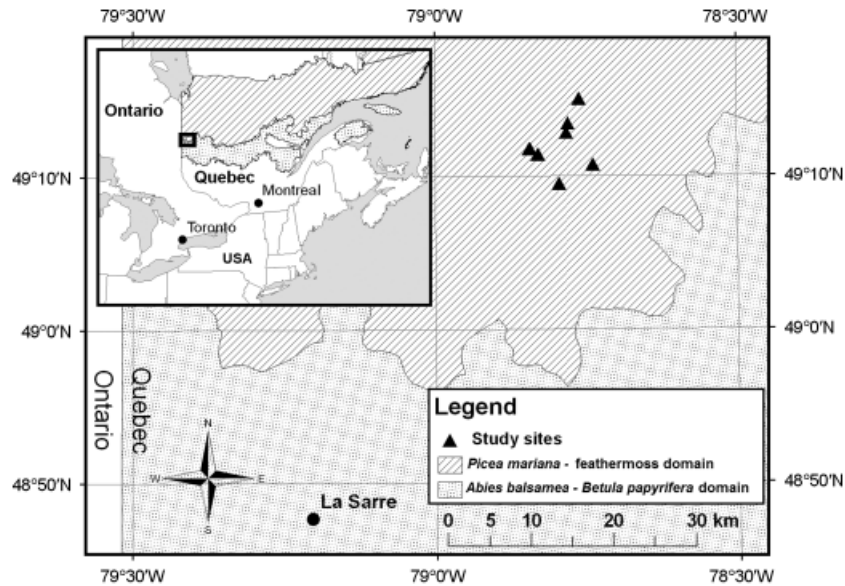


Fig. 1. Map of the study area showing the location of the seven sampling sites.

Sampling design and data collection

Sampling design

During the summer of 2006, seven sites possessing both a mixed composition dominated by *P. mariana* but with heterogeneous presence of *P. tremuloides* (called mixed) and an adjacent pure *P. mariana* stand (called coniferous) were selected in order to compare *Abies* regeneration characteristics between the two stand types. A stand initiation map (Bergeron et al. 2004) and an ecoforestry map (MRNF 2006) were used to choose sites having the same abiotic characteristics (surface deposits, slope and drainage). The seven sites were established in distinct unmanaged units within a 40-km² area (Fig. 1). The stands were even-aged and likely originated from a single fire that occurred around 90 years ago. Time since last fire was determined by coring a number of the dominant trees. At each site, paired 100-m long transects were established about 20 m apart and placed to cross the mixed–coniferous stand transition, thus forming a vegetation gradient with one end in each stand type. Texture of the mineral soil has been verified through granulometric analysis (McKeague 1978). To ensure that the mixed and coniferous stands were not associated with different deposits, a variance analysis (ANOVA) was conducted from samples taken at each transect end, with the ‘transect’ being the random factor and ‘type of stand’ the fixed factor. The analysis did not reveal any differences in clay percentages between transects ($F=0.0020$, $P=0.9648$) and stand types ($F=2.0706$, $P=0.1014$).

Two types of sampling unit were set up: sampling points marked systematically every 5 m and selected *A.*

balsamea individuals sampled within a 5-m wide section along the transects. Sampled trees had to be < 3 m in height and be in good condition, with no trunk or branch damage. Each site had 40 sampling points and 40 selected *A. balsamea*, with the exception of one site where only 11 *A. balsamea* (< 3 m) were present, making a total of 531 sampling units for the seven sites (280 systematic sampling points and 251 selected *A. balsamea*).

Canopy composition

The point-centred quarter method was used to describe the compositional characteristics of the canopy (Cottam & Curtis 1956). At each sampling unit, the species, diameter at breast height (DBH) and distance were noted for the nearest living tree (DBH > 10 cm) in all four directions. A relative dominance index was calculated per species for each sampling unit using the following equation:

Relative dominance

$$= \frac{\text{Total basal area of the species per sampling unit}}{\text{Total basal area of all species per sampling unit}} \times 100$$

The use of the four nearest trees allowed a detailed analysis of environmental heterogeneity, which plays an important role in determining the nature of seedbeds and growth conditions for seedlings and saplings (Greene et al. 1999; Pelletier et al. 1999; Saetre 1999; Légaré et al. 2005). Sampling units with at least one *P. tremuloides* within the four nearest trees were classified as part of the mixed stands. The canopies were mainly composed of *P. tremuloides* and *P. mariana*, but scattered *Pinus banksiana*,

A. balsamea, *B. papyrifera* and *Larix laricina* were also present. The mean distance (MD) of the four point-to-nearest-tree distances measured at each sampling unit was 2.3 m. To ensure that stand densities were comparable between the different sites, we measured the absolute densities per ha ($10\,000\text{ m}^2/\text{MD}^2$) for each transect ($n = 14$) and performed an ANOVA with transects nested in the site factor ($n = 7$). Absolute densities were natural log-transformed for normality. Results showed no significant differences among the seven sites or 14 transects (site: $F = 2.05$, $P = 0.1812$; transect: $F = 1.09$, $P = 0.3719$).

Microsite environments

Understorey species cover (herbs, shrubs and bryophytes), woody debris and leaf litter within a 1-m^2 quadrat centred on the sampling units were estimated using the following seven classes: (1) $< 1\%$; (2) $[1\text{--}5\%]$; (3) $[5\text{--}25\%]$; (4) $[25\text{--}50\%]$; (5) $[50\text{--}75\%]$; (6) $[75\text{--}95\%]$; (7) $[95\text{--}100\%]$. Woody debris were classified using three groups: above the ground, on the ground and decaying. The decaying class of woody debris was defined as wood that could easily be penetrated by a pen to a depth of 3–5 cm. A qualitative substrate type was attributed to each sampling unit given the percentage cover of leaf litter, mosses and *Sphagnum* spp. measured within the 1-m^2 quadrat.

The depth of the organic horizon (LFH layer) was measured for 115 systematically determined sampling units (56 sampling points and 59 selected *A. balsamea*). Measurements taken at sampling points were evenly distributed along the transects in order to describe the conditions of the mixed-coniferous gradient, whereas those obtained from selected *A. balsamea* showed the conditions that support the presence of this species. Samples of the organic horizon were brought back to the laboratory and frozen in order to determine pH, phosphorus concentration (P) and the carbon to nitrogen (C/N) ratio. The C/N ratio can be used as a general indicator of site quality, where low C/N ratios correspond to sites that are rich in nutrients and possess high decomposition rates (Campbell 1978). The forest floor pH was analysed following McKeague (1978). The remainder of the samples were oven-dried at $60\text{ }^\circ\text{C}$ for 24 h and then ground. Percentage C and N content was measured on the dried samples using a LECO CNS-2000 combustion analyser (LECO Corp., MI, USA). Phosphorus content was extracted with a Bray II solution (McKeague 1978) and then analysed colorimetrically with a LACHAT flow analyser (LACHAT Inst., Milwaukee, USA).

In August 2006, light environments were assessed following Parent & Messier (1996). Instantaneous measurements (Q_0) were taken at ground level and above the main understorey vegetation (30 cm above ground) for

each of the 531 sampling units using a LAI-2000 quantum sensor (Li-Cor Inc., Lincoln, NE USA) during completely overcast conditions. Additional measurements were taken at the top of the 251 selected *A. balsamea*. Full light conditions (Q_i) were obtained by placing a second sensor recording continuous measurements with a data logger in an adjacent clearing. Percentage photosynthetic photon flux density ($\% \text{PPFD} = (Q_0/Q_i) \times 100$) represents mean daily light (400 to 700 nm) penetration under the forest canopy.

Abundance and growth of *A. balsamea* regeneration

Abies balsamea regeneration abundance was measured within a 2-m diameter plot centred on each of the 531 sampling units and described using three height groups: seedling (< 30 cm), small sapling (30 to < 100 cm) and tall sapling (100 to 300 cm). This measure aims at evaluating the number of *A. balsamea* (≤ 3 m in height) found at each sampling unit.

Total height, stem diameter at ground level (electronic calibre ± 0.01 mm), annual height increment and crown morphological development were measured in the field for the 251 selected *A. balsamea* (≤ 3 m). Annual height increments were noted for the last 5 years (2002–2006) by precisely locating the terminal bud scars (node) left by the yearly fall of scales that protect the bud of the terminal leader (Parent et al. 2002). The stem length between two nodes corresponds to an annual height increment unit, with the 2006 measurement starting from the terminal leader to the last node. A relative growth index was calculated by dividing the sum of the last 5-year increments ($\text{HG}_{2002\text{--}2006}$) by the total height of the individual.

A mean annual increment value was obtained by averaging height growth for the completed growth seasons ($\text{HG}_{2002\text{--}2005}$). Lateral branches were measured for the last node in order to estimate crown morphological development with a spreading coefficient (C_s). This C_s is described with the following equation:

$$C_s = f / (\Sigma l_{br} / n)$$

where f is the length from the terminal leader, Σl_{br} the sum of lateral branch length, and n , the number of lateral branches. This coefficient indicates the importance of terminal leader growth to lateral branch extension for the last node. It allows rapid estimation of the actual state of the height growth of a tree with an 'umbrella' shape indicating a suppressed state and a 'conical' form generally characterizing a full growth state (Parent & Messier 1995).

In order to assess whether seedlings and saplings were of different ages, 95 systematically determined individuals (approximately one out of three selected *A. balsamea*) were aged. Above- and below-ground parts of the trees were

collected and brought back to the laboratory for dendro-chronological analyses. Trees that grow adventitious roots often possess a reverse taper, i.e. a reduction in the number of growth rings towards the true collar (hypocotyl region) located below ground level (DesRochers & Gagnon 1997). Furthermore, the age of shade-tolerant species is often underestimated due to missing rings in the above-ground stem portions (Morin & Laprise 1997; Parent & Morin 2002). Thus, successive counts on the transverse sections of both the above- and below-ground stem sections were performed to ensure accuracy. Between two and five readings were performed on the above-ground section, depending on height and visual aspect (more readings were made for stems displaying suppressed growth periods, where bud scars were difficult to identify) to ensure no rings were missing at ground level due to previous periods of growth cessation. Beginning at ground level, we tried to find the exact hypocotyl region by cutting the below-ground part into 2–3 cm transverse sections. The transition from stem to root was identified by a shift from the presence of a pith to a central vascular cylinder and by using pointer years from ground level (Esau 1960; DesRochers 1996). The cross-sections were progressively sanded (80–320 grit) and visually cross-dated using the skeleton plot method according to the procedures of DesRochers & Gagnon (1997). Age was assessed from the hypocotyl section with missing ground-level rings being added using pointer years. Ages obtained were minimum ages, as the hypocotyl regions were not exactly located, but determined within the 2–3 cm transverse section.

Statistical analysis

The mean values of the different variables describing *A. balsamea* regeneration abundance and growth were compared between the mixed and coniferous stands using the Wilcoxon nonparametric test, as assumptions of the variance analysis were not met.

In order to obtain an integrated representation of the abundance of the different groups of *A. balsamea* regeneration with canopy composition and the relative effects of environmental variables associated with the mixed–coniferous gradient, a canonical redundancy analysis (RDA) was performed. Response variables (abundance of seedlings, small saplings, tall saplings and total abundance) measured within the 2-m diameter plot were Hellinger-transformed prior to analysis. The Hellinger transformation makes abundance and presence/absence data suitable for analysis with linear methods, such as RDA (Legendre & Gallagher 2001). The explanatory matrix included the following variables measured for the 531 sampling units: relative dominance of *P. tremuloides* and *P. mariana*, light measured at ground level ($light_G$) and

30 cm above ground ($light_{30}$), percentage cover of woody debris (above ground, on the ground and decaying), leaf litter, herbs (grouping all herb species), mosses (grouping moss and lichen species), *Sphagnum* spp. and ericaceous shrubs. Only the relative dominance of *P. tremuloides* and *P. mariana* were used to describe canopy composition as they were the dominant species defining the mixed–coniferous gradient. Only understory species present at more than 5% of the sampling units were retained, with the median value of each class being used for analyses.

The associations between *A. balsamea* regeneration and substrate types (leaf litter, mosses and *Sphagnum* spp.) were determined using a chi-square analysis to test for differences between the observed and expected frequencies of substrates (Scherrer 1984). Instead of using abundances for the 2-m diameter plot, total *A. balsamea* abundance (≤ 3 m) was measured within the 1-m² quadrat and used to describe the occupation rate of the substrate types covering the same surface. A total of 589 *A. balsamea* were present in the 531 quadrats. The observed frequency (f_{obs}) was defined as the number of *A. balsamea* associated with a given substrate type, while the expected frequency (f_{exp}) was the number of *A. balsamea* associated with a substrate type with equal distribution among the substrates ($f_{exp} = (589/531) \times \text{frequency of substrate type}$). A second chi-square analysis was performed to test for associations between *A. balsamea* and woody debris (above ground, on the ground and decaying) representing the three decomposition stages.

Another RDA was performed to illustrate the growth characteristics measured for the 251 selected *A. balsamea* (total height, stem diameter, mean annual increment, relative growth and spreading coefficient) in relation to stand composition and environmental variables. Light at the top of the selected *A. balsamea* ($light_{top}$) was added to the matrix of explanatory variables previously described for the RDA of abundance data. Ordinations were computed with the program CANOCO version 4.5 (Micro-computer power, Ithaca, NY, USA).

The age structure of the *A. balsamea* regeneration was established for the 95 aged individuals. These aged individuals were grouped according to the same height classes used for abundance analyses (seedling (< 30 cm), small sapling (30 to < 100 cm), and tall sapling (100 to 300 cm)). Mean ages were then compared using ANOVA with Tukey's multiple comparison tests. Univariate analyses were performed using JMP IN 5.1 (SAS Institute Inc., Cary, NC, USA).

Results

A comparison of abundance and growth variable means for the mixed and coniferous stands is presented in

Table 1. Comparison of *Abies balsamea* seedling and sapling abundance and growth values between mixed and coniferous stands using the Wilcoxon test. *SD: standard deviation.

	Mean values (SD)*		S	P
	Mixed	Coniferous		
Abundance (n = 531)				
Seedlings	2.16 (0.15)	1.19 (0.20)	42 261	< 0.0001
Small saplings	2.63 (0.15)	0.67 (0.20)	36 721.5	< 0.0001
Tall saplings	1.67 (0.11)	0.60 (0.14)	37 316	< 0.0001
Total	6.47 (0.32)	2.45 (0.43)	35 715	< 0.0001
Growth (n = 251)				
Total height (cm)	108.53 (4.16)	63.01 (7.76)	4437.5	< 0.0001
Diameter (mm)	16.65 (0.61)	10.49 (1.13)	4660	< 0.0001
Mean annual increment (cm)	9.45 (0.37)	5.04 (0.70)	4146.5	< 0.0001
Relative growth	0.46 (0.01)	0.41 (0.02)	5924	0.0181
Spreading coefficient	3.07 (0.11)	1.97 (0.20)	4659	< 0.0001

Table 1. Mean values for all abundance and growth variables were significantly higher for the mixed stands.

The ordination plot (RDA) clearly illustrates the positions of the environmental variables and *A. balsamea* regeneration abundance in relation to stand composition (Fig. 2). The mixed part of the gradient was characterized not only by the presence of *P. tremuloides* and leaf litter, but also by herbs and woody debris. At the opposite end, *P. mariana*-dominated stands were mainly associated with moss cover and to the group formed by ericaceous shrubs, *Sphagnum* spp. and understorey light (light_G and light₃₀). The position of the different groups of *A. balsamea* regeneration (seedling, small sapling and tall sapling) along this gradient indicates an association with the mixed environment. The position of the total *A. balsamea* abundance, i.e. the sum of the three groups, indicates a positive association with litter and *P. tremuloides*, and a negative association to *P. mariana*, moss, understorey light, ericaceous shrubs and *Sphagnum* spp. Taller saplings showed stronger correlations with herbs and decaying woody debris, while seedlings and small saplings were related more to woody debris on the ground. Seedling abundance was less associated to canopy composition compared to the sapling groups. When forest floor properties were included in the analysis (an ordination conducted with a systematically determined subsample of 115 sampling units), higher pH and P concentrations occurred in the humus layers of the mixed environments, whereas high C/N ratios and humus thickness were found associated with the *P. mariana* canopy. Strong negative associations were found between high C/N ratios and the two sapling groups, leaf litter, *P. tremuloides* and decaying woody debris (results not shown).

Both the observed frequencies of total *A. balsamea* regeneration among the different substrates and the classes of woody debris were significantly different than

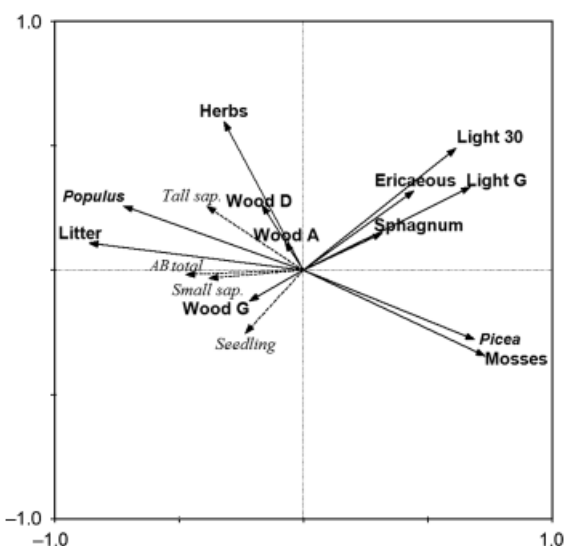


Fig. 2. RDA correlation biplot of *Abies balsamea* regeneration abundance (dashed arrows) and environmental variables (solid arrows). *Seedling*: abundance of *A. balsamea* seedlings (< 30 cm); *Small sap.*: abundance of *A. balsamea* saplings (from 30 to < 100 cm); *Tall sap.*: abundance of *A. balsamea* saplings (from 100 to 300 cm); *AB total*: total abundance of *A. balsamea* (≤ 3 m); *Populus*: relative dominance of *P. tremuloides*; *Picea*: relative dominance of *P. mariana*; *Wood G*: woody debris on the ground; *Wood A*: woody debris above the ground; *Wood D*: decaying woody debris; *Light G*: %PPFD at ground level; *Light 30*: %PPFD 30 cm above the ground. Percentage of variance in the data explained by ordination axes I and II: 17.2%, $n = 531$.

the expected frequencies ($P < 0.001$). There were significantly more *A. balsamea* on leaf litter substrates and less on moss and *Sphagnum* substrates ($P < 0.05$). Positive associations were found only with substrates possessing a maximum percentage cover of leaf litter, i.e. with less than 15% cover of the other substrate types, suggesting that moss and *Sphagnum* substrates are less susceptible to

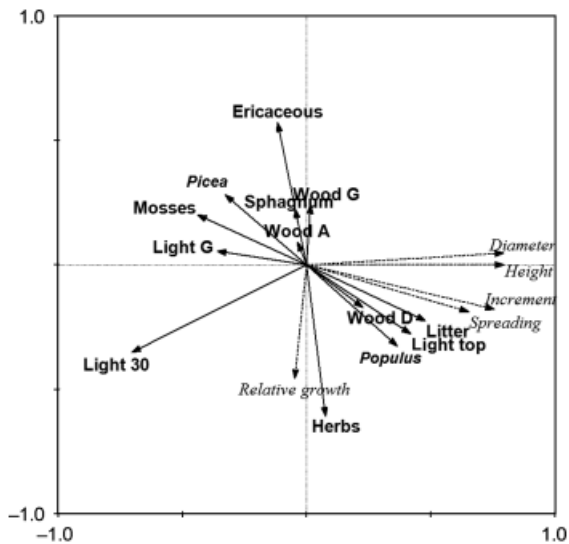


Fig. 3. RDA correlation biplot of *Abies balsamea* regeneration growth characteristics (dashed arrows) and environment variables (solid arrows). *Populus*: relative dominance of *P. tremuloides*; *Picea*: relative dominance of *P. mariana*; Wood G: woody debris on the ground; Wood A: woody debris above the ground; Wood D: decaying woody debris; Light G: %PPFD at ground level; Light 30: %PPFD 30 cm above the ground. Percentage of variance in the data explained by ordination axes I and II: 61.8%, $n = 251$.

occupation by *Abies balsamea*, even if present in small proportions. Significant associations were also found for the three classes of woody debris described separately ($P < 0.05$). The association was highest for decaying woody debris, followed by on-ground debris, and then negative for above-ground woody debris, indicating that *A. balsamea* was associated with the more advanced stages of decomposition.

The RDA biplot performed with the 251 selected *A. balsamea* illustrates that higher values of growth characteristics were all associated with the presence of *P. tremuloides* in the canopy and its related environmental variables (Fig. 3). The spreading coefficient, mean annual increment (HG₂₀₀₂₋₂₀₀₅) and taller individuals (described with stem diameter and total height) were all correlated to leaf litter cover, light measured at the top of the *A. balsamea*, *P. tremuloides* and decaying woody debris. These response variables were also negatively associated with light measured 30 cm above the ground. The position of relative growth, even if still associated with the mixed environment, was related more to herb cover and opposed to the presence of ericaceous shrubs.

The heights of the 95 aged individuals ranged from 16 to 243 cm. The hypocotyl sections were found for 91 of the 95 trees. Cross-dating of the below-ground sections added up to 17 years to the age estimates and only 15 *A. balsamea* were correctly dated at ground level. The mean

Table 2. Comparison of mean ages of the three height groups using ANOVA with Tukey's multiple comparison tests.

Height group	Mean ages	Lower 95%	Upper 95%
Seedlings	17.7	15.6	20.2
Small saplings	25.4	23.8	27.0
Tall saplings	37.2	34.7	39.9

ages of the three height groups were significantly different ($P < 0.05$, $n = 95$) according to Tukey's multiple comparisons test performed on the log-transformed data (Table 2).

Discussion

The results of this study indicate that *A. balsamea* regeneration is generally more abundant when *P. tremuloides* is present in the canopy. Differences in the distribution of the three groups of *A. balsamea* regeneration abundance (seedlings, small saplings and tall saplings) in relation to stand type reveals that the seedling group is probably less influenced by the presence of *P. tremuloides* than the two other groups. This suggests that seedling establishment is not constrained by differences in seedbed availability. Seedlings of larger-seeded species, such as *A. balsamea*, are resistant to various stresses and generally do not require very specific seedbed types (Bakuzis et al. 1965; Simard et al. 1998; Greene et al. 1999). Thus, establishment of seedlings could have occurred over a wide range of substrates, as offered by the sampled mixed-coniferous gradient. However, canopy cover becomes more and more important as seedlings develop to the sapling stage. Duchesneau & Morin (1999) showed that the spatial patterns of newly emerged *A. balsamea* seedlings generally corresponded to seed dispersal, but that seedbed types and understorey light conditions were the main factors explaining seedling mortality. This observed change in spatial patterns of seedlings could explain the differences found in this study between the three groups of *A. balsamea* regeneration, where understorey environments, mainly influenced by canopy composition, would lead to differential survival rates. One can argue that a difference in growth rather than mortality is involved as *A. balsamea*, a shade-tolerant species (Frank 1990), has the ability to persist for long periods in the understorey (Morin & Laprise 1997; Messier et al. 1999). However, results of the dendrochronological analysis showed that saplings were older, suggesting that higher survival rather than better growth explains their higher abundance under the *Populus* canopy.

The higher abundance and better survival and growth of *A. balsamea* under a *P. tremuloides* canopy may be associated with the effects of *Populus* litter. Many studies

have reported the inhibitory effects of leaf litter on conifer regeneration (Koroleff 1954; Simard et al. 1998; Parent et al. 2006). In this study, most of the sampled regeneration had passed the limiting stage of germination, suggesting that *A. balsamea* could, in the long term, benefit from the leaf litter substrate. Moreover, the study sites presented a mixture of broad-leaved and coniferous species and they probably carry less litter than that observed in some previous establishment studies conducted in the *A. balsamea*–*B. papyrifera* domain of the boreal forest. The fact that *P. tremuloides* litter accelerates decomposition rates and nutrient cycling (Van Cleve & Noonan 1975; Légaré et al. 2005) is probably responsible for the better growth observed for *A. balsamea* within the mixed stands. Environmental variables associated with the presence of *P. tremuloides* in the canopy were consistent with these findings. Significant cover of leaf litter, herbs and woody debris was found under *P. tremuloides*, along with high pH and P concentrations in the humus layer. In contrast, *P. mariana*-dominated stands were characterized by the presence of bryophytes, ericaceous shrubs, thick organic layers and high C/N ratios.

Stand development in boreal mixed stands is characterized by a thinning stage leading to a canopy transition, where pioneer tree dominance declines and shade-tolerant conifers take over the main canopy (Chen & Popadiouk 2002). This mechanism could explain the abundance of woody debris found in the mixed stands in comparison to the coniferous environments. Of the three described classes of woody debris, association with *A. balsamea* regeneration was highest with decaying woody debris, which could indicate better growth conditions found in the presence of *P. tremuloides* where higher rates of decomposition provide a greater level of nutrient availability. In the southern *A. balsamea*–*B. papyrifera* domain, stand aging enhances *A. balsamea* regeneration through a reduction of leaf litter and herbaceous vegetation, along with increases in moist humus and rotten logs (Bergeron & Dubuc 1989; Simard et al. 1998). *Populus tremuloides* litter also prevents the establishment of *Sphagnum* spp., which characterize the development of cold, wet and acidic environments (Turetsky 2003). In addition, increased soil temperatures at these latitudes are likely to stimulate microbial activity and nutrient cycling (Chapin et al. 1992). Thus, higher soil temperatures associated with the presence of *P. tremuloides* probably constitutes an advantage for *A. balsamea*, especially north of its zone of dominance. The more acidic environment found under pure *P. mariana* stands is also detrimental to *A. balsamea*, particularly in the coniferous domain where the species' preference for mesic sites is accentuated when compared to the *A. balsamea*–*B. papyrifera* domain (Mesaoud et al. 2007b).

The high levels of understorey light measured in the coniferous stands seem to contradict studies that found that broad-leaved species transmitted more light than conifer-dominated stands (Messier et al. 1998). In fact, the abundance of *A. balsamea* regeneration and other understorey vegetation under the mixed stands probably greatly reduces the light measured at ground level and 30 cm above the ground. Thus, light measured at the top of the sampled *A. balsamea* constitutes the most reliable measure of light available for growth. As expected, these light levels were higher with the presence of broad-leaved species in the canopy and highly associated with the growth of understorey *A. balsamea*. Both vertical and lateral growth were favoured in the presence of a *P. tremuloides* cover. *Abies balsamea* may also benefit from the absence of *P. tremuloides* foliage in spring and autumn (Constabel & Loeffers 1996). Furthermore, increased light and nutrients provides good conditions for the development of dense and tall understorey vegetation that can hamper the establishment and growth of shade-tolerant conifers (Messier et al. 1998). However, the benefits that come with this rich environment when compared to pure *P. mariana* stands probably overcome the negative effects of abundant competitors. In fact mixed stands support less and less herbaceous vegetation with time as succession progresses (Simard et al. 1998).

Most of the growth characteristics (height, stem diameter, spreading coefficient and annual height increment) measured from selected *A. balsamea* individuals were positively associated with the presence of *P. tremuloides*, along with higher light levels measured on top of these selected individuals and abundance of decaying woody debris. Relative growth assesses the overall growth of all selected *A. balsamea* individuals without being masked by the effect of the higher annual height increments of taller individuals. The relative growth index seems to be less influenced by canopy composition but indicates a negative effect of ericaceous shrubs on the growth of *A. balsamea* seedlings and saplings. Ericaceous shrubs are generally detrimental to conifer growth, which is attributed partly to allelopathy (Chapin 1983; Titus et al. 1995; Mallik 2003). This allelopathic effect also seems to inhibit many conifer ectomycorrhizae, subsequently affecting their regeneration (Mallik 2003). Mycorrhizal fungi are known to play a major role in a number of ecological processes within the boreal forest (Read et al. 2004). Simard et al. (1997) found a net carbon transfer from *B. papyrifera* to *Pseudotsuga menziesii* seedlings through ectomycorrhizae, thus suggesting that mycorrhizal networks between pioneer species and shaded seedlings could promote the establishment of shade-tolerant species. In the *A. balsamea*–*B. papyrifera* boreal forest of Quebec, some studies showed that mycorrhizal

fungi distributions were influenced by the relative proportions of host tree species (Kernaghan et al. 2003; DeBellis et al. 2006). Further studies should investigate the underground links affecting *A. balsamea* regeneration in the presence of *P. tremuloides*.

Conclusion

Our results suggest that the presence of *P. tremuloides* in the *P. mariana*–feathermoss domain favours *A. balsamea* regeneration through enhanced growth conditions that ensure a higher survival rate for *Abies* seedlings. The easily decomposable *P. tremuloides* litter accelerates nutrient cycling and hinders the development of a thick forest floor layer, thus greatly altering conditions that otherwise provide a competitive advantage to *P. mariana*. This natural process, coupled with warmer temperatures and industrial logging, could accelerate the northward expansion of the *A. balsamea*–*B. papyrifera* bioclimatic domain into the coniferous domain. Investigating some of the mechanisms by which *P. tremuloides* influences *A. balsamea* regeneration constitutes the first step for global understanding of a long-term process that could lead to a shift in species dominance and to the redistribution of bioclimatic domain limits. Moreover, this study acknowledges the relevance of integrating facilitation processes with the prediction of species responses to climate change and to the development of strategies for maintaining the diversity and functional integrity of boreal forest ecosystems.

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