# Natural canopy gap disturbances and their role in maintaining mixed-species forests of central Quebec, Canada[1]

**Daniel D. Kneeshaw and Marcel Prévost**

**Abstract:** Until recently, natural dynamics of mixedwood stands have been largely ignored, resulting in the transformation of many North American mixedwoods into conifer- or hardwood-dominated stand types. The goal of this study was to examine canopy gap dynamics in balsam fir (*Abies balsamea* (L.) Mill.) – yellow birch (*Betula alleghaniensis* Britt.) mixedwoods to better understand possible mechanisms for species coexistence. Gap proportion in 12 study stands varied between 9% and 30% of the total stand area, while gap size varied from 20 to 2100 $m^2$. Balsam fir mortality was the primary cause of gap formation. Balsam fir and mountain maple (*Acer spicatum* Lamb.) dominated the tree and shrub regeneration layers, respectively. Shrub competition slows the natural filling of gaps by tree species. Our results indicate that yellow birch is most abundant in gaps over 800 $m^2$ and balsam fir in those under 200 $m^2$. Transition models showed that the greater longevity of yellow birch than balsam fir ensured its maintenance as a dominant. Dominant species coexistence thus results from divergent use of available resources through time and space. Forest management should maintain variability in harvest timing and size because the use of one gap size or a single rotation age will lead to an imbalance in species proportion relative to natural stands.

**Résumé :** Jusqu'à récemment, la dynamique naturelle des peuplements mixtes a été largement ignorée, ce qui a mené à la transformation de plusieurs peuplements mixtes d'Amérique du Nord en peuplements dominés par des conifères ou des feuillus. Le but de cette étude était d'examiner la dynamique des trouées dans le couvert de peuplements mixtes composés de sapin baumier (*Abies balsamea* (L.) Mill.) et de bouleau jaune (*Betula alleghaniensis* Britt.) pour améliorer la compréhension des mécanismes potentiels de coexistence entre les espèces. La proportion des trouées dans les 12 peuplements étudiés se situait entre 9 % et 30 % de la superficie totale des peuplements alors que les trouées couvraient de 20 à 2 100 $m^2$. La mortalité du sapin baumier était la cause principale de la formation des trouées. Le sapin baumier et l'érable à épis (*Acer spicatum* Lamb.) dominaient les strates de régénération formées respectivement par des arbres et des arbustes. La compétition exercée par les arbustes ralentit le repeuplement naturel des trouées par des espèces arborescentes. Nos résultats indiquent que le bouleau jaune est l'espèce la plus abondante dans les trouées de plus de 800 $m^2$ alors que le sapin baumier domine les trouées de moins de 200 $m^2$. Des modèles de transition ont indiqué que la longévité supérieure du bouleau jaune par rapport à celle du sapin baumier assure son maintien dans la strate dominante. La coexistence des espèces dominantes est donc le résultat de l'utilisation différente des ressources disponibles en fonction du temps et de l'espace. L'aménagement forestier devrait maintenir la variabilité de l'âge et de la taille de la récolte parce l'utilisation d'une seule taille de trouée ou d'un seul âge de récolte mènera à un déséquilibre dans la proportion des espèces par rapport à ce qui est observé dans les peuplements naturels.

[Traduit par la Rédaction]

## Introduction

The coexistence of balsam fir (*Abies balsamea* (L.) Mill.) and yellow birch (*Betula alleghaniensis* Britt.) within the balsam fir – yellow birch bioclimatic domain can be considered a paradox because these two dominant species have markedly different functional traits yet occur together in the same forest ecosystem. Balsam fir is a short-lived, shade-tolerant conifer with large seeds, while yellow birch is a small-seeded, long-lived, and intermediately shade-tolerant deciduous species. Many theories have been developed, based primarily on modeling, to address factors that permit species coexistence (Chesson 1986; Loehle 2000; Hubbell 2001; Kelly and Bowler 2002). Although equivocal, studies

---

Received 15 November 2006. Accepted 5 June 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 14 September 2007.

**D.D. Kneeshaw.**[2] Département des sciences biologiques, Centre d'étude de la forêt, Université du Québec à Montréal, C.P. 8888, Succursale Centre-ville, Montréal, QC H3P 3PC, Canada.
**M. Prévost.** Direction de la recherche forestière, Forêts Québec, Ministère des Ressources naturelles et de la Faune, 2700, rue Einstein, Québec, QC G1P 3W8, Canada.

[1] This article is one of a selection of papers published in the Special Forum IUFRO 1.05 Uneven-Aged Silvicultural Research Group Conference on Natural Disturbance-Based Silviculture: Managing for Complexity.

[2] Corresponding author (e-mail: kneeshaw.daniel@uqam.ca).

doi:10.1139/X07-112

of natural dynamics in some tropical and temperate forests have suggested that disturbances can ensure the maintenance of species with different ecological niches (Denslow 1987; Gravel et al. 2006). It has also been suggested that gap-based mortality in combination with differing longevities can ensure the maintenance of long-lived tree species (Lertzman 1995; Woods 2000; Kelly and Bowler 2002). Loehle (2000) identified a number of different tree characteristics including longevity, shade tolerance, size, and reproduction as important factors enabling trees to coexist following disturbances.

The primary natural disturbance affecting resources in temperate balsam fir – yellow birch mixedwood forests is canopy gaps, although little work has been done to quantify how gaps affect the natural dynamics of these forests (Archambault et al. 1997; Hébert 2003). In boreal mixedwoods to the north, large canopy openings may maintain shade-intolerant individuals such as trembling aspen (*Populus tremuloides* Michx.), whereas smaller openings may lead to increases in shade-tolerant species such as balsam fir and eastern white cedar (*Thuja occidentalis* L.) or permit the invasion of preestablished shade-tolerant shrub competitors such as mountain maple (*Acer spicatum* Lamb.) (Frelich and Reich 1995; Kneeshaw and Bergeron 1998, 1999). In balsam fir – yellow birch mixedwoods, the prevalence of competing shrub species, such as mountain maple, suggests that studies limited to only commercial tree species may overlook an important part of the natural dynamics (Archambault et al. 1997).

In recent years, it has been suggested that biodiversity objectives can be attained by basing forest management on natural disturbances (Lieffers and Beck 1994; Bergeron and Harvey 1997; Angelstam 1998). Although there is strong consensus for the need to develop more ecologically acceptable forestry practices, the knowledge needed to accomplish this is often lacking (MacDonald 1995). This is especially true for mixedwood forests for which past management practices have resulted in many stands being converted to pure hardwood or conifer stands. Management of mixedwood forests is difficult due to their compositional complexity and structure. Gap-based silviculture, which has been suggested for mixedwood forests (Coates and Burton 1997), would thus require knowledge of the natural gap regime and the response of important species to different-sized canopy openings (Coates and Burton 1997; Archambault et al. 1998). For example, yellow birch, because of its intermediate shade tolerance (Kneeshaw et al. 2006), may require multiple tree openings over time for successful recruitment. There is, however, little knowledge about the gap sizes required to regenerate this commercially valuable, long-lived species or about the compositional dynamics that naturally occur in these forests. A better understanding of the natural processes that ensure species coexistence is thus a crucial step in planning silvicultural strategies for these mixedwood forests.

The objectives of this study are to (*i*) describe the natural gap disturbance regime for yellow birch – balsam fir stands, (*ii*) determine how gaps affect natural stand dynamics, particularly species coexistence over time, and (*iii*) provide knowledge on natural gap dynamics for managing these mixed forests. Our primary hypothesis is that the natural gap regime, in combination with the different longevities of the two dominant species, is responsible for their continued maintenance in these systems. Specifically, we propose that (*i*) large, multiple-tree gaps will favour yellow birch recruitment whereas small single tree gaps will favour fir, (*ii*) yellow birch will be successful because of its greater longevity, and (*iii*) shrub recruitment will delay forest succession in gaps but not alter compositional trajectories.

## Study area

The study area is in the Portneuf region of central Quebec, Canada (approximately 47°N, 72°W), within the balsam fir – yellow birch bioclimatic domain (Saucier et al. 1998). Balsam fir, yellow birch, and red spruce (*Picea rubens* Sarg.) are the dominant canopy species. Important concentrations of red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), paper birch (*Betula papyrifera* Marsh.), and pin cherry (*Prunus pensylvanica* L.f.) also occur in some stands. A variety of other tree species such as American beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), largetooth aspen (*Populus grandidentata* Michx.), white spruce (*Picea glauca* (Moench) Voss), and American mountain-ash (*Sorbus americana* Marsh.) are occasionally found. Mountain maple, striped maple (*Acer pensylvanicum* L.), and hobblebush (*Viburnum alnifolium* Marsh.) are important elements of the understory shrub community.

The study sites are near the southern edge of the Laurentian foothills and a hilly topography is characteristic of the region. The podzol soils are developed from deep glacial till (Canada Soil Survey Committee 1992). The regional climate has been characterized as subpolar, subhumid, and continental (Robitaille and Saucier 1998). The region normally has 88–115 frost-free days (Canadian Climate Program 1982) and receives between 1100 and 1400 mm of annual precipitation (22%–26% as snow). Mean maximum daily temperatures occur in July (23.8–24.8 °C) whereas minimum daily temperatures occur in January (–18.9 to –21.6 °C) (Canadian Climate Program 1993).

## Methods

Twelve stands having no evidence of recent cutting (e.g., cut stumps) and varying in size from 2 to 30 ha were examined. All of the studied stands presented old-growth characteristics including a wide range of tree sizes and ages as well as abundant coarse woody debris. Individual tree ages were highly variable and minimum ages, from cores taken at stump height (30 cm), varied from 80 to 253 years for sampled canopy dominants, although the oldest sampled trees exceeded 150 years in all stands. No sign of recent stand reinitiating fire was observed in any of the sampled stands. All sampled stands were dominated by yellow birch and balsam fir and were located on mesic sites. More detailed descriptions of the composition, density, and basal area of the studied mixedwood stands are presented in Table 1.

Canopy gaps were evaluated using the transect approach proposed by Runkle (1992). Twelve band transects, varying in length from 110 to 550 m for a total of 2966 m, were located a minimum of 25 m from any open area (roads, har-

**Table 1.** Mean, SD, and minimum and maximum density and basal area of live trees greater than 9.1 cm DBH by species in the yellow birch – balsam fir stands under study.

| | Density (stems·ha$^{-1}$) | | | | Basal area (m$^2$·ha$^{-1}$) | | | |
|---|---|---|---|---|---|---|---|---|
| Species | Mean | SD | Minimum | Maximum | Mean | SD | Minimum | Maximum |
| Yellow birch | 480 | 1324 | 250 | 3650 | 10.8 | 7.8 | 1.8 | 24.9 |
| Paper birch | 46 | 161 | 0 | 750 | 1.0 | 4.3 | 0.0 | 4.5 |
| Red spruce | 49 | 38 | 0 | 1250 | 2.6 | 3.9 | 0.0 | 5.3 |
| Red maple | 38 | 78 | 0 | 2250 | 1.1 | 2.4 | 0.0 | 8.7 |
| Pin cherry | 28 | 39 | 0 | 3250 | 0.3 | 0.9 | 0.0 | 3.2 |
| Balsam fir | 1334 | 2720 | 250 | 9250 | 5.6 | 7.4 | 0.1 | 14.7 |
| Mountain maple | 7 | 16 | 0 | 20 | <0.1 | <0.1 | 0.0 | 0.1 |
| Striped maple | 15 | 14 | 0 | 500 | 0.1 | 0.2 | 0.0 | 0.6 |
| Sugar maple | 12 | 29 | 0 | 150 | 1.4 | 3.3 | 0.0 | 0.6 |
| Others | 14 | 27 | 0 | 500 | 0.6 | 0.9 | 0.0 | 2.2 |
| Total | 2023 | 444 | 500 | 6250 | 23.6 | 2.8 | 10.5 | 29.2 |

vested areas, etc.) and at least 10 m from the edges of other stand types (e.g., plantations, forests having experienced partial cutting, etc.). The proportions of each transect covered by canopy and canopy gaps were measured and each intersected canopy gap was evaluated in detail. Gap area was estimated as the distance (along axes as described below) from crown edge to crown edge as viewed from a vertical projection from the ground. The distance from the base of a tree stem surrounding the opening to the base of a tree stem on the opposite side of the gap was used to define the extended gap area. Area of elliptical canopy gaps was evaluated by measuring two axes, the longest transversal axis and an axis at a right angle, and then applying the formula for calculating the area of an ellipse (Runkle 1992). Gaps with more irregular forms were measured by increasing the number of perpendicular axes; this varied between 1 for small elliptical gaps and 12 perpendicular axes in the largest, most irregular gaps (Kneeshaw and Bergeron 1998).

Within each gap, dead trees over 9.1 cm diameter at breast height (DBH) were quantified and identified to species and the mode of death (windthrow, defoliation by the spruce budworm (*Choristoneura fumiferana* Clem.), senescence, or unknown) was determined. Regeneration was evaluated by counting the number of individuals by species within predefined size classes: 0–20 cm in height, 21–100 cm, 101–200 cm, 201 cm in height to 4 cm diameter at the base, and 4–8 cm diameter at the base. The largest size class individuals were counted in the entire gap area whereas seedlings in the four smallest classes were counted in a 2 m wide band running along the axes used to measure gap area. Shrub density by species was visually estimated (percent cover) in a 4 m$^2$ quadrat located every 2 m along the entire length of the regeneration transects. The estimations from each quadrat were then averaged to give an overall per gap estimation. Hemispherical photographs were taken in the forest understory and in gaps at seedling height (defined as 1 m above ground level) and analysed using the GLA program (Fraser et al. 1999) to quantify the photosynthetically active radiation.

Stand composition, density, and basal area of the forest as a whole as well as seedling density were determined using plot data from the Ministère des Ressources naturelles et de la Faune du Québec. Plots were within the yellow birch – balsam fir stand type and within the area circumscribed by the study transects. Each of the ten 400 m$^2$ plots that were used contained information on tree species composition, density, DBH of each tree, and tree state (live or dead).

Comparisons with silvicultural scenarios to use gap openings in these forests were made using calculations based on circular gap forms and diameters of 10, 20, 30, 40, 50, and 60 m. These gap sizes were chosen to represent a gradient that is currently operationally used or suggested for different forest types in Quebec (Ministère des Ressources naturelles du Québec 2003). Gap sizes were then calculated as a function of gap diameter ($D$) to canopy height ($H$) as per previous studies (Runkle 1981; Lertzman and Krebs 1991; Kneeshaw and Bergeron 1998). The $D/H$ ratios tested were 0.5, 1, 1.5, 2, 2.5, and 3. Based on an average canopy height of 20 m in the study area, perfectly circular gap areas would thus be 79, 314, 707, 1257, 1963, and 2827 m$^2$.

Computer simulations were used to estimate light conditions in each gap based on the diameter of the gap opening, a 20 m average canopy height, and the latitude of the study area. Modeling of light availability in gaps follows the approaches detailed in Canham (1988) and Dai (1996).

### Analyses

Transition probabilities were calculated for the different species based on overstory mortality and understory regeneration. Only regenerating individuals greater than 1 m in height were included because they were considered to have a better chance of being recruited into the canopy than smaller individuals. Probabilities were calculated based on observed transitions occurring in gaps (sensu Kneeshaw and Bergeron 1998) rather than for each tree using the ratio of dead individuals to live individuals by species, as originally proposed by Horn (1975). Analyses were performed for each of five gap size classes (0–200, 201–400, 401–600, 601–800, and >800 m$^2$) as well as for all gap sizes pooled. This latter analysis was done because it has been shown that species response to canopy opening can vary with gap size in northern forests (Kneeshaw and Bergeron 1998). We also performed analyses for different species longevities (Lertzman 1995) to evaluate whether coexistence of the different species, particularly the two dominant species, could be explained in part by tree species life spans.

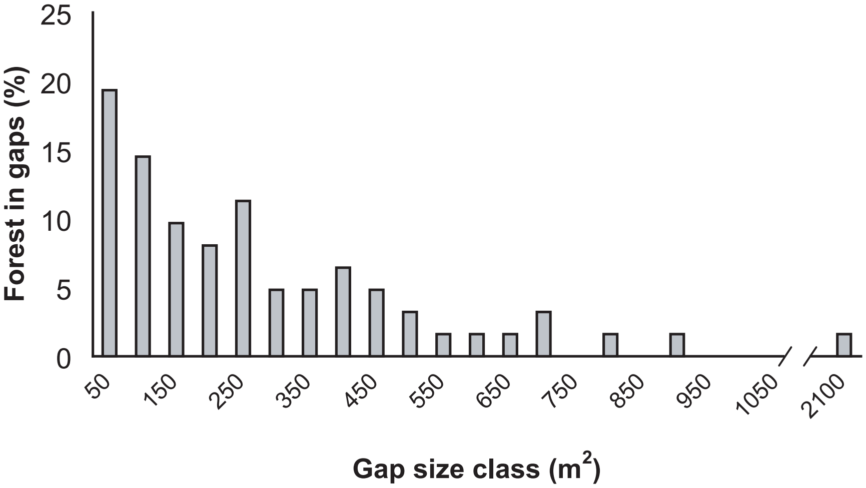
Relationships of regeneration abundance by species to light

**Table 2.** Comparison of canopy gap regime with silvicultural proposal of gaps (based on 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 *D*/*H* circular gaps with 20 m canopy height) and approximately 25% area cut every entry.

| | Natural gaps | | | | Silvicultural proposal (*D*/*H* ratio) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Minimum | Maximum | 0.5 | 1.0 | 1.5 | 2.0 | 2.5 | 3.0 |
| Gap size ($m^2$) | 270 | 314 | 18 | 2120 | 79 | 314 | 707 | 1257 | 1963 | 2827 |
| Light availability (% of full light) | 19 | 8 | | | 38 | 54 | 59 | 68 | 77 | 86 |
| Rotation length (years) | | | 106 | 213 | 100 | 100 | 100 | 100 | 100 | 100 |
| Forest in gaps (% of area) | 18.7 | 7.0 | 8.5 | 29.6 | 25 | 25 | 25 | 25 | 25 | 25 |

**Note:** For silvicultural proposals, gap size and light availability are the calculated values. Forest rotations can be calculated based on time taken to grow to the canopy and area of the forest in gap (rotation = % area affected/time taken for gap to be closed) (Frelich 2002). In managed stands, entries are expected every 25 years with 25%–35% of the trees being harvested in contrast with natural stands where gaps could occur throughout the rotation period.

**Fig. 1.** Size distribution of studied canopy gaps in the 12 yellow birch – balsam fir stands under study. Numbers represent the upper bounds of the class such that the first class varies from 1 to 50 $m^2$ in size and so on.



and gap size were performed using Pearson correlations with variables transformed when necessary to preserve statistical assumptions. Spearman correlations were used (i.e., for gap maker size relationships) when transformations did not correct for nonnormality or heteroscedasicity. Proportions of species recruitment under different species of gap maker were analysed using $\chi^2$ tests. All statistical analyses were performed using SAS version 8.02 (SAS Institute Inc. 1999).

## Results

### Gaps and tree mortality

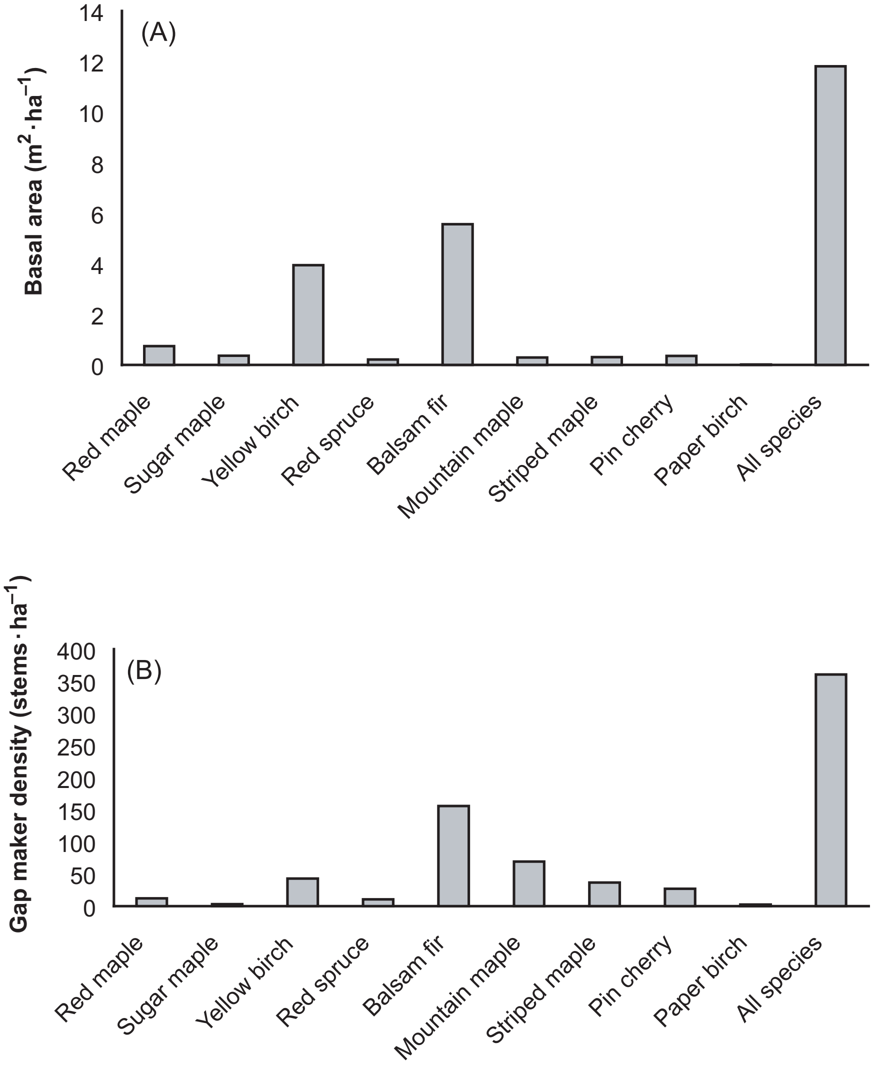
The percentage of forest in gaps averaged 18.7% of the area and ranged from 8.5% to 29.6% (Table 2). Gap size regime varied from 18 to 2120 $m^2$ with most gaps occurring in the smallest size classes (Fig. 1). The average size of natural gaps was 270 $m^2$ (SD 314 $m^2$) and the median was 180 $m^2$.

Light in the understory of closed canopy natural forests varied between 7% and 11% of full light. In natural openings, the quantity of light being received averaged 19% (SD 8%). In modeled openings, light varied among treatment types. Modeled light conditions in the proposed silvicultural gaps (i.e., with a canopy height to opening diameter ratio of 0.5–3 as explained in the Methods) varied from 38% to 86% (Table 2).

Natural gaps were created by the death of nine different species. The most commonly occurring gap maker was balsam fir in terms of both basal area and stem density (Fig. 2). The next most abundant gap maker in terms of basal area and density was yellow birch followed by pin cherry, red maple, and red spruce. Although the number of dead fir was almost four times higher than the number of dead yellow birch, the difference in basal area was much smaller (Fig. 2A versus Fig. 2B). Furthermore, the difference in terms of canopy gap area produced as a result of balsam fir mortality versus yellow birch mortality was even smaller because yellow birch crowns are generally larger than balsam fir crowns for stems of equivalent diameter. Dead mountain maple, with around 70 stems·$ha^{-1}$ was also high in numbers, but since mountain maple rarely attains more than 7 m in height, its death would rarely have caused an overstory gap. An important number of dead striped maple (35 stems·$ha^{-1}$) was also observed, but similar to mountain maple, this species is generally an understory shrub.

Differences in total (living and dead) stem densities were small, with balsam fir only slightly outnumbering yellow birch (287 to 208 stems/ha, respectively) (Table 1). Red spruce was the next most abundant species with 89 stems·$ha^{-1}$, while red maple, the fourth most abundant species, had only one third that number of stems. Yellow birch accounted for almost one third of the total stand basal area (9.9 $m^2 \cdot ha^{-1}$) followed by balsam fir (7.8), red spruce (4.6), and red maple (2.2). Basal areas of the other species were negligible.

**Fig. 2.** Dead tree distribution by species in studied canopy gaps by (A) basal area and (B) stem density. Balsam fir had significantly greater dead basal area than all trees except yellow birch. No other significant differences were found (Bonferonni, $p < 0.10$). Balsam fir had significantly greater dead stems than all species except mountain maple. No statistical differences were found between other species.



## Regeneration in mixedwood forests and gaps

The most common woody species in the regeneration (<1 m in height) and understory sapling layer (>1 m) in our gaps was mountain maple with total average densities of about 15 000 stems·ha$^{-1}$ in gaps (Fig. 3). In the larger size classes (>1 m in height), it was 10 times more abundant than the most abundant commercial tree species, balsam fir ($p < 0.01$) (Fig. 3B). Among commercial tree species, no significant differences were noted in the abundance of their regeneration, although there was a statistically nonsignificant tendency for yellow birch and balsam fir to remain as dominant species (Fig. 3B).

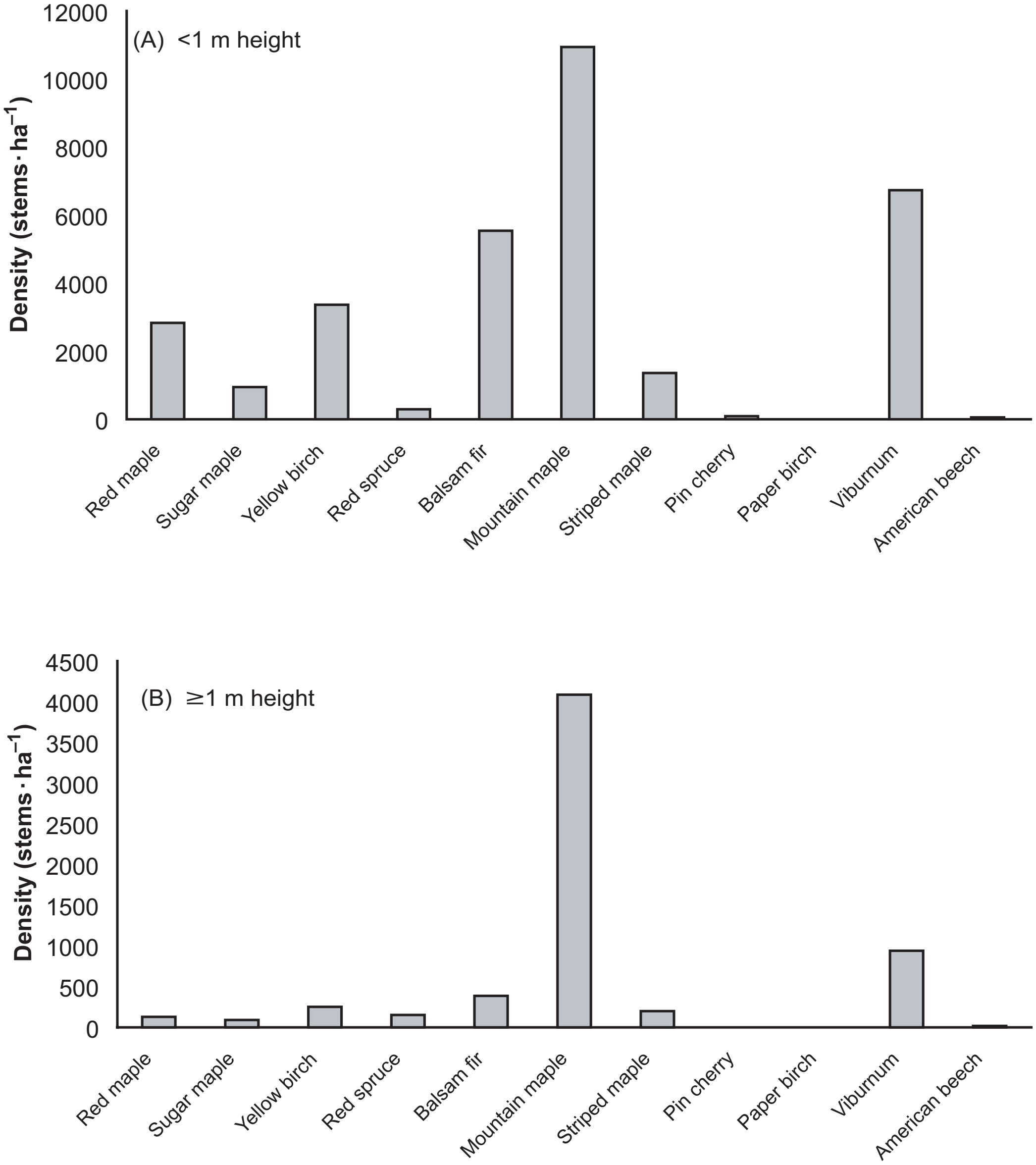
The most common shrubby species found in these forest gaps were mountain maple, beaked hazel (*Corylus cornuta* Marsh.), and hobblebush. No direct relationship between shrub species and light availability was detected ($p > 0.10$) with the exception of Canada yew (*Taxus canadensis* Marsh.), which was negatively correlated with light ($r = -0.62$, $p < 0.01$). This may explain why Canada yew was present in the understory of closed forests and relatively rare in gaps.

## Gap size and stand dynamics

Yellow birch ($r = 0.39$, $p < 0.01$) and balsam fir ($r = 0.27$, $p < 0.01$) were the most abundant gap makers in large natural gaps (>600 m$^2$). In terms of the regeneration layer, yellow birch, red maple, mountain maple, and hobblebush increased in density with gap size ($r$ = 0.85, 0.61, 0.31, and 0.30, respectively). Mountain ash and pin cherry also appeared to be associated with larger gaps, but small sample sizes did not permit us to test for significant relationships. Shrubs in the largest size class (>4 m in height and <10 cm DBH) were also found to increase in abundance as gap size increased ($r$ = 0.51 for mountain maple and 0.92 for striped maple).

Our results show a change in species replacement transition probabilities from small to large gaps, assuming equal gap ages (Table 3). They also confirm the importance of considering competing species. When considering trees only, balsam fir had the highest transition probabilities in gaps caused by the mortality of any species up to a gap size of 600 m$^2$. In larger gaps, red spruce and yellow birch had greater probabilities of recruiting than balsam fir. Red

**Fig. 3.** Average density of seedlings by species in the studied canopy gaps (A) <1 m in height and (B) ≥1 m in height. Only mountain maple is significantly different from the other species for both panels (Bonferroni, $p < 0.01$).



spruce did not recruit well in gaps greater than 800 m$^2$. Most species recruited best in gaps created by conspecifics. Notable exceptions were yellow birch, red spruce, and pin cherry, which recruited preferentially in balsam fir caused gaps (Fig. 4). Paper birch also recruited well under red maple, although there was little red maple mortality, so this may not be an ecologically meaningful tendency. With shrubs included in the analyses, mountain maple had great success recruiting in gaps of all sizes independent of the species of overstory tree mortality (Table 3*b*). Hobblebush also performed well in gaps greater than 200 m$^2$, often having the second greatest transition probabilities after mountain maple.

When differential tree life span is considered, balsam fir, which does not live as long as many of its conspecifics, does not maintain its dominant status in most of the gap sizes investigated (Table 3). Instead, yellow birch increases in relative proportion based on current transition probabilities due to its much greater longevity. With shrubs included in the analyses, shrub longevity (which in all cases is less than 50 years) limits their ability to maintain dominance of a site.

## Discussion

Coexistence of dominant species has often been linked to divergent use of niches that permit different species to maintain a balance in respective abundances through time and space (Chesson 2000). Multiple factors have been identified in models of species coexistence including shade tolerance, reproduction, tree size, and longevity (Loehle 2000). In our work, each of these factors has been identified as permitting the coexistence of the two dominant species, balsam fir and yellow birch, as well as in maintaining companion species such as red spruce. As proposed in our initial hypothesis, heterogeneity in the natural gap regime in combination with differences in species silvics seems to ensure multiple species coexistence in these forests.

**Table 3.** Gap replacement probabilities (in terms of percentage of final species composition based on density) using Markov transition matrices.

| | Equal ages | | | | | Different longevities | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Gap size ($m^2$) | Yellow birch | Red spruce | Balsam fir | Others | Shrubs | Yellow birch | Red spruce | Balsam fir | Others | Shrubs |
| **(*a*) Without including the shrub layer** | | | | | | | | | | |
| <200 | 13.5 | 11.2 | 55.5 | 19.8 | | 36.7 | 12.0 | 25.4 | 25.9 | |
| 201–400 | 25.1 | 23.8 | 28.5 | 22.6 | | 53.0 | 21.8 | 4.9 | 20.3 | |
| 401–600 | 8.8 | 9.4 | 56.4 | 25.4 | | 25.7 | 12.8 | 27.3 | 34.2 | |
| 601–800 | 17.2 | 30.5 | 10.2 | 42.1 | | 33.7 | 32.8 | 0.2 | 33.3 | |
| 801+ | 88.8 | 2.3 | 6.7 | 2.2 | | 98.0 | 0.9 | 0.2 | 0.9 | |
| Overall | 18.8 | 14.7 | 44.9 | 21.6 | | 41.8 | 15.2 | 20.1 | 22.9 | |
| **(*b*) Including the shrub layer** | | | | | | | | | | |
| <200 | 3.8 | 0.8 | 16.2 | 2.9 | 76.3 | 37.0 | 3.0 | 31.4 | 12.8 | 15.8 |
| 201–400 | 4.7 | 2.9 | 9.2 | 4.1 | 79.1 | 42.4 | 11.3 | 13.4 | 15.8 | 17.1 |
| 401–600 | 0.1 | 0.3 | 1.4 | 2.1 | 96.1 | 0.7 | 2.8 | 5.7 | 18.0 | 72.8 |
| 601–800 | 3.8 | 2.2 | 0.3 | 3.7 | 90.0 | 43.7 | 10.9 | 0.6 | 18.0 | 26.8 |
| 801+ | 16.1 | 1.2 | 0.3 | 0.1 | 82.3 | 96.5 | 1.3 | 0.1 | 0.2 | 1.9 |
| Overall | 4.3 | 1.2 | 12.4 | 2.9 | 79.2 | 37.3 | 5.8 | 19.0 | 14.1 | 23.8 |

**Note:** The left side of the table presents data from a traditional model using equal ages whereas the right side of the table presents results from a model based on different tree longevities. The upper part of the table is based on transitions without the woody shrub layer whereas the lower part of the table includes the shrub layer.

Our first specific hypothesis was that varying size gaps influence species success in recruitment, since differences in shade tolerance should be reflected by species associations with distinct gap sizes. Our results support this idea, as balsam fir recruited with greater success in smaller openings whereas yellow birch recruited better in larger openings. Hébert (2003), also working in the balsam fir – yellow birch domain, reported similar results.

We also hypothesized that the differing longevity of the dominant species may be an important factor ensuring the maintenance of the less competitive (in terms of shade tolerance) yellow birch with the extremely shade-tolerant balsam fir (Kneeshaw et al. 2006). This follows earlier theories that long-lived tree species may be maintained in forests due to the occurrence of temporal as well as spatial niches (Chesson and Warner 1981; Chesson 2000). In our study, traditional Markov analyses, which do not take into account the different ages of the species, suggest that balsam fir and shrub species will dominate sites (Table 3). However, the inclusion of longevity into the species replacement transitions (similar to Lertzman 1995) shows that the long-lived yellow birch is able to dominate in these mixedwood stands. In natural stands in our region, balsam fir will die earlier but be recruited a number of times during the life span of a yellow birch. Thus, even though the models we have used are relatively simple, they illustrate that the inclusion of longevity is crucial to account for species dynamics in these forests.

Although not explicit in our original hypotheses, tree size seemed also to be an important factor in explaining tree coexistence. Yellow birch attains larger diameters and has a larger crown size compared with balsam fir of similar diameter classes (2.5 times the same balsam fir DBH). This suggests that because of their greater size, a few yellow birch can ensure canopy dominance. Basal area may thus be a more important factor than abundance in explaining some aspects of species coexistence on a site.

Yellow birch also had better recruitment in gaps created by the mortality of balsam fir than in gaps created by its own mortality. Contrary to reciprocal replacement models that suggest that a species recruits better under competitors than under itself (Woods 1979), we found that only yellow birch exhibited this tendency. In contrast, balsam fir tended to recruit best beneath dead balsam fir trees and not under yellow birch. Two possibilities may explain why yellow birch recruited best beneath balsam fir. Because of the deep shade cast beneath balsam fir trees (Messier et al. 1998), there is less balsam fir advance regeneration than under yellow birch. Subsequent overstory balsam fir mortality permits the establishment of other species because there are more available sites. Alternatively, the relatively higher mortality rates of balsam fir resulted in larger gaps that are favourable to yellow birch establishment.

Our data thus show that multiple factors explain the coexistence of the two dominant species. Species longevity, shade tolerance, different associations with the gap size disturbance spectrum, and tree size differences between yellow birch and balsam fir are all responsible for the maintenance of this forest type. Although these differences ensure species coexistence, they complicate the prediction of mixed-species stand development (Larson 1992). Furthermore, other tree species in these mixedwood forests such as red spruce are also maintained due to interspecific differences. For example, red spruce is larger than balsam fir, occupies a larger growing space, is smaller seeded, and can thus disseminate seeds farther. Red spruce is also generally considered less tolerant than balsam fir but more so than yellow birch and tends to be found in gaps of intermediate size (Burns and Honkala 1990). Its much greater longevity than fir ensures the continued maintenance of red spruce in natural forests, although competition with balsam fir represents an important aspect of natural red spruce recruitment (Seymour 1992; Fortin 2005; Dumais and Prévost 2007).

**Fig. 4.** Species recruitment under gap makers of different species. The zero line represents recruitment that would be expected if there was an equal chance to recruit under that species. Positive values indicate greater recruitment under that species. Negative values indicate that recruitment is less than would be expected if recruitment was evenly partitioned under all dead species.

## Competition

Competition with shrubs and herbaceous species has been identified as an important factor limiting tree seedling success in many forest types (Brand 1986; Harvey et al. 1995; Ricard and Messier 1996; Bourgeois et al. 2004). Our study shows that shrub competition from species such as mountain maple has a significant influence on stand dynamics in our initial Markovian transition models (Table 3*a*). In similar mixedwood forests, Archambault et al. (1998) demonstrated that mountain maple is a strong competitor after clear-cutting. However, when we consider species longevity, then shrub dominance decreases. Tree seedlings must, however, first outgrow shrub competitors, and thus, as proposed in our final hypothesis, natural forest rotations may require long periods. Other empirical studies have shown that mountain maple initially outgrows balsam fir after gap disturbances caused by spruce budworm (Kneeshaw and Bergeron 1999; Sarvaala 2000; Aubin et al. 2005). Replacement of mountain maple by tree seedlings may effectively require at least one rotation of the shrub species, which could take up to 50 years (Sarvaala 2000).

## Implications for mixedwood forest management

The use of knowledge of ecosystem dynamics to improve management has long been proposed (Grime 1980) and is the fundamental basis of many silvicultural systems (Smith et al. 1996). Our results suggest that the natural species mix of these forests is maintained by a number of different factors from multiple life attributes to disturbance characteristics. This thus emphasizes the need for the use of a varied silviculture to maintain the integrity of these mixed forests. It is the heterogeneity of the natural disturbance regime and differences in species ecological characteristics that permit the maintenance of multiple species in these forests. Management of balsam fir – yellow birch forests for all tree species will thus require managers to avoid homogenization of silvicultural techniques (i.e., the targeting of a single approach), which could tend to favour one species. In mixedwood forests from the Southern Hemisphere, it has similarly been suggested that flexible management using a variety of treatments will be needed to maintain all species (Kennard and Putz 2005).

Specifically, we found that although yellow birch is most successful in larger natural openings (>800 m$^2$), none of the measured natural gaps exceeded 2000 m$^2$ (approximately 0.2 ha). These natural disturbances are thus small compared with the clearcuts that have traditionally been used in this forest (Laflèche et al. 2000; Hébert 2003). It could be argued that even if yellow birch benefits from larger gaps, harvest openings should not exceed the sizes identified if natural conditions are to be emulated. Archambault et al. (1998) observed decreases in both yellow birch and balsam fir and increases in paper birch and shrub species 20 years after clear-cutting.

The abundance of large shrubs was also positively correlated with opening size. Many researchers also report that shrub species, such as mountain maple, may increase in abundance in clearcuts or where disturbances lead to abundant overstory mortality (Batzer and Popp 1985; Kneeshaw and Bergeron 1996, 1999; Archambault et al. 1997, 1998). However, we did not find a significant relationship between light and shrub density in this study. This may be due to greater availability of below-ground resources, as shrub species such as mountain maple have been reported to be most abundant on rich sites (Post 1970; Lei and Lechowicz 1990). Without control of these competitors, increases in rotation lengths should be expected (Batzer and Popp 1985). Alternatively, forest managers may (if the public permits) use herbicides or mechanical weeding to favour yellow birch or choose to use smaller openings in combination with weeding treatments to favour balsam fir regeneration over most other species. Establishment of red spruce is also likely to be favoured in smaller canopy gaps (Dumais and Prévost 2007).

In terms of promoting yellow birch seedling establishment, it is well accepted that a sound silvicultural strategy is to produce soil surface disturbance during harvest (Nyland 2002). Historically, however, sufficient yellow birch regeneration has naturally occurred to ensure its dominance in Quebec's mixedwood forests. This reflects the role of understory substrates such as decaying woody debris, which may be reduced after harvesting (Tinker and Knight 2000). Silvicultural strategies that ensure a continued recruitment of deadwood should thus prove beneficial to the success of yellow birch in managed forests.

Our data also show that a gap-based silvicultural model that does not account for the differential life spans of the dominant species will probably not optimize wood production goals on these rich mixedwood sites. Balsam fir has a higher mortality rate than either red spruce or yellow birch due to its shorter longevity and high vulnerability to the spruce budworm as well as stem and butt rots (MacLean 1984; Burns and Honkala 1990). Fixing a common rotation length based on balsam fir longevity would disadvantage the co-occurring species whereas fixing rotation lengths based on yellow birch or red spruce longevity would inevitably lead to loss of balsam fir wood volume to mortality. Natural turnover time of the forest is estimated to vary from 100 to over 200 years (Table 2) whereas rotation in the managed forest does not exceed 100 years in Quebec (Pothier and Savard 1998; Ministère des Ressources naturelles du Québec 2003). Approaches such as irregular shelterwoods, in which species are harvested based on their age of maturity, may be worth considering for mixedwood forests composed of species with different longevities.

### Conclusion

Natural dynamics provide a useful reference or template for sustainable forest management. However, the concept requires serious thinking about adapting silvicultural interventions and the trade-offs involved. If a natural species composition is to be maintained, a range of opening sizes and rotation ages for the different species should be created, as they have important roles in species coexistence. Logistically or operationally, however, it may be difficult to harvest gaps at different time intervals to promote the coexistence of the different species. An approach that provides the conditions necessary for the recruitment and maintenance of all species instead of imitating patterns of gap size and form may prove to be most successful. Based on our results, we suggest that forest management systems that emulate natural processes both spatially and temporally should be more successful than those that address only spatial concerns.

## Acknowledgements

A number of people have made this research possible. We would like to thank Éric Saulnier and Jean-Pierre Lapointe for their help with the field work and Dominic Sénécal, Ève Lauzon, and Gerardo Reyes for help with the manuscript. Following reviews of this manuscript, we would like to thank two anonymous reviewers and the Associate Editor for their time and comments. We would also like to recognize financial support from the FQRNT Fonds forestier for the field work and subsequent support from the FQRNT and Natural Sciences and Engineering Research Council of Canada.

## References

Angelstam, P.K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. J. Veg. Sci. **9**: 593–602. doi:10.2307/3237275.

Archambault, L., Morissette, J., and Bernier-Cardou, M. 1997. Succession forestière après feu dans la sapinière à bouleau jaune du Bas-Saint-Laurent, Québec. For. Chron. **6**: 702–710.

Archambault, L., Morissette, J., and Bernier-Cardou, M. 1998. Forest succession over a 20-year period following clearcutting in balsam fir -– yellow birch ecosystems of eastern Quebec. For. Ecol. Manag. **102**: 61–74. doi:10.1016/S0378-1127(97)00109-6.

Aubin, I., Messier, C., and Kneeshaw, D.D. 2005. Population structure and growth acclimation of mountain maple along a successional gradient in the southern boreal forest. Ecoscience, **12**: 540–548. doi:10.2980/i1195-6860-12-4-540.1.

Batzer, H.O., and Popp, M.P. 1985. Forest succession following a spruce budworm outbreak in Minnesota. For. Chron. **61**: 75–80.

Bergeron, Y., and Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Québec. For. Ecol. Manag. **92**: 235–242. doi:10.1016/S0378-1127(96)03924-2.

Bourgeois, L., Messier, C., and Brais, S. 2004. Mountain maple and balsam fir early response to partial and clear cut harvesting in the boreal mixedwoods of northern Québec. Can. J. For. Res. **34**: 2049–2059. doi:10.1139/x04-080.

Brand, D.G. 1986. A competition index for predicting the vigour of planted Douglas-fir in southwestern British Columbia. Can. J. For. Res. **16**: 23–29.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. U.S. Dep. Agric. Agric. Handb. 654. Vol. 2.

Canada Soil Survey Committee. 1992. The Canadian system of soil classification. Publ. 1646. Agriculture Canada, Ottawa, Ont.

Canadian Climate Program. 1982. Canadian climate normals 1951–1980. Vol. 6. Frost. Environment Canada, Atmospheric Environment Service, Downsview, Ont.

Canadian Climate Program. 1993. Canadian climate normals 1961–1990. Québec. Environment Canada, Atmospheric Environment Service, Downsview, Ont.

Canham, C.D. 1988. An index for understory light levels in and around canopy gaps. Ecology, **69**: 1634–1638. doi:10.2307/1941664.

Chesson, P.L. 1986. Environmental variability and the coexistence of species. *In* Community ecology. *Edited by* J. Diamond and T.J. Case. Harper & Row, New York. pp. 240–256.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. **31**: 343–366. doi:10.1146/annurev.ecolsys.31.1.343.

Chesson, P.L., and Warner, R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. Am. Nat. **117**: 923–943. doi:10.1086/283778.

Coates, K.D., and Burton, P.J. 1997. A gap-based approach for the development of silvicultural systems to address ecosystem management objectives. For. Ecol. Manag. **99**: 339–356.

Dai, X. 1996. Influence of light conditions in canopy gaps on forest regeneration: a new gap light index and its application in a boreal forest in east-central Sweden. For. Ecol. Manag. **84**: 187–197. doi:10.1016/0378-1127(96)03734-6.

Denslow, J.S. 1987. Tropical rain forest gaps and tree species diversity. *In* The ecology of natural disturbance and patch dynamics. *Edited* by S.T.A. Pickett and P.S. White. Academic Press, New York.

Dumais, D., and Prévost, M. 2007. Red spruce conservation in managed forest of Québec: importance of some physiological and ecological characteristics. A review. For. Chron. **83**: 378–392.

Fortin, M. 2005. Étude rétrospective de la croissance en diamètre du sapin baumier (*Abies balsamea* (L.) Mill.) et de l'épinette rouge (*Picea rubens* Sarg.) en peuplements mixtes après une coupe à diamètre limite. For. Chron. **81**: 791–800.

Fraser, G.W., Canham, C.D., and Lertzman, K.P. 1999. Gap light analyzer (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright 1999. Simon Fraser University, Burnaby, B.C., and the Institute of Ecosystem Studies, Millbrook, N.Y.

Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen forests. Cambridge University Press, Cambridge, U.K.

Frelich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. Ecol. Monogr. **65**: 325–346. doi:10.2307/2937063.

Gravel, D., Canham, C.D., Beaudet, M., and Messier, C. 2006. Reconciling niche and neutrality: the continuum hypotheses. Ecol. Lett. **9**: 399–409. doi:10.1111/j.1461-0248.2006.00884.x. PMID:16623725.

Grime, J.P. 1980. An ecological approach to management. *In* Amenity grassland: an ecological perspective. *Edited by* I.H. Rorison and R. Hunt. John Wiley & Sons, Inc., New York. pp. 13–55.

Harvey, B.D., Leduc, A., and Bergeron, Y. 1995. Early postharvest succession in relation to site type in the southern boreal forest of Quebec. Can. J. For. Res. **25**: 1658–1672.

Hébert, R. 2003. Are clearcuts appropriate for the mixed forest of Québec? For. Chron. **79**: 664–671.

Horn, H.S. 1975. Forest succession. Sci. Am. **232**: 90–98.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Monographs in population biology. Princeton University Press, Princeton, N.J.

Kelly, C.K., and Bowler, M.G. 2002. Coexistence and relative abundance in forest trees. Nature (Lond.), **417**: 437–440. doi:10.1038/417437a. PMID:12024212.

Kennard, D.K., and Putz, F.E. 2005. Differential responses of Bolivian timber species to prescribed fire and other gap treatments. New For. **30**: 1–20.

Kneeshaw, D.D., and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Québec's southwestern boreal forest. Can. J. For. Res. **26**: 888–898.

Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southern boreal forest. Ecology, **79**: 783–794.

Kneeshaw, D.D., and Bergeron, Y. 1999. Spatial and temporal patterns of seedling recruitment within spruce budworm caused canopy gaps. Ecoscience, **6**: 214–222.

Kneeshaw, D.D., Kobe, R., Coates, D., and Messier, C. 2006. Sapling size influences shade tolerance ranking among southern boreal tree species. J. Ecol. **94**: 471–480. doi:10.1111/j.1365-2745.2005.01070.x.

Laflèche, V., Ruel, J.C., and Archambault, L. 2000. Évaluation de la coupe de protection de la régénération et des sols comme méthode de régénération de peuplements mélangés du domaine bioclimatique de la sapinière à bouleau jaune de l'est du Québec, Canada. For. Chron. **76**: 653–663.

Larson, B.C. 1992. Pathways of development in mixed-species stands. *In* The ecology and silviculture of mixed-species forests. *Edited by* M.J. Kelty, B.C. Larson, and C.D. Oliver. Kluwer Academic Publishers, Norwell, Mass. pp. 3–10.

Lei, T.T., and Lechowicz, M.J. 1990. Shade adaptation and shade tolerance in saplings of three *Acer* species from eastern North America. Oecologia, **84**: 224–228.

Lertzman, K.P. 1995. Forest dynamics, differential mortality rates and variable transition probabilities. J. Veg. Sci. **6**: 191–204. doi:10.2307/3236214.

Lertzman, K.P., and Krebs, C.J. 1991. Gap-phase structure of a sub-alpine old-growth forest. Can. J. For. Res. **21**: 1730–1741.

Lieffers, V.J., and Beck, J.A., Jr. 1994. A semi-natural approach to mixedwood management in the prairie provinces. For. Chron. **70**: 260–264.

Loehle, C. 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. Am. Nat. **156**: 14–33. doi:10.1086/303369. PMID:10824018.

MacDonald, G.B. 1995. The case for boreal mixedwood management: an Ontario perspective. For. Chron. **71**: 725–734.

MacLean, D.A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. For. Chron. **60**: 273–279.

Messier, C., Parent, S., and Bergeron, Y. 1998. Characterization of understory light environment in closed mixed broadleaf-conifer boreal forests: effects of overstory and understory vegetation. J. Veg. Sci. **9**: 511–520. doi:10.2307/3237266.

Ministère des Ressources naturelles du Québec. 2003. Manuel d'aménagement forestier. 4$^{\text{ième}}$ éd. Ministère des Ressources naturelles du Québec, Direction des programmes forestiers, Québec, Qué.

Nyland, R.D. 2002. Site preparation. *In* Silviculture: concepts and applications. 2nd ed. *Edited by* S. Spoolman. McGraw-Hill, New York pp. 86–116.

Post, L.J. 1970. Dry matter production of mountain maple and balsam fir in northwestern New Brunswick. Ecology, **51**: 548–550. doi:10.2307/1935397.

Pothier, D., and Savard, F. 1998. Actualisation des tables de production pour les principales espèces forestières du Québec. Ministère des Ressources naturelles du Québec, Direction de la recherche forestière, Québec, Qué.

Ricard, J.P., and Messier, C. 1996. Abundance, growth and allometry of red raspberry (*Rubus idaeus*) along light gradient in a northern hardwood forest. For. Ecol. Manag. **81**: 153–160. doi:10.1016/0378-1127(95)03643-1.

Robitaille, A., and Saucier, J.P. 1998. Paysages régionaux du Québec méridional. Ministère des Ressources naturelles du Québec, Direction de la gestion des stocks forestiers et Direction des relations publiques, Québec, Qué.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology, **62**: 1041–1051. doi:10.2307/1937003.

Runkle, J.R. 1992. Guidelines and sample protocol for sampling forest gaps. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-283.

Sarvaala, M. 2000. Mountain maple dynamics in Québec's southwestern boreal forest. M.Sc. thesis, University of Helsinki, Helsinki, Finland.

SAS Institute Inc. 1999. SAS user's guide. SAS Institute Inc., Cary, N.C.

Saucier, J.P., Bergeron, J.F., Grondin, P., and Robitaille, A. 1998. The land regions of Southern Québec. 3rd version. One element in the hierarchical classification system developed by Québec's Ministère des Ressources naturelles. Ministère des Ressources naturelles du Québec, Direction de la gestion des stocks forestiers, Québec, Qué.

Seymour, R.S. 1992. The red spruce –– balsam fir forest of Maine: evolution of silvicultural practice in response to stand development patterns and disturbances. *In* The ecology and silviculture of mixed-species forests. *Edited by* M.J. Kelty, B.C. Larson, and C.D. Oliver. Kluwer Academic Publishers, Norwell, Mass. pp. 217–244.

Smith, D.M., Larson, B.C., Kelty, M.J., and Ashton, P.M.S. 1996.

The practice of silviculture: applied forest ecology. John Wiley & Sons, Inc., New York.

Tinker, D.B., and Knight, D.H. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems (N.Y., Print), **3**: 472–483. doi:10.1007/s100210000041.

Woods, K.D. 1979. Reciprocal replacement and the maintenance of codominance in a beech–maple forest. Oikos, **33**: 31–39. doi:10.2307/3544508.

Woods, K.D. 2000. Long-term change and spatial pattern in a late successional hemlock northern hardwood forest. J. Ecol. **88**: 267–282. doi:10.1046/j.1365-2745.2000.00448.x.