

silviculture

Patch Cutting in Temperate Mixedwood Stands: What Happens in the Between-Patch Matrix?

Patricia Raymond, Marcel Prévost, and Hugues Power

Over the last two decades, patch cutting systems have been applied in Eastern Canada to regenerate uneven-aged yellow birch (*Betula alleghaniensis* Britton)-conifer stands. Yet, we still know very little about how the trees located in the between-patch matrix respond to treatments. This study compares growth, recruitment, and tree mortality of yellow birch, red maple (*Acer rubrum* L.), balsam fir (*Abies balsamea* [L.] Mill.), and red spruce (*Picea rubens* Sarg.) in three 50% patch cutting treatments with 20-, 30-, and 40-m diameter circular gaps combined with 33% single-tree cutting in the matrix between patches and an uncut control. After 10 years, the positive effects of cutting treatments on recruitment and growth were nullified by mortality, resulting in nonsignificant changes in stand net merchantable basal area. The mortality rate modeled at the tree level was highest for trees with larger diameters, defects, and high crown ratios. Trees with small diameters and those located along the border of harvest gaps had the largest increments in basal area. This study questions the use of patch cutting in mixed uneven-aged stands comprising an important component of short-lived balsam fir. Silvicultural systems utilizing nonsystematic placement of variably sized gaps may prove more beneficial for managing wood production and complexity in yellow birch-conifer stands.

Keywords: hardwoods, uneven-aged management, hybrid regeneration methods, harvest gaps, mixedwood silviculture

In Eastern Canada's temperate mixedwood forest, yellow birch (*Betula alleghaniensis* Britton) is among the most valuable tree species for wood production. This mid shade-tolerant species benefits from soil disturbance and requires high light levels to regenerate (Willis et al. 2015). Silvicultural systems using gaps, such as group selection and patch cutting, are often recommended for managing yellow birch in both northern hardwoods (Leak and Filip 1977, Leak et al. 1987, Webster and Lorimer 2002, Pin et al. 2013) and mixed yellow birch-conifer stands (Ministère des Ressources naturelles, de la Faune et des Parcs 2003). For mixed-species stands, the harvest gaps create a variety of niches that can promote coexistence and maintain species diversity (Coates and Burton 1997). They have been under assessment in Eastern Canada since the late 1990s for regenerating yellow birch-conifer stands (Prévost et al. 2010b, Beaudet et al. 2014, Prévost and Charette 2015). Short-term results in uneven-aged stands of this forest type indicate that harvest

gaps of moderate size (with a diameter larger than the equivalent of one tree height; $>1H$) usually succeed in establishing yellow birch but can also fail to regenerate shade-tolerant conifers such as red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* [L.] Mill.) (Prévost et al. 2010b, Beaudet et al. 2014, Prévost and Charette 2015).

Although the effects of patch cutting on regeneration dynamics are important, a broader assessment of this silvicultural system would involve determining the effects on the growth and yield of residual trees, particularly when partial harvests are applied in the residual stand matrix to remove high-mortality risk trees, improve residual stand quality, and favor regeneration (Nyland 2002, p. 533–536). Aside from producing wood for the next harvest, the residual stand plays a role in maintaining a forest cover containing seed trees and in tempering both within- and between-patch microclimate for regeneration. To date, however, knowledge of these

Manuscript received March 4, 2015; accepted November 12, 2015; published online January 14, 2016.

Affiliations: Patricia Raymond (patricia.raymond@mffp.gouv.qc.ca), Gouvernement du Québec, Ministère des Forêts, de la Faune et des Parcs, Direction de la recherche forestière, Quebec City, QC, Canada. Marcel Prévost (marcel.prevost@mffp.gouv.qc.ca), Gouvernement du Québec, Ministère des Forêts, de la Faune et des Parcs. Hugues Power (hugues.power@mffp.gouv.qc.ca), Gouvernement du Québec, Ministère des Forêts, de la Faune et des Parcs.

Acknowledgments: We thank four anonymous reviewers and the associate editor for providing judicious comments. We are in debt to Alejandro A. Royo, Daniel Dumais, and Jean-Pierre Saucier for diligently reviewing previous versions of this article, and to Josianne DeBlois and Isabelle Auger for their statistical advice. Special thanks go to Eric Saulnier, Jean-Pierre Lapointe, Julie Forgues, Maurice Gagnon, Carlo Gros-Louis, Daniel Guimond, Gabriel Pilote, and numerous summer students for their excellent fieldwork throughout the years. We also acknowledge Brigitte Bigué, Jean-Martin Lussier, André Rouleau, and Daniel Tremblay for their active participation during the initial planning and establishment of the silvicultural experiment. This study is part of Project 142332018 of the Direction de la recherche forestière, Ministère des Forêts, de la Faune et des Parcs du Québec.

This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; square centimeters (cm²): 1 cm² = 0.155 in.²; meters (m): 1 m = 3.3 ft; square meters (m²): 1 m² = 10.8 ft²; millimeters (mm): 1 mm = 0.039 in.; hectares (ha): 1 ha = 2.47 ac.

stand-level effects in a thinned residual matrix remain poorly documented, although literature reports for other silvicultural systems using gaps in northeastern mixedwood forests exist (e.g., expanding-gap irregular shelterwood; Arseneault et al. 2011, Arseneault and Saunders 2012, Saunders and Arseneault 2013). Namely, Arseneault et al. (2011) reported a significant growth and regeneration response on a distance up to 18 m in the unharvested forest adjacent to patches. They also emphasized how scarce knowledge of edge effects in gap-based systems is. Other results gleaned from partial cutting studies indicate that conifers and the short-lived balsam fir in particular grow faster with the enhanced light conditions, but have a higher rate of mortality than their competitors (Hatcher 1960, Prévost et al. 2010a, Martin et al. 2014). Hence, it is critical to assess the stand-level and species-specific effects on wood production in the between-patch matrix of forest types dominated by a mixture of long-lived species and containing high proportions of balsam fir.

Mixed-species stands composed of species with differing traits (e.g., longevity, shade tolerance, crown or root structure, and phenology) can be more productive than pure stands because of the optimized resource exploitation related to the differential above-ground and below-ground niche selection by species (Man and Liefers 1999, Brassard et al. 2011, Waskiewicz et al. 2013). According to Pretzsch (2014), the benefits of mixed-species composition go far beyond simple niche complementarity in crown geometries among species (e.g., Thorpe et al. 2010, Bayer et al. 2013) that maximizes occupancy of canopy space. Rather, he argues, environmental cues in mixed stands trigger a much larger variation in crown geometry than is typically found in pure stands (“true mixing effects” *sensu* Forrester 2013), thereby optimizing stand productivity, resilience, and stability. However, this interspecific variation in crown geometry in response to the local environment remains poorly understood, particularly in mixedwood stands. Nevertheless, a few studies have found that species can exhibit considerable variation in crown geometry in response to both resource (e.g., light and space) availability and competitor identity (Maguire et al. 1998, Thorpe et al. 2010, Bayer et al. 2013, Dieler and Pretzsch 2013). Gap creation directly alters the intensity of competition and the environment around residual trees (Vepakomma et al. 2011, Prévost and Raymond 2012). Thus, to fully understand the efficacy of silvicultural practices such as patch cutting on tree- and stand-level dynamics, it is necessary to elucidate how the combination of harvest gap creation and partial cutting between patches affects tree morphological characteristics that directly influence long-term growth and survival.

The high proportion of edge effects (*sensu* Bradshaw 1992) that result from the use of patch-cutting systems may have additional impacts on trees located along the periphery of the gaps (Arseneault and Saunders 2012). These systems typically create circular gaps with a diameter to canopy height ratio between 1 and 2 (1H–2H) (Nyland 2002, p. 252) that greatly increases light transmission within the opening (e.g., 2–3× relative to that for uncut forest; Prévost and Raymond 2012). They also result in a spatially heterogeneous distribution of light, with a maximum irradiance in the northern part of gaps at high latitudes (Canham et al. 1990, Raymond et al. 2006, Prévost and Raymond 2012). Trees along the gap periphery benefit from the increased resource availability with greater radial growth (Pedersen and Howard 2004, Arseneault et al. 2011, Vepakomma et al. 2011, Stan and Daniels 2014) but can develop asymmetrical crown and bole shapes because of the heterogeneous distribution of sunlight after gap creation (Brisson 2001, Muth and Bazzaz 2002, Getzin and Weigand 2007). In the specific

case of yellow birch reserved as seed trees, exposure along the edges of large gaps could affect stem quality, given its proneness to epicormic branching after severe canopy opening (Trimble and Seegrist 1973, Rey-Lescure 1982). Therefore, it is relevant to contrast the individual responses of trees located at the periphery of gaps along with those of trees located further in the between-patch matrix.

In a former study, we characterized the effects of different cutting treatments (patch cutting with 20-, 30-, and 40-m gaps, 1-ha patch clearcut, and uncut control) on the microenvironment and early regeneration dynamics of yellow birch-conifer stands (Prévost et al. 2010b, Prévost and Raymond 2012). The aim of this article is to assess the stand- and tree-level effects 10 years after patch cutting in the between-patch matrix of the same stands. Specifically, we quantified how cutting treatments affected the radial growth, mortality, and recruitment of merchantable trees (>90 mm dbh) in the residual stand matrix and whether the effects varied by species or among locations within the treated areas. We expected the following: that patch cutting with partial cutting between gaps will increase the growth and decrease mortality of residual trees relative to uncut controls, enhancing stand development as measured by the change in quadratic mean diameter (QMD) and basal area (BA); that the increased resource availability in the between-patch matrix will benefit the development of basal area of small balsam fir more than that of other species because of its high degree of morphological plasticity; and that trees along the periphery of gaps will have the largest growth increments.

Materials and Methods

Site Description

The study was carried out near Rivière-à-Pierre, approximately 80 km northwest of Québec City, QC, Canada. The region is characterized by a high-hill topography with rounded summits (Robitaille and Saucier 1998). Mean monthly temperatures (1981–2010) vary from -14.6°C in January to 17.3°C in July (using BioSIM) (Régnière and Bolstad 1994). On average, the region receives 1,253 mm of precipitation annually, with 31% falling as snow. The experiment is located at the margins of the balsam fir-yellow birch and the sugar maple (*Acer saccharum* Marsh.)-yellow birch bioclimatic domains (Saucier et al. 2009). It was established in high-quality uneven-aged yellow birch-conifer stands located at two sites, 10 km from each other. The soil was classified as a humo-feric podzol. Before cutting, the first site (Lac Poissonneux) had a mean BA of 31 m^2/ha with 44% yellow birch, 31% balsam fir, 14% red spruce, and 5% red maple (*Acer rubrum* L.). The second site (Lac des Étangs) averaged 28 m^2/ha with 44% yellow birch, 17% balsam fir, 15% red spruce, and 11% red maple. The remaining BA at both stands comprised companion species, among them sugar maple, pin cherry (*Prunus pensylvanica* L. f.), white birch (*Betula papyrifera* Marsh.), and striped maple (*Acer pensylvanicum* L.). Preliminary historical analysis by Lussier et al. (2000) indicated that these stands were disturbed repeatedly by spruce budworm (*Choristoneura fumiferana* Clemens) epidemics. The infestations of 1912 and 1947 stimulated tree growth and regeneration the most, presumably because of partial mortality. A partial cutting (salvage) was also applied at the first site during 1947–1948. Stands were uneven-aged and contained more than three age classes (Lussier et al. 2000). Precut diameter

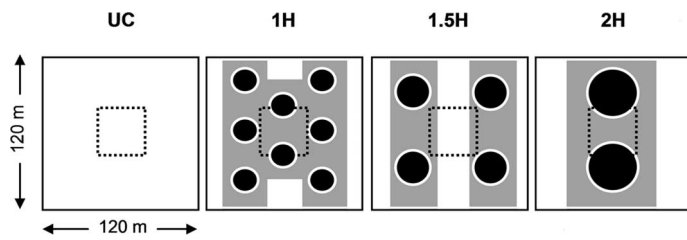


Figure 1. Layout of an experimental block (repetition) comprising four treatments: uncut control (UC) and three patch cutting treatments (1H, 1.5H, and 2H). Cutting established systematic gaps across a comparable area for each treatment (1H: 8 × 20-m diameter gaps; 1.5H: 4 × 30-m diameter gaps; 2H: 2 × 40-m diameter gaps) as well as 33% of stocking by single-tree cutting in the between-patch matrix. Dotted lines indicate the central plots and areas in gray the border plots.

distribution generally followed a reverse J-shaped diameter distribution (Supplemental Figure S1[■]). The majority of trees had a dbh smaller than 50 cm.

Experimental Design

The experiment, established in October 1999, contains four complete randomized blocks (two blocks per site) and four treatments. Selected treatments consist of three different patch sizes (20-, 30-, or 40-m diameter) corresponding to 1, 1.5, and 2 times dominant tree heights (1H, 1.5H, and 2H; H = 20 m in this study) and an uncut control (Figure 1). Gaps were evenly distributed on a 120- × 120-m experimental unit, with similar proportions of total area in gaps in each treatment (1H: 8 gaps, 17.5% of area; 1.5H: 4 gaps, 19.6%; 2H: 2 gaps, 17.5%). In addition, one-third of the BA in the residual stand matrix was harvested. This treatment of the matrix had objectives similar to those for single-tree selection cutting: (1) to harvest high-risk trees; (2) to improve stand vigor and quality; (3) to favor the regeneration of shade-tolerant conifers; and (4) to enhance tree growth and recruitment. However, because of the difficulty in maintaining a balanced diameter distribution in mixed stands (Seymour and Kenefic 1998), there was no attempt to sustain a reverse-J distribution as with the traditional selection system (see Arbogast 1957). Trees were cut in all diameter classes after species-based tree marking accounting for longevity, vigor, quality, and seed tree potential. Balsam fir, red maple, and paper birch were harvested as a priority, whereas vigorous red spruce and yellow birch were maintained in the stand for both wood and seed production. With the combination of patch and matrix cutting, 50% of merchantable BA was harvested from each experimental unit.

Stand-level effects on wood production of the between-patch matrix were documented for each 40- × 40-m central plot (hereafter called the central plot). To assess the edge effects on individual tree characteristics, we expanded the sampling area to include the edge of gaps (hereafter called border plot). Border plots were located around the central plot and included the major portion of gaps. Figure 1 shows the location and configuration of the central and border plots within the four treatments.

Tree Measurements

The first measurement was done in the central plots before harvesting in 1999, with subsequent measurements during fall

2000 (central and border plots, year 1 after treatment), 2004 (center), 2005 (border), 2009 (center), and 2010 (border). All trees with a dbh (1.3 m dbh larger than 90 mm (merchantable dbh) were numbered and tallied for dbh and species. Tree condition (alive, dead, or harvested) was also recorded at each measurement. In border plots, trees were classified in two locations: edge trees (i.e., tree with a crown adjacent to a harvest gap) or not. Projected crown radii along cardinal directions were measured in 1999, 2000, 2005, and 2010. Total height (m) and height from the tree base to the first live branch (>1 cm) of the crown on the main stem (clear bole length) were measured in 1999, 2000, 2009, and 2010. Visible defects that could affect tree survival and growth (*sensu* Majcen et al. 1990, Guillemette et al. 2008) were recorded in the central plots in 1999, 2004, and 2009. Defects include cankers, holes, decay, injury, insect damage, lean ($\geq 30^\circ$), and proportion of crown with dead branches.

Plot- and Tree-Level Variable Calculation

Stand density (no. of trees/ha), QMD, and merchantable BA were computed from the living trees of >90 mm dbh and for the four main tree species (yellow birch, red maple, red spruce, and balsam fir). In addition, the ratio of tree dbh over stand QMD, the BA of all trees with a dbh larger than the subject tree (BAL), the ratio of total height over dbh (H/D), and the ratio of crown length over tree height (CR) were also calculated for each tree. Crown surface area was also estimated from crown radii and crown length measurements. The shape of the crown was assumed to be conical for conifer and parabolic for hardwood species (Prévost et al. 2010a). We calculated plot- and tree-level variables from the 1999 measurement within the central plot (excluding trees that were harvested the same year), in 2000 within the central and border plots, in 2004 within the central plot, and in 2005 within the border plots.

Statistical Analysis

Stand-Level Assessment

Change in QMD and BA.—We analyzed stand-level changes in quadratic mean diameter (Δ QMD) and basal area (Δ BA), as well as species-specific changes in these variables (Δ QMD_s and Δ BA_s, respectively) in the central plots both immediately after cutting (1999) and 10 years later (2009). We used the changes in QMD and BA_s as metrics to quantify how each species was affected by treatments. ANOVAs were performed with the MIXED procedure (SAS 9.3; SAS Institute, Inc., Cary, NC), where blocks were tested as random effects and treatments and species as fixed effects. In addition, because variation in stand conditions among plots and treatments can affect growth responses, we tested precut BA (and BA_s) or immediately postcut BA (and BA_s) as covariates (for immediate effects and for 10-year effects, respectively). This procedure first required testing the homogeneity of slopes assumption. If the full model failed to reject the hypothesis of no interaction between the covariate and the main effect ($P > 0.05$), the interaction was removed, resulting in an equal slopes model testing only the covariate. However, in cases where the covariate × main effects interaction was significant, we used an unequal slopes model, and treatment differences were tested for three levels of the BA_s covariate: low (first quartile, 2.37 m²/ha or 177 mm/QMD_s), average (mean, 7.25 m²/ha or 234 mm/QMD_s), and high (third quartile, 11.0 or 279 mm/QMD_s) (Littell et al.

[■] Supplementary data are available with this article at <http://dx.doi.org/10.5849/forsci.15-023>.

Table 1. Species-level changes in ΔQMD_s and ΔBA_s for the four main species immediately after treatment.

Variable	Level of covariate	Species	Estimate	<i>P</i> value	Treatment	Estimate	<i>P</i> value
ΔQMD_s (mm)	NA	YB	6.364	0.458	1H	-4.713	0.595
		RM	8.774	0.320	1.5H	-10.913	0.002
		RS	-8.798	0.342	2H	-3.660	0.691
		BF	-32.055	<0.001			
ΔBA_s (m ² /ha)	Low	YB	-1.299	0.339	1H	-1.595	0.006
		RM	-0.938	0.072	1.5H	-0.576	0.311
		RS	-0.788	0.309	2H	-1.157	0.055
		BF	-1.413	0.107			
	Mean	YB	-2.074	0.002	1H	-3.990	<0.001
		RM	-2.808	0.001	1.5H	-2.970	<0.001
		RS	-4.230	<0.001	2H	-3.552	<0.001
		BF	-4.904	<0.001			
	High	YB	-2.670	<0.001	1H	-5.830	<0.001
		RM	-4.245	0.001	1.5H	-4.810	<0.001
		RS	-6.876	<0.001	2H	-5.392	<0.001
		BF	-7.586	<0.001			

Since the species interacted significantly with the covariate, ANOVAs were performed at three levels: low (first quartile = 2.37 m²/ha), mean (7.25 m²/ha), and high precut BA_s (third quartile = 11 m²/ha). Treatments consist of patch cutting using three circular gap sizes (20-, 30-, and 40-m diameter) corresponding to 1, 1.5, and 2 times tree heights (1H, 1.5H, and 2H) combined to 33% single-tree cutting in the matrix and an uncut control. NA, not applicable; YB, yellow birch; RM, red maple; RS, red spruce; BF, balsam fir.

2006). Homogeneity of the variance and normality of residuals were graphically checked. When nonhomogeneity or nonnormality was detected, the variance of the residuals was modeled with the REPEATED option of the MIXED procedure. We estimated the species and treatments parameters with the LSMEAN function and the ILINK option.

Recruitment and mortality.—We estimated tree recruitment to the 9.0-cm dbh class in the central plots over a 10-year period. We classified trees as recruits if they were not recorded at the first measurement but recorded at the last. Red maple was excluded from recruitment analyses since it proved negligible for the 10-year period. We considered trees that were alive in 1999 but dead in 2009 (excluding harvested trees) as having died during the 10-year period. We performed stand-level analysis of mortality on the ratio between the species merchantable BA of the trees that died ($BA_{s10dead}$) over the species merchantable BA of living trees in 1999 (excluding harvested trees) ($BA_{s0living}$). Recruitment and mortality at the stand level were analyzed with the GLIMMIX procedure (SAS Institute, Inc. 2011) with the Laplace estimation method, enabling the use of a likelihood-based model selection method (Bolker et al. 2008). Blocks and treatments nested in blocks were used as random effects in the model. Recruitment was modeled with a negative binomial distribution and a log link function (White and Bennetts 1996), whereas mortality was modeled with a binomial distribution and logit link function. Species and treatments were considered as fixed effects. The LSMEAN function with the ILINK option was used to obtain the species- and treatment-specific estimates of recruitment and mortality. Comparisons between groups with polynomial contrasts were performed with the LSMESTIMATE function and the SIMULATE option.

Tree-Level Assessment

Mortality models.—We modeled tree-level mortality binary variables with the data from the central plots (to include the stem defects in the model) over two continuous 5-year periods (1999–2004 and 2004–2009). We tested dbh, dbh/QMD, H/D, BAL, crown ratio, crown radius, crown surface area, presence of defects, species, and group of treatments as explanatory variables in the model. All predictors and their simple interactions were entered in a full model, and model simplification was

performed using a backward selection technique based on the Akaike criterion (Akaike 1973). To avoid problems of convergence, selection of fixed effects was made without random effects with the GLIMMIX procedure. However, random effects (blocks and treatments nested in blocks) were entered in the final model to estimate parameters (Fortin et al. 2008). Model goodness of fit was assessed with a Hosmer-Lemeshow test (Hosmer and Lemeshow 2000, p. 147–156).

Tree growth models.—We used trees from the central and the border plots to model the tree-level change in merchantable BA (ΔBA_s). Growth periods were 1999–2004 and 2004–2009 in central plots and 2000–2005 and 2005–2010 in border plots. BA_t was estimated from the difference between values at the end and at the beginning of the growth periods (cm²/year). BA_t was modeled with a linear regression using the MIXED procedure. Blocks, treatments nested in blocks, and plots nested in treatments were included as random effects. Correlation between two observations of the same trees was modeled with the REPEATED statement. The same predictors were tested as in the tree-level mortality model. To avoid collinearity, if two predictors showed a variance inflation factor larger than 10, they were entered separately in the model (Kleinbaum et al. 1998, p. 241). We log-transformed the dependent variable to meet the assumptions of normality and homogeneity of variance. The smear factor was used to correct the bias when returning to the original scale (Duan 1983). Model selection was conducted similarly to the method used for the tree-level mortality model, with the difference that random effects were used from the beginning of the selection procedure.

Results

Immediate Stand-Level Effects

Changes in QMD and BA

ΔQMD within the central plots did not differ among treatments immediately after treatment but did among species ($P = 0.642$ and $P = 0.008$, respectively) (Supplemental Table S2). Species-level analyses showed that harvesting significantly affected only balsam fir, decreasing QMD by 32 mm (Table 1). As a result of the cutting, BA of the residual stand between the gaps was decreased by 6.65 m²/ha, but without differences among cutting treatments (1H, 1.5H, and 2H) (Supplemental Table

Table 2. Species-level Δ QMD_s and Δ BA_s, no. of recruits/ha, and BA_{s10dead}/BA_{s0living} for the central plots 10 years after treatment.

Variable	Level of covariate	Species	Estimate	P value	Treatment	Estimate	P value
Δ QMD _s (mm)	NA	YB	21.759	<0.001	1H	27.435	<0.001
		RM	26.049	<0.001	1.5H	33.551	<0.001
		RS	35.189	<0.001	2H	23.601	<0.001
		BF	26.09	<0.001	Control	24.499	0.001
Δ BA _s (m ² /ha)	Low	YB	1.963	0.004	1H	0.720	0.066
		RM	0.210	0.321	1.5H	1.043	0.001
		RS	0.519	0.010	2H	0.388	0.063
		BF	0.084	0.695	Control	0.626	0.088
	Mean	YB	1.626	<0.001	1H	-0.092	0.875
		RM	0.692	0.249	1.5H	0.813	0.027
		RS	2.356	<0.001	2H	1.570	<0.001
		BF	-1.264	0.030	Control	1.119	<0.001
	High	YB	1.367	<0.001	1H	-0.716	0.557
		RM	1.063	0.223	1.5H	0.637	0.312
		RS	3.767	<0.001	2H	2.478	<0.001
		BF	-2.301	0.031	Control	1.497	0.002
No. of recruits/ha	NA	YB	9.930	<0.001	1H	20.515	<0.001
		RS	4.951	<0.001	1.5H	13.876	<0.001
		BF	36.443	<0.001	2H	17.286	<0.001
					Control	4.423	0.005
BA _{s10dead} /BA _{s0living}	NA	YB	0.053	0.002	1H	0.234	0.015
		RM	0.133	0.077	1.5H	0.102	0.067
		RS	0.018	0.338	2H	0.064	0.062
		BF	0.383	<0.001	Control	0.040	0.079

When the fixed effect (species or treatment) interacted significantly with the covariate, ANOVAs were performed at three levels of the covariate distribution (mean, first, and third quartiles). They were 2.37, 7.25, and 11 m²/ha for postcut BA_s and 177, 234, and 279 mm for postcut QMD. The mortality rate was computed as the proportion of 10-year BA_s in dead trees (BA_{s10dead}) over BA_s in living trees in 1999 (excluding harvested trees). The number of recruits was too low for red maple to allow analysis. See Table 1 for the description of species. NA, not applicable.

S2). In contrast, BA_s changed significantly between species, but the effects interacted with the level of the precut BA_s covariate ($P < 0.001$). No differences were observed among species at low levels of precut BA_s, but there were significant differences at the average and high levels of precut BA_s (Table 1). Contrasts indicate that BA_s was reduced more for balsam fir than for other tree species at those levels (Table 3).

10-Year Stand-Level Effects

Changes in QMD and BA

Ten years after treatment, average stand QMD for residual trees within the central plots increased by 31 mm ($P = 0.001$), without differences in Δ QMD among treatments ($P = 0.502$). When tested at the species level, the change in QMD_s did not differ among species (Supplemental Table S2). Mean stand BA increased by 2.03 m²/ha ($P = 0.020$) but with no differences among treatments ($P = 0.171$). Species-level BA_s varied among species and treatments, depending on the degree of postcut BA_s (see Supplemental Table S2 for significant covariate \times main effect interactions). After 10 years, only yellow birch and red spruce increased in BA_s at all levels of the covariate. Balsam fir BA_s decreased at mean and high levels of the covariate, whereas red maple remained unchanged (Table 2). Red spruce had the best 10-year growth response with 3.80 m²/ha at the high covariate level (33% gain). Increases in mean species BA over 10 years were greatest in treatments with the large gaps (2H) and the uncut controls, at mean and high levels of postcut BA_s (Table 2). Patch cutting with intermediately sized gaps (1.5H) only significantly increased BA_s at low to mean levels of postcut BA_s. Those with small gaps (1H) did not affect species-level BA_s over 10 years. Contrasts confirm that the average increase in BA_s was lower by 1.26 m²/ha in treatments with small gaps, compared with the others, at the mean covariate value (Table 3).

Recruitment and Mortality

For the central plots, the number of trees recruited to the merchantable class over the 10-year period within the matrix between

patches differed among species, but not among treatments (Supplemental Table S2). We found that the recruitment into the merchantable size class was higher for balsam fir (36 stems/ha) than for yellow birch (10 stems/ha) and red spruce (5 stems/ha) (Tables 2 and 3). The mortality rate differed among species and treatments (Supplemental Table S2). Both balsam fir (38%) and yellow birch (5%) exhibited significant mortality over 10 years (Tables 2 and 3). Mortality was marginally significant ($P = 0.077$) for red maple, representing 13% of postcut BA_s. Significant mortality (23% BA loss) occurred only in the treatments with the smallest gaps (Tables 2 and 3).

Variation in the Components of Net Growth in BA

Overall, despite the fact that patch cutting treatments did not exert strong effects on the net change in merchantable BA within the central plots, differences did occur in growth, recruitment, and mortality (Figure 2) across treatments and species. Balsam fir showed the highest variation, especially for mortality (10–60% of postcut BA_s) and recruitment (2–31% of postcut BA_s). Yellow birch had the least variation in growth and mortality (14 and 7% of postcut BA_s, respectively). Within the uncut control these varied little, with the proportion of postcut BA in growth and mortality remaining at lower levels than in the patch cutting treatments.

10-Year Tree-Level Effects

Modeling of Mortality and Growth in BA

Probabilities of mortality over 5-year periods varied greatly among species within the central plots. Balsam fir and red maple had the highest probabilities, whereas red spruce and yellow birch had the smallest (Figures 3 and 4). Factors increasing the probabilities of mortality were the proximity to harvest gaps (border trees) and tree characteristics such as diameter, presence of defects, and crown ratio (all $P \leq 0.001$) (Table 4). For trees without defects, probabilities remained at less than 10% for red spruce and yellow birch (except for yellow birch at ≥ 34 cm dbh in cutting treatments) (Figure 3). In the matrix of patch cutting treatments, trees with defects and high crown ratios (e.g., >55%) had a higher probability of dying. We

Table 3. Results of the polynomial contrasts for species-level analysis for the central plots.

Effects	Variable	Test	Covariate level	Estimate	df	P value
Immediately after the cut	Δ QMD (mm)	BF versus other species	NA	-34.168	29	0.004
	Δ BA _s (m ² /ha)	BF versus other species	Low	-0.405	28	0.636
		BF versus other species	Mean	-1.867	28	0.006
After 10 years	Δ BA _s (m ² /ha)	BF versus other species	High	-2.990	28	0.003
		BF versus other species	Low	-0.813	33	0.018
		BF versus other species	Mean	-2.822	33	<0.001
		BF versus other species	High	-4.366	33	<0.001
		1H versus other treatments	Mean	-1.259	33	0.039
	No. of recruits/ha	BF versus other species	NA	NA*	32	0.003
		BA _{s10dead} /BA _{s0living}	BF versus YB	NA	NA*	49
	BA _{s10dead} /BA _{s0living}	BF versus RM	NA	NA*	49	0.194
		BF versus RS	NA	NA*	49	0.011
		1H versus other treatments	NA	NA*	49	0.008

See Tables 1 and 2 for the description of species and variables.

* Because of the link function between the response and the predicting variables (logit for mortality and log for recruits), the estimate contrasts could not be reported. NA, not applicable.

also found an interaction between crown radius and crown ratio ($P < 0.001$) (Table 4), indicating that the positive relationship of crown ratio on mortality is stronger for trees with narrower crowns (e.g., 100–350 cm) than for trees with larger crowns (e.g., >350 cm) (not shown). Moreover, trees with smaller crown radii and greater crown ratios had higher probabilities of mortality than trees with larger crown radii and smaller crown ratios (Figures 3 and 4).

Tree-level annual growth in BA (BA_t) differed by species, treatments, location within the stand, dbh, crown ratio, and crown radius (Table 4). Growth in BA_t increased with diameter for all species except for yellow birch (Figures 5 and 6). Trees grew better in BA_t if located around the periphery of gaps ($P < 0.001$) and if they had larger crown radius ($P < 0.001$) and smaller crown ratios ($P < 0.001$). Large conifers (e.g., ≥ 30 cm dbh) located at the periphery of gaps had a 6% greater BA_t growth relative to that of individuals of

equivalent dbh in the uncut controls (Figures 5 and 6). Nevertheless, the overall combined effects of treatments with dbh ($P < 0.001$) (Table 4) indicate that the magnitude of response to patch cutting was higher for smaller trees. For example, small conifers (e.g., 10 cm dbh) located at the periphery of gaps showed a 94% greater basal area growth relative to those in the uncut controls (Figures 5 and 6).

Discussion

Stand-Level Response to Patch Cutting

We expected that the net change in residual stand basal area would be higher in the matrix of patch cutting treatments than in the control, because the partial cutting should reduce potential mortality and increase residual tree growth. The patch cutting treatments successfully targeted mature balsam fir and increased stand

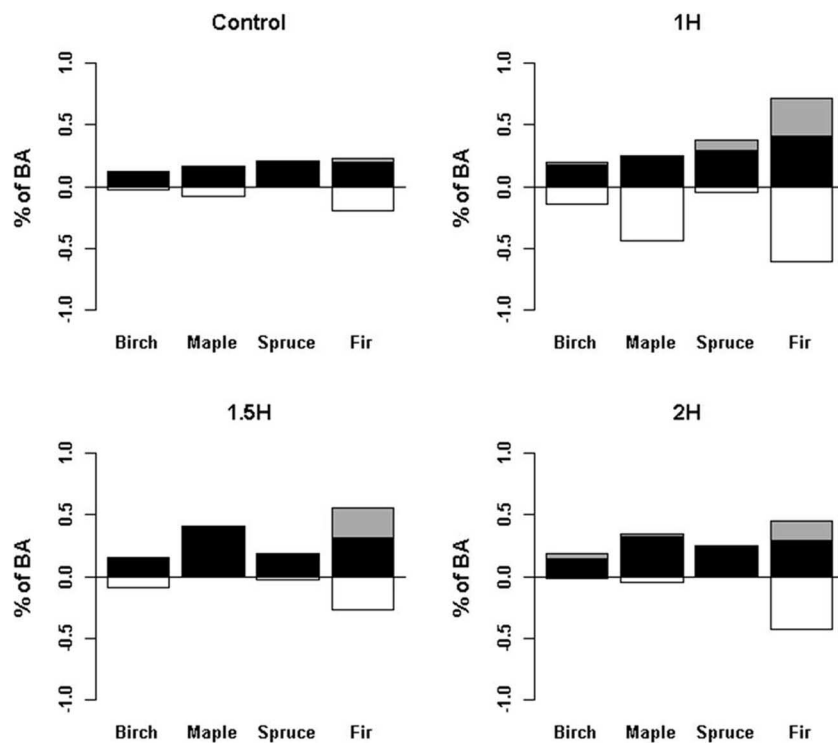


Figure 2. Net change in stand merchantable BA by treatment and species within the central plots after 10 years, following the components of net growth: growth (dark gray), recruitment (light gray), and mortality (white). Data were standardized as a percentage of postcut BA to facilitate comparisons.

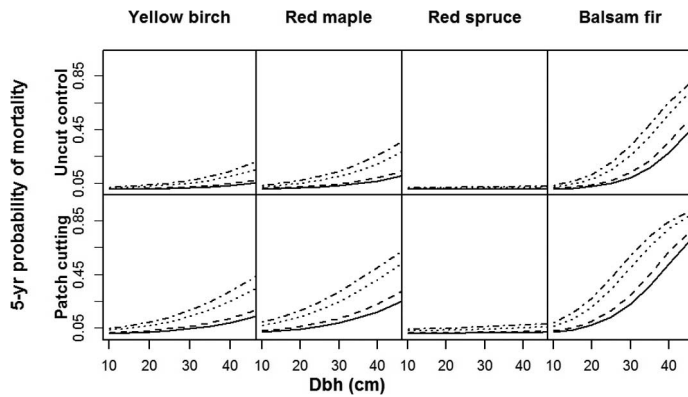


Figure 3. Five-year probability of mortality by species within the central plots as a function of dbh, crown ratio, presence of defects, and treatment. Trees with 35% crown ratio and no defects are represented by a full line, 35% crown ratio with defects by a dotted line, 55% crown ratio without defects by a dashed line, and 55% crown ratio with defects by a dashed and dotted line. Crown radius was held constant at 275 cm in equations.

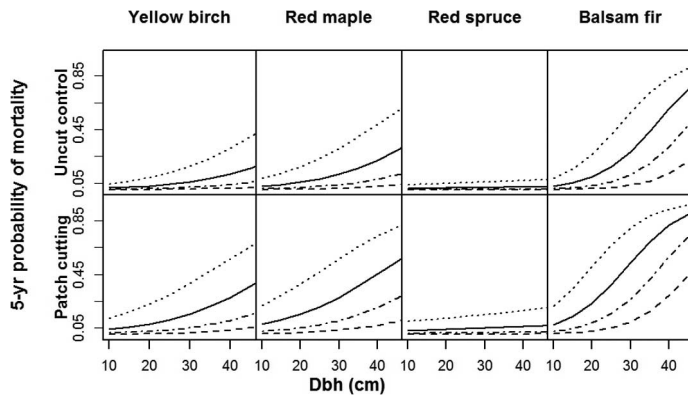


Figure 4. Five-year probability of mortality by species within the central plots as a function of dbh, crown radius, and treatment. Trees with 150-cm crown radius without defects are represented by a full line, 150-cm crown radius trees with defects by a dotted line, 400-cm crown radius trees without defects by a the dashed line, and 400-cm crown radius trees with defects by a dashed and dotted line. Crown ratio was held constant at 45% in equations.

QMD. However, net growth did not significantly increase total 10-year basal area compared with that for the control. Under high latitude, a lag period in tree growth is common, but response usually occurs within 10 years after cutting (Thorpe and Thomas 2007). Partial cutting studies in mixedwood stands indicate that gains in net growth are possible after 10 years if the mortality rate is low (Prévost and Dumais 2013, 2014). However, high variability can also explain the lack of differences between treated plots and uncut controls (Arseneault et al. 2011). In our study, we observed a greater variation in recruitment, growth, and mortality in the patch cutting treatments compared to that for the control over the 10-year period (Figure 2). Recruitment of new stems above 90 mm increased by 3–4 times compared with that for the control. Yet, despite cutting one-third of the basal area from within the matrix, mortality increased by 2–6 times (Table 2) and offset effects of the treatment on 10-year residual tree growth and recruitment in this mixedwood forest type. Our study confirms that as in other partial cutting studies, residual tree mortality is a critical factor that can determine the success or failure of partial harvests (Thorpe and Thomas 2007).

Table 4. Parameters of the tree-level models for the combined central and border plots.

Variable	Parameter	Estimate	<i>P</i> value
Mortality rate	Intercept	-8.1175	<0.001
	Dbh	0.0133	<0.001
	YB	-0.0866	0.807
	RS	0.2520	0.641
	RM	0.6152	0.334
	Healthy versus defect	-1.2192	<0.001
	Treatment	1.0704	<0.001
	Patch matrix versus border	3.2979	0.001
	Crown radius (CRad)	-0.0033	0.204
	Crown ratio (CRat)	0.0566	<0.001
	Dbh × YB	-0.0058	<0.001
	Dbh × RS	-0.0112	<0.001
	Dbh × RM	-0.0058	0.017
	CRad × CRat	-0.0001	<0.001
	BA _t growth (m ² /ha)	Intercept	-5.5599
LnDbh		1.0529	<0.001
CRat		-0.0118	<0.001
YB		2.6874	<0.001
RS		-0.9013	0.106
RM		1.5620	0.045
Treatment		3.2077	<0.001
Patch matrix versus patch border		-0.2990	<0.001
LnCRad		0.5444	<0.001
LnDbh × YB		-0.6050	<0.001
LnDbh × RS		0.1326	0.219
LnDbh × RM		-0.3220	0.030
LnDbh × treatment		-0.5530	<0.001

Mortality rates and BA_t growth based on 5-year periods. See Table 1 for the description of species.

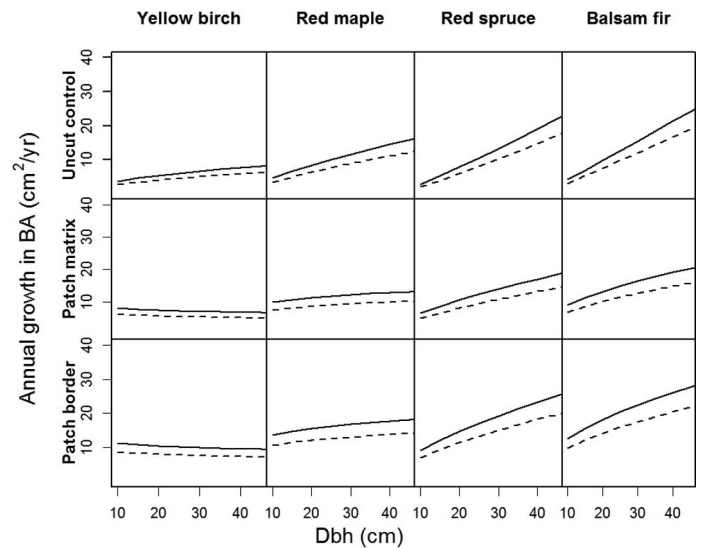


Figure 5. Annual change in stem merchantable BA by species within the central and border plots as a function of dbh, crown ratio, and treatment. Patch border is a specific case of trees located in the between-patch matrix, but adjacent to a gap (edge trees). Solid lines represent 35% crown ratio and dashed lines 55% crown ratio.

Our results shed light on how silvicultural treatments affect species-specific responses within mixed-species stands. Contrary to our expectation, balsam fir did not benefit the most from the partial cutting within the matrix. We found greater balsam fir growth and recruitment than with other species in response to treatments and also higher mortality. This result is common after partial cutting (Hatcher 1960, Fortin et al. 2008, Prévost and Dumais 2013, Martin et al. 2014). Our data show that most balsam fir trees did not

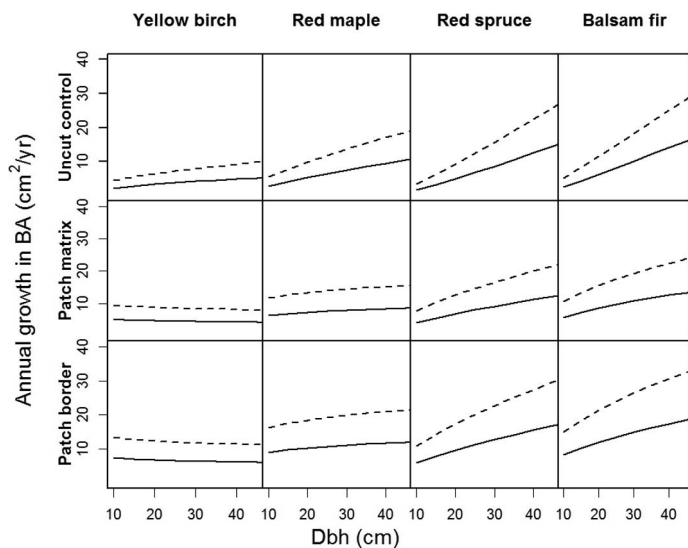


Figure 6. Annual change in stem merchantable BA by species within the central and border plots as a function of dbh, crown radius, and treatment. Patch border is a specific case of trees located in the between-patch matrix, but adjacent to a gap (edge trees). Solid lines represent 150-cm crown radius and dashed lines 350-cm crown radius.

blow down (not shown). Rather, they died standing, possibly due to stress or accelerated senescence. We also observed that long-lived species such as yellow birch and red spruce had more modest increments, but lower mortality rates. Overall, red spruce benefited the most from the enhanced growing conditions with a high basal area increment and a very low mortality rate. Although red spruce usually grows more slowly than balsam fir in early growing stages (Davis 1989, Dumais and Prévost 2014), its greater longevity makes it more persistent in the long-term stand dynamics (Fraver and White 2005). Differences among the species indicate that longer-term study of their dynamics is essential for an accurate modeling of the forest responses within this complex ecosystem.

Tree-Level Response to Patch Cutting

Although crown shape may vary for a given diameter and height in mixedwood stands because of interspecific competition (e.g., Bayer et al. 2013), our tree-level mortality risk model is among the first to rigorously relate mortality risk in mixedwood stands with a complex of factors such as tree longevity, vigor, size, and crown attributes (see Fortin et al. 2008 and Guillemette et al. 2008 for similar results in northern hardwood forests). In our study, trees with narrower crowns had a higher mortality risk than trees with wider crowns, probably because they were located in subordinate crown positions where light is limited and crown expansion is restricted (Gilmore and Seymour 1997). Our results also revealed a positive relationship between the mortality risk and high live crown ratio, which contrasts with the trends reported in the literature (e.g., Monserud and Sterba 1999).

Our work quantifying relationships between tree growth and crown attributes allowed us to assess under field conditions the theoretical “true mixing effects” that Pretzsch (2014) described through intraspecific shifts in size, shape, and inner space filling of crowns. Regardless of species, trees with smaller diameters and possessing narrower crowns (Bechtold 2003) exhibited the greatest growth response to the increased light availability found in the gaps

after harvests (Prévost and Raymond 2012). Most likely, small trees experienced more intense competition before treatment in lower crown positions, whereas those with larger diameter and wider crowns were already in more favorable positions in the upper canopy, which limited their response to treatment (Prévost and Dumais 2013). Similar trends have also been documented after selection cutting in northern hardwood stands, where smaller hardwood trees showed better diameter growth than larger ones (Eyre and Zillgitt 1953, Kiernan et al. 2008, Swift et al. 2012). Nonetheless, conifers with large diameters and wide crowns had the best growth regardless of treatments because they support a large amount of foliage biomass and have consequently a higher photosynthesis production (Landsberg and Sands 2011). Red spruce and balsam fir were the species that increased the most in individual-tree growth, even at large diameters. This suggests that these species possess a high phenotypic plasticity (*sensu* de Kroon et al. 2005). We also found that live crown ratio was inversely correlated to basal area growth. Because the live crown ratio decreases with increasing tree size (results not shown), trees with high crown ratios were typically present in the intermediate and oppressed canopy positions and probably possess lower stem growth rates due to the limited light availability (Maguire et al. 1998, Vanninen and Mäkelä 2000, Dyer et al. 2010). Still, as predicted, increases in annual growth as a function of either the live crown ratio or crown radius were most pronounced for trees along the periphery of the gaps, presumably due to increased light availability and space for tree development (Pedersen and Howard 2004, Dyer et al. 2010). Knowledge about these types of tree interactions within the interspecific environment is highly relevant for further development of individually based growth models in mixed-species stands (Pretzsch 2014).

Implications for Management

Gap-based silvicultural approaches were developed from an ecological perspective, based on the perceived natural dynamics of forested systems (Coates and Burton 1997). Yet, landowners and forest managers must determine how these approaches affect wood production objectives. We conclude that despite a relatively high harvesting intensity in our study, use of systematically located patches combined with partial cutting resulted in a suboptimal harvest of the potential mortality, particularly of balsam fir. However, the poor 10-year gain in net growth in the between-patch matrix raises concerns regarding the application of patch cutting systems in mixed stands comprising an abundant component of short-lived balsam fir. In these uneven-aged yellow birch-conifer stands, mortality occurs at a scale smaller than that of patches. Hence, these mini-clearcuts and the partial cutting could not capture the majority of the potential mortality. Meanwhile, young trees such as yellow birch poles were harvested in haste, whereas they could still contribute to net growth in BA during the next cutting cycle. For these reasons, the patch cutting system does not seem well adapted to such complex uneven-aged mixedwood stands. Yet, we need to monitor longer-term effects, including the contribution of the regenerating patches to the overall stand basal area and wood quality (e.g., epicormic branching) to complete this assessment.

Indeed, more flexible silvicultural systems enabling harvest of most of the potential balsam fir mortality could be more effective in uneven-aged mixedwood stands, particularly if they allow managers to choose gap location at a finer scale. Such silvicultural systems which harvest small groups of trees or single trees (e.g., 100–300 m²) enhance the regeneration of shade-tolerant conifers (Dumais

and Prévost 2014, Prévost and Charette 2015), as has proven challenging with gap sizes (314–1,256 m²) typically used with patch cutting systems (Prévost et al. 2010b, Beaudet et al. 2014). Although gap-based approaches still have importance for managing mixed-species stands and promoting diversity, the systematic creation of gaps, as is done in our patch cutting treatments, decreases flexibility for tree selection to control mortality and best simulate the growth of desired tree species. Moreover, silvicultural systems utilizing variably sized gaps appear more promising for managing complexity and wood production in yellow birch-conifer stands (Kneeshaw and Prévost 2007, Duchesne and Prévost 2012).

Literature Cited

- AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle. P. 267–281 in *Second international symposium on information theory*, Petrov, B.N., and F. Csaki (eds.). Akademiai Kiado, Budapest, Hungary.
- ARBOGAST, C. JR. 1957. *Marking guides for northern hardwoods under the selection system*. USDA For. Serv., Stn. Pap. 56, Lake States Forest Experiment Station, St. Paul, MN. 21 p.
- ARSENAULT, J.E., AND M.R. SAUNDERS. 2012. Incorporating canopy gap-induced growth responses into spatially implicit growth model projections. *Ecol. Model.* 237:120–131.
- ARSENAULT, J.E., M.R. SAUNDERS, R.S. SEYMOUR, AND R.G. WAGNER. 2011. First decadal response to treatment in a disturbance-based silviculture experiment in Maine. *For. Ecol. Manage.* 262:402–412.
- BAYER, D., S. SEIFERT, AND H. PRETZSCH. 2013. Structural crown properties of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in mixed versus pure stands revealed by terrestrial laser scanning. *Trees* 27:1035–1047.
- BEAUDET, M., S. BÉDARD, M.-C. LAMBERT, AND J. HAMEL. 2014. *Effets réels quinquennaux des coupes de jardinage par trouées et des coupes de jardinage par parquets pratiquées de 2000 à 2005 en forêt feuillue et mixte [Five-year results of group and patch selection cutting conducted operationally from 2000 to 2005 in hardwood and mixedwood forests]*. Dir. Rech. For., Mém. Rech. For. no. 172, Gouvernement du Québec, Ministère Ressources naturelles, Québec, QC, Canada. 41 p.
- BECHTOLD, W.A. 2003. Crown-diameter prediction models for 87 species of stand-grown trees in the Eastern United States. *South. J. Appl. For.* 27:269–278.
- BOLKER, B.M., M.E. BROOKS, C.J. CLARK, J.R. POULSEN, M.H.H. SEVENS, AND J.-S.S. WHITE. 2008. Generalized linear mixed models: A practical guide for ecology and evolution. *Trends Ecol. Evol.* 24:127–135.
- BRADSHAW, F.J. 1992. Quantifying edge effect and patch size for multiple-use silviculture—A discussion paper. *For. Ecol. Manage.* 48:249–264.
- BRASSARD, B.W., H.Y.H. CHEN, Y. BERGERON, AND D. PARÉ. 2011. Differences in fine root productivity between mixed- and single-species stands. *Funct. Ecol.* 25:238–246.
- BRISSON, J. 2001. Neighborhood competition and crown asymmetry in *Acer saccharum*. *Can. J. For. Res.* 31:2151–2159.
- CANHAM, C.D., J.S. DENSLOW, W.J. PLATT, J.R. RUNKLE, T.A. SPIES, AND P.S. WHITE. 1990. Light regimes beneath closed canopies and treefall gaps in temperate and tropical forests. *Can. J. For. Res.* 20:620–631.
- COATES, K.D., AND P.J. BURTON. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *For. Ecol. Manage.* 99:337–354.
- DAVIS, W.C. 1989. *The role of released advance growth in the development of spruce-fir stands in eastern Maine*, PhD Dissertation, Yale Univ., New Haven, CT. 104 p.
- DE KROON, H., H. HUBER, J.F. STUEFER, AND J.M. VAN GROENENDAEL. 2005. A modular concept of phenotypic plasticity in plants. *New Phytol.* 166:73–82.
- DIELER, J., AND H. PRETZSCH. 2013. Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-species stands. *For. Ecol. Manage.* 295:97–108.
- DUAN, N. 1983. Smearing estimate: A nonparametric retransformation method. *J. Am. Stat. Ass.* 78(383):605–610.
- DUCHESNE, L., AND M. PRÉVOST. 2012. Canopy disturbance and intertree competition: Implications for tree growth and recruitment in two yellow birch-conifer stands in Quebec, Canada. *J. For. Res.* 18(2):168–178.
- DUMAIS, D., AND M. PRÉVOST. 2014. Physiology and growth of advance *Picea rubens* and *Abies balsamea* regeneration following different canopy openings. *Tree Physiol.* 34:194–204.
- DYER, J.H., S.T. GOWER, J.A. FORRESTER, C.G. LORIMER, D.J. MLADENOFF, AND J.I. BURTON. 2010. Effects of selective tree harvests on aboveground biomass and net primary productivity of a second growth northern hardwood forest. *Can. J. For. Res.* 40:2360–2369.
- EYRE, F.H., AND W.M. ZILLGITT. 1953. *Partial cuttings in northern hardwoods of the Lake States: Twenty-year experimental results*. USDA For. Serv., Tech. Bull. LS-1076, Lake States Forest Experiment Station, St. Paul, MN. 124 p.
- FORRESTER, D.I. 2013. The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. *For. Ecol. Manage.* 213:282–292.
- FORTIN, M., S. BÉDARD, J. DEBLOIS, AND S. MEUNIER. 2008. Predicting individual tree mortality in northern hardwood stands under uneven-aged management in southern Québec, Canada. *Ann. For. Sci.* 65(2):205.
- FRAVER, S., AND A.S. WHITE. 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *J. Veg. Sci.* 16:597–610.
- GETZIN, S., AND K. WEIGAND. 2007. Asymmetric tree growth at the stand level: Random crown patterns and the response to slope. *For. Ecol. Manage.* 242:165–174.
- GILMORE, D.W., AND R.S. SEYMOUR. 1997. Crown architecture of *Abies balsamea* from four canopy positions. *Tree Physiol.* 17:71–80.
- GUILLETTE, F., S. BÉDARD, AND M. FORTIN. 2008. Evaluation of a tree classification system in relation to mortality risk in Québec northern hardwoods. *For. Chron.* 84(6):886–899.
- HATCHER, R.J. 1960. *Mortality and regeneration following partial cutting at Lake Edward, P.Q. Canada*, Department of Forest, Forest Research Division, Government of Canada, Ottawa, ON, Canada. 21 p.
- HOSMER D.W. JR., AND S. LEMESHOW. 2000. *Applied logistic regression*, 2nd ed. John Wiley & Sons, New York. 375 p.
- KIERNAN, D.H., E. BEVILACQUA, AND R.D. NYLAND. 2008. Individual-tree diameter growth model for sugar maple trees in uneven-aged northern hardwood stands under selection system. *For. Ecol. Manage.* 256:1579–1586.
- KLEINBAUM, D.G., L.L. KLUPPER, K.E. MULLER, AND A. NIZAM. 1998. *Applied regression analysis and other multivariable methods*. Duxbury Press, Pacific Grove, CA. 798 p.
- KNEESHAW, D.D., AND M. PRÉVOST. 2007. Natural canopy gap disturbances and their role in maintaining mixed-species forests of central Quebec, Canada. *Can. J. For. Res.* 37:1534–1544.
- LANDSBERG, J., AND P. SANDS. 2011. *Physiological ecology of forest production: Principles, processes and models*. Academic Press, San Diego, CA. 352 p.
- LEAK, W.B., AND S.M. FILIP. 1977. Thirty-eight years of group selection in New England northern hardwoods. *J. For.* 75:641–643.
- LEAK, W.B., D.S. SOLOMON, AND P.S. DEBALD. 1987. *Silvicultural guide for Northern hardwood types in the Northeast (revised)*. USDA For. Serv., Res. Pap. NE-603, Northeastern Forest Experiment Station, Broomall, PA. 35 p.
- LITTELL, R.C., G.A. MILLIKEN, W.W. STROUP, R.D. WOLFINGER, AND O. SCHABENBERGER. 2006. *SAS for mixed models*, 2nd ed. SAS Institute, Inc., Cary, NC. 840 p.

- LUSSIER, J.-M., R. GAGNÉ, AND G. BÉLANGER. 2000. Analyse dendroécologique des bétulaies jaunes à sapin de la région de Portneuf: Résultats préliminaires [Dendrochronological analysis of balsam fir-yellow birch stands in the Portneuf region: Preliminary results]. P. 24–30 in *2^e Atelier SSAM: de la recherche à la pratique* (Conference proceedings), Sainte-Catherine-de-la-Jacques-Cartier, QC, Canada.
- MAGUIRE, D.A., J.C. BRISSETTE, AND L. GU. 1998. Crown structure and growth efficiency of red spruce in uneven-aged, mixed-species stands in Maine. *Can. J. For. Res.* 28:1233–1240.
- MAJCNEN, Z., Y. RICHARD, M. MÉNARD, AND Y. GRENIER. 1990. *Choix des tiges à marquer pour le jardinage d'érablières inéquiennes* [Choice of trees to mark for selection cutting in uneven-aged sugar maple stands]. Dir. Rech. Dév. Mém. no. 96, Gouvernement du Québec, Ministère Énergie et des Ressources (Forêts), Québec, QC, Canada. 96 p.
- MAN, R., AND V.J. LIEFFERS. 1999. Are mixtures of aspen and white spruce more productive than single species stands? *For. Chron.* 75(3):505–513.
- MARTIN, A., J.P. CASPERSEN, M.M. FULLER, T.A. JONES, AND S.C. THOMAS. 2014. Temporal dynamics and causes of postharvest mortality in a selection-managed tolerant hardwood forest. *For. Ecol. Manage.* 314:183–192.
- MONSERUD, R.A., AND H. STERBA. 1999. Modeling individual tree mortality for Austrian forest species. *For. Ecol. Manage.* 113(2):109–123.
- MINISTÈRE DES RESSOURCES NATURELLES, DE LA FAUNE ET DES PARCS. 2003. *Manuel d'aménagement forestier* [Forest management manual], 4th ed. Quebec City, QC, Canada. 245 p. Available online at www.mffp.gouv.qc.ca/publications/forets/amenagement/manuel.pdf; last accessed Feb. 12, 2015.
- MUTH, C.C., AND F.A. BAZZAZ. 2002. Tree canopy displacement at forest gap edges. *Can. J. For. Res.* 32:247–254.
- NYLAND, R.D. 2002. *Silviculture: Concepts and application*, 2nd ed. McGraw-Hill, New York. 682 p.
- PEDERSEN, B.S., AND J.L. HOWARD. 2004. The influence of canopy gaps on overstory tree and forest growth rates in a mature mixed-age, mixed-species forest. *For. Ecol. Manage.* 196:351–366.
- PIN, D., G. LESSARD, AND F. GUILLEMETTE. 2013. Les coupes de jardinage avec cohortes juxtaposées [Selection cutting systems with juxtaposed cohorts]. P. 604–627 in *Le guide sylvicole du Québec, Tome 2: Les concepts et l'application de la sylviculture*, Larouche, C., F. Guillemette, P. Raymond, and J.-P. Saucier (eds.). Ministère des Ressources naturelles Les Publications du Québec, Quebec City, QC, Canada.
- PRETZSCH, H. 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For. Ecol. Manage.* 327:251–264.
- PRÉVOST, M., AND L. CHARENTE. 2015. Selection cutting in a yellow birch-conifer stand, in Quebec, Canada: Comparing the single-tree and two hybrid methods using different sizes of canopy opening. *For. Ecol. Manage.* 357:195–205.
- PRÉVOST, M., AND D. DUMAIS. 2013. Decennial growth and mortality following uniform partial cutting in yellow birch-conifer stands. *Can. J. For. Res.* 43:224–233.
- PRÉVOST, M., AND D. DUMAIS. 2014. Shelterwood cutting in a boreal mixed-wood stand: 10-year effects of the establishment cut on growth and mortality of merchantable residual trees. *For. Ecol. Manage.* 330:94–104.
- PRÉVOST, M., D. DUMAIS, AND D. POTHIER. 2010a. Growth and mortality following partial cutting in a trembling aspen-conifer stand: Results after 10 years. *Can. J. For. Res.* 40:894–903.
- PRÉVOST, M., AND P. RAYMOND. 2012. Effect of gap size, aspect and slope on available light and soil temperature after patch-selection cutting in yellow birch-conifer stands, Quebec, Canada. *For. Ecol. Manage.* 274:210–221.
- PRÉVOST, M., P. RAYMOND, AND J.-M. LUSSIER. 2010b. Regeneration dynamics after patch cutting and scarification in yellow birch-conifer stands. *Can. J. For. Res.* 40:357–369.
- RAYMOND, P., A.D. MUNSON, J.-C. RUEL, AND K.D. COATES. 2006. Spatial patterns of soil microclimate, light, regeneration, and growth within silvicultural gaps of mixed tolerant hardwood-white pine stands. *Can. J. For. Res.* 36:639–651.
- RÉGNÈRE, J., AND P. BOLSTAD. 1994. Statistical simulation of daily air temperature patterns in eastern North America to forecast seasonal events in insect pest management. *Environ. Entomol.* 23:1368–1380.
- REY-LESCURE, E. 1982. Distribution des gourmands sur les fûts de 25 essences en bordure de déboisement [Distribution of epicormic sprouts on the stems of 25 species located at the edge of cutovers]. *Can. J. For. Res.* 12:687–698.
- ROBITAILLE, A., AND J.-P. SAUCIER. 1998. *Paysages régionaux du Québec méridional* [Regional landscapes of meridional Québec]. Les Publications du Québec, Sainte-Foy, QC, Canada. 213 p.
- SAS INSTITUTE, INC. 2011. *The Glimmix procedure in SAS/STAT 9.3 user's guide*. Available online at support.sas.com/documentation/cdl/en/statug/63962/HTML/default/viewer.htm#glimmix_toc.htm; last accessed Jan. 14, 2014.
- SAUCIER, J.-P., P. GRONDIN, A. ROBITAILLE, J. GOSSELIN, C. MORNEAU, P.J.H. RICHARD, J. BRISSON, ET AL. 2009. Écologie forestière [Forest ecology]. P. 165–316 in *Manuel de foresterie*, 2nd ed., Ordre des ingénieurs forestiers du Québec (ed.). Éditions Multimondes, Quebec City, QC, Canada.
- SAUNDERS, M.R., AND J.E. ARSENEAULT. 2013. Potential yields and economic returns of natural disturbance-based silviculture: A case study from the Acadian Forest Ecosystem Research Program. *J. For.* 111(3):175–185.
- SEYMOUR, R.S., AND L.S. KENEFIC. 1998. Balance and sustainability in multi-aged stands: A northern conifer case study. *J. For.* 96(7):12–17.
- STAN, A.B., AND L.D. DANIELS. 2014. Growth releases across a natural canopy gap-forest gradient in old-growth forests. *For. Ecol. Manage.* 313:98–103.
- SWIFT, D.E., D.H. KIERNAN, E. BEVILACQUA, AND R.D. NYLAND. 2012. Predicting future diameter of sugar maple in uneven-aged stands of west-central New Brunswick and New York. *For. Chron.* 88:420–425.
- THORPE, H.C., R. ASTRUP, A. TROWBRIDGE, AND K.D. COATES. 2010. Competition and tree crowns: A neighbourhood analysis of three boreal tree species. *For. Ecol. Manage.* 259:1586–1596.
- THORPE, H.C., AND S.C. THOMAS. 2007. Partial harvesting in the Canadian boreal: Success will depend on stand dynamic responses. *For. Chron.* 83:319–325.
- TRIMBLE, G.R. JR., AND D.W. SEEGRIST. 1973. *Epicormic branching on hardwood trees bordering forest openings*. USDA For. Serv., Res. Pap. NE-154, Northeastern Forest Experiment Station, Upper Darby, PA. 6 p.
- VANNINEN, P., AND A. MÄKELÄ. 2000. Needle and stem wood production in Scots pine (*Pinus sylvestris*) trees of different age, size and competitive status. *Tree Physiol.* 20:527–533.
- VEPAKOMMA, U., B. ST-ONGE, AND D. KNEESHAW. 2011. Response of a boreal forest to canopy opening: Assessing vertical and lateral tree growth with multi-temporal lidar data. *Ecol. Appl.* 21(1):99–121.
- WASKIEWICZ, J., L. KENEFIC, A. WEISKITTEL, AND R. SEYMOUR. 2013. Species mixture effects in northern red oak-eastern white pine stands in Maine, USA. *For. Ecol. Manage.* 298:71–81.
- WEBSTER, C.R., AND C.G. LORIMER. 2002. Single-tree versus group selection in hemlock-hardwood forests: Are smaller openings less productive? *Can. J. For. Res.* 32:591–604.
- WHITE, G.C., AND R.E. BENNETTS. 1996. Analysis of frequency count data using negative binomial distribution. *Ecology* 77(8):2549–2557.
- WILLIS, J.L., M.B. WALTERS, AND K.W. GOTTSCHALK. 2015. Scarification and gap size have interacting effects on northern temperate seedling establishment. *For. Ecol. Manage.* 347:237–246.