Precommercial thinning of overtopping aspen to release coniferous regeneration in a boreal mixedwood stand

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ABSTRACT

We used precommercial thinning (PCT) to accelerate natural succession in an 8-year-old, even-aged stratified mixture, in which trembling aspen (*Populus tremuloides*) overtopped a dense understory of balsam fir (*Abies balsamea*) and spruce (*Picea mariana*, *P. glauca*). In addition to an unthinned control, we applied three residual aspen spacings (2.5, 3.0 and 3.5 m) while retaining all understory conifers, and a 3.0-m spacing retaining only small conifers (<1/3 of the aspen crop tree height). PCT improved survival of spruce, increased diameter growth of aspen by 90% and doubled diameter and height growth of conifers, without differences among spacings or between levels of conifer retention after 10 years. The level of conifer retention did not affect aspen growth response, but appeared to influence the occurrence of browsing on aspen and balsam fir. Retaining only small conifers decreased regeneration density of balsam fir in favour of abundant vegetative reproduction of red maple (*Acer rubrum*) and beaked hazelnut (*Corylus cornuta*). Live crown characteristics and stand structure indicate that thinning caused a shift from overtopping of aspen to an intimate mixture of species sharing the growing space. This study confirms PCT as a means of accelerating natural succession in a boreal mixedwood stand, thereby securing the coniferous component at the early stage of development.

Key words: ecosystem-based forest management; hardwood conversion; stratified species mixture; precommercial thinning; live crown characteristics.

RÉSUMÉ

Nous avons utilisé l'éclaircie précommerciale (EPC) afin d'accélérer la succession naturelle dans un mélange équié stratifié de 8 ans, dans lequel le peuplier faux-tremble (*Populus tremuloides*) surplombait une dense régénération de sapin baumier (*Abies balsamea*) et d'épinette (*Picea mariana*, *P. glauca*). En plus d'un témoin non éclairci, nous avons appliqué trois espacements résiduels entre les trembles (2,5, 3,0 et 3,5 m) en conservant tous les conifères du sous-étage, et un espacement de 3,0 m en conservant seulement les petits conifères (<1/3 de la hauteur du tremble éclairci). L'EPC a amélioré la survie de l'épinette, augmenté la croissance en diamètre du tremble de 90% et doublé la croissance en diamètre et en hauteur des conifères, sans différences entre les espacements ou entre les niveaux de rétention des conifères après 10 ans. Le niveau de rétention des conifères n'a pas affecté la réponse de croissance du tremble, mais a semblé influencer la fréquence du broutement sur le tremble et le sapin. La rétention des petits conifères seulement a diminué la densité de la régénération de sapin au profit d'une abondante reproduction végétative d'érable rouge (*Acer rubrum*) et de noisetier à long bec (*Corylus cornuta*). Les caractéristiques des cimes vivantes et la structure du peuplement indiquent que l'éclaircie a amené le peuplement à passer d'une dominance du tremble à un mélange intime d'espèces se partageant l'espace de croissance. Cette étude confirme que l'EPC est un moyen d'accélérer la succession naturelle dans un peuplement mixte boréal, en assurant le maintien de la composante résineuse dès le stade initial.

Mots-clés: aménagement écosystémique; enfeuillement; mélange stratifié d'espèces; éclaircie précommerciale; caractéristiques des cimes vivantes.

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Introduction

Precommercial thinning (PCT) is used in young forest stands to redistribute growing space to a reduced number of residual trees (Smith *et al.* 1997). These crop trees benefit from increased light (Pothier and Margolis 1991, Prévost and Gauthier 2012), water and nutrients (Thibodeau *et al.* 2000), while the felled trees are left to decay on the ground and contribute to nutrient cycling (e.g., Sterba 1988). Moreover, PCT may have beneficial effects on soil fertility through increases in soil temperature, decomposition rates, and nitrogen pools over the short-term (Thibodeau *et al.* 2000). Several studies have shown that PCT is effective in reducing stand density, increasing the growth rate of selected trees, adjusting species composition, and improving overall stand quality from the earliest stages of development (e.g., Brissette *et al.* 1999).

Historically, PCT was practiced to avoid stagnation in dense pure stands originating from natural or artificial seeding (Smith *et al.* 1997). Several PCT experiments were therefore conducted in pure or nearly pure (ca. $\geq 75\%$ basal area, BA) stands (e.g., Karsh *et al.* 1994), in mixtures with conifers (Brissette *et al.* 1999, Weiskittel *et al.* 2009) or hardwoods (Voorhis 1990, Nicholson *et al.* 2010). Generally, both conifer and hardwood species benefit from increased resource availability with gains in diameter at breast height (DBH) that increase with spacing. For the two species groups however, high branch retention on the lower bole (Weiskittel *et al.* 2009, Nicholson *et al.* 2010), and low wood density and lumber strength (Zhang *et al.* 2006) may result from wide spacing. Consequently, the trade-off between diameter gain and subsequent quality of the wood products is an important consideration when choosing an intensity of PCT (Nicholson *et al.* 2010).

In the Canadian boreal forest, PCT increased DBH growth of balsam fir (*Abies balsamea* (L.) Mill.) (Pothier 2002, Pitt and Lanteigne 2008, Zhang *et al.* 2009), red spruce (*Picea rubens* Sarg.) (Pitt and Lanteigne 2008), and to a lesser extent jack pine (*Pinus banksiana* Lamb.) (Zhang *et al.* 2006). The effects observed on black spruce (*Picea mariana* (Mill.) B.S.P.) were weak or even negligible in some experiments (e.g., McClain *et al.* 1994, Fleming *et al.* 2005), but good growth responses have been obtained on productive sites (Karsh *et al.* 1994, Newton and Weetman 1994). Experiments conducted in the eastern United States and Canada also have reported significant DBH growth increases to PCT for northern hardwoods including paper birch (*Betula papyrifera* Marsh.) and red maple (*Acer rubrum* L.) (Voorhis 1990, Nicholson *et al.* 2010, Leak and Yamasaki 2012, Swift *et al.* 2017). For trembling aspen (*Populus tremuloides* Michx.), the literature on PCT is rather equivocal, with either increases in individual tree DBH (e.g., Rice *et al.* 2001) or no response (e.g., Penner *et al.* 2001). As a result, the implementation of PCT in aspen stands is still under debate, given that this shade-intolerant species readily regenerates through root suckering and self-thins (Perala 1990).

In the Canadian boreal mixedwood forest, a dense aspen cover of sucker origin often overtops an understory of balsam fir and spruce (*Picea glauca* (Moench) Voss, *P. mariana*), which survived as advance growth or became established post-harvest. The widespread presence of aspen on the land-

scape and the increasing protection of conifer advance growth in current management practices (Groot *et al.* 2005) should favour development of this type of even-aged stratified mixture along successional pathways (Smith *et al.* 1997). In such stands, PCT has traditionally prioritized conifers over early successional broadleaved species (e.g., Pitt and Bell 2005), whereas growing species in mixtures has received little attention so far (e.g., Bokalo *et al.* 2007, Kabzems *et al.* 2016). For example, Rice *et al.* (2001) suggested that PCT be considered as a means of increasing aspen diameter and allowing conifer ingress to be established within the resultant openings. A more recent PCT experiment (Prévost and Gauthier 2012) tested different spacings of aspen, while preserving sparse balsam fir regeneration. This experiment yielded promising results, as PCT increased growth of both the residual aspen and the understory fir. This response prompted the initiation of the present study in a typical stratified mixture that contained a denser understory of both fir and spruce. This allowed us to assess post-thinning development of an intimate species mixture.

In addition to maintaining the conifer fraction in order to prevent hardwood conversion (Prévost and Gauthier 2012), favouring species mixtures may present some advantages over pure stands. For instance, spatial complementarity among tree crowns may allow better exploitation of light and other resources (Williams *et al.* 2017). In the case of aspen and white spruce in the boreal mixedwood forest, Man and Lieffers (1999) concluded that these species may avoid competition and produce greater yields in mixture because of the physical separation of their canopies, and their differential shade-tolerance, phenology and soil resource utilization. Aspen could even positively affect spruce growth by enhancing litter decomposition and nutrient cycling (Van Cleve *et al.* 1983). Among other possible advantages of species mixtures are increased resilience against insect and disease outbreaks (Su *et al.* 1996) and a greater diversity of forest products (MacDonald 1995).

This study presents the results of a PCT experiment that was aimed at accelerating natural succession in a stratified mixture, in which aspen overtopped a dense understory of fir and spruce. The principal objective was to define a spacing that would be beneficial to both aspen crop trees and released understory conifers. A secondary objective was to assess two different levels of advance growth protection: (1) retaining conifers of all heights; and, (2) retaining only small conifers, i.e., $< 1/3$ the height of the aspen crop tree within a 2-m inter-tree radius, which is the operational standard in Quebec. We present the 10-year effects of PCT on DBH, height, BA and crown characteristics of aspen crop trees and understory conifers. We hypothesized that (i) aspen DBH growth would be proportional to spacing (Rice *et al.* 2001), (ii) conifers will be released and their DBH and height growth would be proportional to aspen spacing, (iii) the level of conifer advance growth retention would not affect growth of aspen in the overstory, (iv) PCT in overstory aspen would be more beneficial to balsam fir than to spruce (Prévost *et al.* 2016), and (v) PCT would affect natural ingress of fir and spruce after treatment (Prévost and Gauthier 2012).

Material and Methods

Site description

The study site was located in the balsam fir – yellow birch bioclimatic domain (region 4d), in the High Hills of Charlevoix and Saguenay (Saucier *et al.* 2009), about 160 km northeast of Québec City, Quebec, Canada (47° 55' N, 70° 04' W). Mean daily maximum temperature (1981–2010, Petit-Saguenay station) is recorded in July (23.5 °C) and minimum temperature is recorded in January (–18.8 °C), with a mean annual temperature of 3.1 °C. The region annually receives 1041 mm of precipitation on average, with 31% falling as snow (MDDELCC 2016).

The previous stand was clearcut in 1997 before the growing season (based on annual rings), with protection of the conifer advance regeneration, and regenerated naturally. For all saplings ≥ 1 cm DBH, stand density was 31 400 stems/ha, with 78% commercial species including aspen (44%), red maple (18%), balsam fir (9%), paper birch (6%) and spruce ($\sim 2/3$ *P. mariana* and $\sim 1/3$ *P. glauca*) (1%). The stand was at an early stage of the even-aged stratified mixture as described by Smith *et al.* (1997), in which aspen was 4–6 m and conifers were 2–3 m in height. Noncommercial species (22%) included mountain maple (*Acer spicatum* Lamb.) (9%), beaked hazelnut (*Corylus cornuta* Marsh.) (6%), striped maple (*Acer pensylvanicum* L.) (3%) and other species (willow (*Salix* spp.) and pin cherry (*Prunus pensylvanica* L. f.), 4%). The soil was a sandy loam with a mesic drainage on a less than 10% northwest-facing slope.

Experimental design

The experiment consisted of four complete randomized blocks, each one containing five treatments: an unthinned control (CON); three targeted residual aspen spacings (2.5, 3.0 and 3.5 m) retaining coniferous regeneration of all sizes (referred to as 2.5A, 3.0A and 3.5A); and a 3.0-m spacing retaining only small coniferous regeneration (3.0S), i.e., felling all advance growth $\geq 1/3$ of the aspen crop tree height within a 2-m radius. Treatments of each block were contiguous and distributed across the slope, using slope position as blocking factor. Each experimental unit measured 50 m $\times$ 50 m (0.25 ha) and contained a 20 m $\times$ 20 m centre plot (400 m²) from which precise measurements were taken. In each 400-m² plot, sixteen 4-m² subplots (2 m $\times$ 2 m) were installed in a systematic grid pattern to measure regeneration.

PCT was carried out in late September 2004 at the end of the 8th growing season after the clearcut. Aspen stems that were retained were marked prior to treatment according to the targeted spacing and their overall quality. These latter criteria included tree height and diameter, and the absence of injury, infection or insect damage. To avoid selection of poor quality stems, spacing was lowered by 1 m of the targeted spacing (i.e., 1.5 m instead of 2.5 m). All other stems, except for the conifers that were retained, were felled using spacing saws. Cut stems were left to decay on the ground, while preventing their physical contact with crop trees to avoid injuries to the live individuals.

Vegetation monitoring

In August 2004 and prior to thinning, all saplings (≥ 1.3 m in height) located in each 400-m² plot were tallied by species and

DBH class (1, 2, 4, 6, 8 and 10 cm). This inventory was used to estimate the initial stem density at stand-level. After thinning, all residual saplings in each plot were tagged in October and November 2004. Species, DBH, total height, crown height and four crown radii (N, E, S and W) were then recorded as year 0 measurements. In the unthinned control, saplings were tagged and measured in the 4-m² subplots only. At post-treatment years 1–5, 7 and 10 (2005–2009, 2011 and 2014), DBH and total height of all tagged stems were measured, whereas crown height and crown radii were measured only at years 5 and 10. Presence of mechanical injuries, infections or insect damage, together with traces of browsing by moose (*Alces alces*) or snowshoe hare (*Lepus americanus*), were recorded across all measurement years. Finally, all commercial species and major noncommercial species were counted by height class (1–5, 6–30, 31–60, 61–100, 101–200, 201–300 and >300 cm) in the regeneration subplots at years 1–3, 5, 7 and 10 post-thinning.

Statistical analyses

DBH, height and BA measured at years 0–5, 7 and 10 after PCT, and live crown characteristics measured at years 0, 5 and 10, were analyzed by species for aspen, fir and spruce (pooled white and black spruces). Regeneration density measured at post-thinning years 1–3, 5, 7 and 10, was also analyzed separately by species (aspen, paper birch, red maple, spruce, fir, mountain maple, striped maple, beaked hazelnut and pin cherry). Linear mixed models with repeated measurements were used, with a variance-covariance matrix to take into account the correlation between measurements that were performed on the same experimental units. The choice of this matrix was made using goodness-of-fit and parsimony criteria, while taking into account the unequal time intervals and maintaining consistency among the set of analyses. PCT treatments, measurement years and their interaction were introduced into the model as fixed-effect factors, whereas blocks and experimental units were considered as random effects. For DBH, height, BA, crown characteristics and regeneration density of each species, the pre-thinning (2004) density of saplings ≥ 1.3 m in height was tested as a covariate. It was included in the model when significant, in which case the equal slopes hypothesis was tested (non-significant interaction of covariate and fixed effects when the covariate is in the model). Data for decennial mortality and occurrence of browsing were analyzed separately for each commercial species and expressed in % (100 $\times$ number of stems that died or were browsed from years 1–10 / number of stems at year 0).

A priori specific contrasts of treatments were tested as follows: *i*) PCT retaining all coniferous regeneration (mean of 2.5A, 3.0A and 3.5A) vs. the unthinned control; *ii*) PCT retaining small coniferous regeneration (3.0S) vs. the control; *iii*) pairwise among the three PCT retaining all coniferous regeneration (2.5A vs. 3.0A, 2.5A vs. 3.5A and 3.0A vs. 3.5A); and *iv*) PCT retaining all vs. small coniferous regeneration (3.0A vs. 3.0S). The first two contrasts were tested along with a one-sided alternative in favour of PCT treatments for DBH and height, and in favour of the control for BA. The third contrast was also a one-sided alternative in favour of the wider spacing for DBH and height, and two-sided for BA. The

fourth contrast was two-sided for all variables. For tree mortality, browsing, live crown characteristics and regeneration density, all tests were two-sided. Orthogonal polynomial decomposition of the time effect (linear, quadratic and cubic) was performed, taking into account the unequal time intervals by using the ORPOL function of the IML SAS procedure (v. 9.4, SAS Institute Inc., Cary, NC). For significant interactions between main factors, contrasts were compared at years 0, 5 and 10 for DBH, height, BA and crown characteristics, whereas the time effect was decomposed for every PCT treatment. For regeneration density, the same contrasts were compared at years 1, 5 and 10, but time intervals for years 1–2, 2–3, 3–5, 5–7, 7–10, 1–5 and 5–10 were tested for every treatment, in order to detect pulses in recruitment or mortality. Homogeneity of variances and normality were assessed on scaled residuals using standard graphical methods, together with the Brown and Forsythe's test (homogeneity) and the Shapiro-Wilk's test (normality). When required, data were transformed ($\sqrt{x}$) to improve homogeneity of variance, although they are presented in their original form in the Results section. The level of significance was 0.05 for all analyses and tests.

Analyses were performed using the MIXED procedure of SAS for DBH, height, BA, live crown characteristics and regeneration density, and the GLIMMIX procedure for mortality and browsing, using the logit-link function. The Kenward-Roger approximation was used to estimate the denominator degrees of freedom in the ANOVA models. A simulation-based approach was used to assess differences while considering tests multiplicity in all cases where a factor or an interaction was significant. In the case of interactions,

the 0.05 error rate was applied within each fixed level of the main factors, as a separate-family approach (Westfall *et al.* 2011). The approach of Braat *et al.* (2008) was used to transform all tests to their one-sided form to deal with the simultaneous application of one-sided and two-sided tests. A limitation of this framework is that in the case of two-sided tests, adjusted confidence intervals are used to assess significance rather than the usual adjusted *p*-values.

Results

Ten-year tree mortality and browsing

After 10 years, tree mortality was related to PCT for trembling aspen ($p < 0.001$, not presented) and spruce ($p = 0.017$). Aspen mortality was higher in the unthinned CON (52%) than in every PCT treatment (4–7%, $p \leq 0.004$). Similarly, spruce mortality was higher in the CON (24%) than in PCT treatments that retained all conifers (2.5A, 3.0A and 3.5A: 3–4%, $p = 0.010$), and appeared to be higher than in the PCT treatment that retained only small conifers (3.0S: 0% mortality, therefore excluded from the test). PCT tended to affect browsing on balsam fir ($p = 0.060$) and aspen ($p = 0.095$) by lowering the mean occurrence on fir in treatments 2.5A, 3.0A and 3.5A (3% vs. 11% in the CON, $p = 0.057$) and increasing the occurrence on aspen in the treatment 3.0S (19% vs. 3% in the unthinned CON, $p = 0.093$).

Growth

DBH, height and BA

An interaction of PCT with time (PCT $\times$ T) was found in DBH of trembling aspen, balsam fir and spruce (all $p < 0.001$, Table 1; Fig. 1). For each species, the DBH was comparable

Table 1. Analysis of variance and probabilities ($P > F$) for trembling aspen, balsam fir and spruce DBH, height and BA measured 0, 1, 2, 3, 4, 5, 7 and 10 years after PCT and crown characteristics measured 0, 5 and 10 years after PCT: unthinned control, 2.5-, 3.0- and 3.5-m aspen spacings protecting all understory conifers and a 3.0-m spacing protecting only small understory conifers (<1/3 of the retained aspen height).

Source of variation	df	DBH	Height	BA	df	Crown width	Crown length	Bole length	Live crown ratio
Trembling aspen									
PCT	4	0.005	0.417	0.042	4	<0.001	0.010	0.379	<0.001
Time (T)	7	<0.001	<0.001	<0.001	2	<0.001	<0.001	<0.001	<0.001
PCT $\times$ T	28	<0.001	0.469	0.059	8	0.004	<0.001	0.044	<0.001
Covariate	1	<0.001	<0.001	0.001	1	–	0.029	<0.001	–
Balsam fir									
PCT	4	0.311	0.485	0.008	4	0.001	0.391	0.126	0.409
Time (T)	7	<0.001	<0.001	<0.001	2	<0.001	<0.001	<0.001	0.003
PCT $\times$ T	28	<0.001	<0.001	0.010	8	0.560	<0.001	0.332	<0.001
Covariate	1	–	–	0.002	1	–	–	–	–
Spruce									
PCT	4	0.362	0.590	0.533	4	0.182	0.284	0.169	0.538
Time (T)	7	<0.001	<0.001	<0.001	2	<0.001	<0.001	<0.001	0.001
PCT $\times$ T	28	<0.001	<0.001	0.785	8	0.040	<0.001	0.008	<0.001
Covariate	1	–	–	0.015	1	–	–	–	–

Note: The variance-covariance matrix was spatial power for all variables and species, except for crown width of aspen and fir (variance components). *df* = degrees of freedom of the numerator. Denominator degrees of freedom, according to Kenward-Roger: PCT = 6.5 to 42.0, T = 12.1 to 105.0, PCT $\times$ T = 18.8 to 105.0, Covariate = 3.0 to 14.1. Significant *p*-values are presented in **boldface type**. A dash indicates that the covariate was not significant and was removed from the model.

Fig. 1. DBH and total height related to species and PCT treatment: unthinned control, 2.5-, 3.0- and 3.5-m aspen spacings protecting all understory conifers (respectively 2.5A, 3.0A and 3.5A), and a 3.0-m spacing protecting only small understory conifers (3.0S), at years 0–5, 7 and 10 post-thinning.

among treatments immediately post-thinning (year 0). However, the DBH was higher in treatments 2.5A, 3.0A and 3.5A (5.9–6.4 cm), and 3.0S (6.5 cm) than in the CON (4.9 cm) at years 5 and 10 (respectively 7.9–8.8, 9.0 and 6.1 cm) for aspen ($p \leq 0.002$), and at year 10 for fir (all 6.1, 6.4 and 3.7 cm, $p \leq 0.016$) and spruce (5.7–8.0, 6.7 and 3.6 cm, $p \leq 0.036$). The time effect was a linear increase in aspen DBH, with growth rates of 0.41–0.51 cm/year in PCT treatments and 0.24 cm/year in the CON. For the two conifers, the decennial DBH increase was also linear in the CON (both 0.19 cm/year). In PCT treatments, cubic (sigmoidal) time effects were related to variations in growth rates that resulted in mean increases of 0.34–0.46 cm/year for fir and 0.32–0.51 cm/year for spruce.

A significant PCT $\times$ T interaction was found in height of fir and spruce, while only a time effect was found in height of aspen (all $p < 0.001$, Table 1; Fig. 1). The height of each conifer was comparable among treatments at years 0 and 5. Both species were taller in treatments 2.5A, 3.0A and 3.5A (fir: 527–543 cm, spruce: 513–592 cm), and 3.0S (respectively 523 and 526 cm) than in the CON (361 and 365 cm) at year 10 ($p \leq 0.048$). Cubic time effects following thinning (all $p < 0.001$) resulted in mean increases of 28–31 cm/year for fir and 27–33 cm/year for spruce. For aspen, a quadratic time effect was related to an increasing growth rate over time. PCT did not affect aspen height growth.

An interaction was also found in BA of balsam fir ($p = 0.010$, Table 1; data not shown). Balsam fir BA was not

statistically different between 3.0A (2.8 m²/ha) and 3.0S (0.6 m²/ha) at year 0, but was higher in 3.0A than in 3.0S at both years 5 (6.2 vs. 2.0 m²/ha) and 10 (10.3 vs. 3.8 m²/ha), due to the magnitude of their linear increase (0.75 vs. 0.31 m²/ha/year, both $p < 0.001$). Single effects of PCT ($p = 0.042$) and time ($p < 0.001$) were found in BA of aspen. As a whole, aspen BA was significantly lower in all PCT treatments compared to the CON. For instance, BA was 1.2–1.9 vs. 10.2 m²/ha at year 0, 2.9–4.5 vs. 17.2 m²/ha at year 5 and 5.5–8.1 vs. 23.7 m²/ha at year 10, with a linear increase ($p < 0.001$) of 0.43–0.62 m²/ha/year in PCT treatments and 1.35 m²/ha/year in the CON. Only a time effect was found in BA of spruce, with an overall increase of 0.11 m²/ha/year.

Live crown characteristics

PCT and time interacted in the responses for crown length and live crown ratio of the three species, and for crown width and bole length of aspen and spruce ($p \leq 0.044$, Table 1; Figs. 2 and 3). All crown characteristics of the three species were comparable among treatments at year 0 and the four PCT treatments showed enhanced crown development over the 10-year period. The PCT effect on crown width, crown length and live crown ratio was detected at years 5 and 10 for aspen ($p \leq 0.009$), but only at year 10 for conifers ($p \leq 0.049$). For instance, at year 10, crown length in PCT treatments and the CON were 492–560 vs. 315 cm for aspen, 393–423 vs. 240 cm for fir, and 391–469 vs. 246 cm for spruce. At this time, bole length of spruce was lower in the 3.0S (78 cm) than in the

Fig. 2. Bole length (grey bar) and live crown length (empty bar) of trembling aspen (A), balsam fir (F) and spruce (S) related to PCT treatment: unthinned control, 2.5-, 3.0- and 3.5-m aspen spacings protecting all understory conifers (respectively 2.5A, 3.0A and 3.5A), and a 3.0-m spacing protecting only small understory conifers (3.0S), at years 0, 5 and 10 post-thinning

Fig. 3. Live crown width of trembling aspen, balsam fir and spruce related to PCT treatment: unthinned control (CON), 2.5-, 3.0- and 3.5-m aspen spacings protecting all understory conifers (respectively 2.5A, 3.0A and 3.5A), and a 3.0-m spacing protecting only small understory conifers (3.0S), at years 0, 5 and 10 post-thinning. Error bars represent standard error of treatment means (n = 4)

Table 2. Analysis of variance and associated probabilities ($P > F$) with repeated measurements (1, 2, 3, 5, 7 and 10 years post-thinning) of regeneration density (stems/ha, >30 cm in height) related to species and PCT treatment: unthinned control, 2.5-, 3.0- and 3.5-m aspen spacings protecting all understory conifers, and a 3.0-m spacing protecting only small understory conifers (<1/3 of the retained aspen height).

Source of variation	df	Trembling aspen	Paper birch	Red maple	Spruce	Balsam fir	Mountain maple	Striped maple	Beaked hazelnut	Pin cherry
PCT	4	0.203	0.198	<0.001	0.910	0.040	0.425	0.639	0.037	0.013
Time (T)	5	<0.001	<0.001	<0.001	0.323	<0.001	<0.001	<0.001	0.006	<0.001
PCT $\times$ T	20	<0.001	0.041	0.427	0.996	0.576	0.607	0.266	0.203	0.617
Covariate	1	–	–	<0.001	–	<0.001	–	<0.001	0.020	–

Note: Data were transformed for all species ($\sqrt{x}$). The variance-covariance matrix was spatial power for all species. *df* = degrees of freedom of the numerator. Denominator degrees of freedom, according to Kenward-Roger: PCT = 12.5 to 15.3, T = 58.5 to 75.0, PCT $\times$ T = 59.5 to 74.9. Significant *p*-values are presented in **boldface type**. A dash indicates that the covariate was not significant and was removed from the model.

Fig. 4. Density of trembling aspen regeneration (stems/ha, >30 cm in height) related to PCT treatment: unthinned control (CON), 2.5-, 3.0- and 3.5-m aspen spacings protecting all understory conifers (respectively 2.5A, 3.0A and 3.5A), and a 3.0-m spacing protecting only small understory conifers (3.0S), at years 1–3, 5, 7 and 10 post-thinning. Error bars represent standard error of treatment means ($n = 4$)

3.0A (123 cm) treatment. PCT did not clearly influence bole length of aspen and fir, despite the significant PCT $\times$ T interaction for aspen.

A PCT effect was found in crown width of balsam fir ($p = 0.001$, Table 1; Fig. 3), while an effect of time was also detected in crown width and bole length of this species (both $p < 0.001$; Fig. 2). For the 10-year period, fir had wider crowns in treatments 2.5A, 3.0A and 3.5A (169–177 cm), and 3.0S (176 cm) than in the CON (142 cm, both $p = 0.001$). The time effect was linear for these variables, and for crown width of fir, this resulted in a mean decennial gain of 8 cm/year.

Regeneration dynamics

A PCT $\times$ T interaction was found for density of trembling aspen and paper birch >30 cm in height ($p \leq 0.041$, Table 2; Fig. 4). At year 1 post-thinning, aspen density was lower in the CON (14 100 stems/ha) than in all PCT treatments (22 100–28 000 stems/ha, $p \leq 0.006$). Conversely, density in the CON (10 500 stems/ha) was higher than in treatments 2.5A, 3.0A and 3.5A (4100–6500 stems/ha, $p = 0.001$) at year 5, and higher (6400 stems/ha) than in all PCT treatments (1100–1400 stems/ha, both $p < 0.001$) at year 10. The time effect indicated that significant aspen mortality mainly

Fig. 5. Density of red maple and balsam fir regeneration (stems/ha, >30 cm in height) related to PCT treatment: unthinned control (CON), 2.5-, 3.0- and 3.5-m aspen spacings protecting all understory conifers (respectively 25A, 30A and 35A), and a 3.0-m spacing protecting only small understory conifers (30S), at years 1–3, 5, 7 and 10 post-thinning. Error bars represent standard error of treatment means ($n = 4$)

occurred in years 1–5 in treated units (all $p < 0.001$) and in years 5–10 in the CON. Despite the PCT $\times$ T interaction that was found for paper birch density, contrasts of interest within the PCT treatments were not significant.

PCT affected regeneration density (>30 cm in height) of red maple, balsam fir, beaked hazelnut and pin cherry ($p \leq 0.040$, Table 2; Figs. 5 and 6). Over the 10-year period, more red maple was found in the 2.5A, 3.0A and 3.5A (9900–16 800 stems/ha, $p = 0.001$), and 3.0S (19 100 stems/ha, $p < 0.001$) than in the CON (8700 stems/ha). The 3.0S also contained less balsam fir (4800 vs. 9500 stems/ha, $p = 0.030$) and more hazelnut (12 500 vs. 2800 stems/ha, $p = 0.049$) than the CON. The 3.5A tended to contain more pin cherry than the 2.5A (2100 vs. 600 stems/ha, $p = 0.062$). Finally, time effect was significant for the density of red maple, balsam fir, mountain maple, stripe maple, beaked hazelnut and pin cherry ($p \leq 0.006$, Table 2). Significant recruitment was detected in years 1–2 for all species, except pin cherry. Thereafter, decreases in density were observed for red maple (years 3–5, 7–10), mountain maple (years 2–3, 3–5), striped maple (years 7–10) and pin cherry (years 2–3), while balsam fir and beaked hazelnut density did not significantly change over time. Year 10 density was 9800, 8300, 4300, 2700, 6600 and 200 stems/ha, respectively, for red maple, fir, mountain maple, striped maple, hazelnut and cherry. PCT and time did not affect the density of spruce regeneration.

Discussion

Mortality and browsing

Over the 10-year period of this study, half of the aspen stems died standing in the control. This is consistent with high natural mortality that has been observed in young aspen stands (e.g., Bokalo *et al.* 2007) and exemplifies the self-thinning ability of this pioneer species (Perala 1990). Our results indicate that PCT lowered aspen mortality, while greatly improving spruce survival. Indeed, decennial spruce mortality was high in the control (24%) relative to PCT treatments (0–4%), indicating that aspen self-thinning was not sufficient to sustain an adequate understory light environment for white spruce (Nienstaedt and Zasada 1990) and black spruce (Viereck and Johnston 1990), which are less shade-tolerant than balsam fir. Height growth of balsam fir has already been related to available solar radiation in a comparable PCT experiment (Prévost and Gauthier 2012). In the present study, increased light availability not only improved growth of both conifers (Fig. 1), but also critically enhanced spruce survival. This suggests that PCT may be used to enhance the spruce component at an early stage of development in boreal mixed-wood stands where spruce is more desirable than balsam fir, given its better wood properties and resistance to spruce budworm (*Choristoneura fumiferana* Clem.).

It is not totally unclear how PCT affected browsing. Our experimental units were relatively small and did not allow a

Fig. 6. Density of beaked hazelnut and pin cherry regeneration (stems/ha, >30 cm in height) related to PCT treatment: unthinned control (CON), 2.5-, 3.0- and 3.5-m aspen spacings protecting all understory conifers (respectively 25A, 30A and 35A), and a 3.0-m spacing protecting only small understory conifers (30S), at years 1–3, 5, 7 and 10 post-thinning. Error bars represent standard error of treatment means ($n = 4$)

clear interpretation of herbivore movement behaviour (e.g., Leblond *et al.* 2010). In addition, the occurrence of browsing was noted without identification of damage types. Nevertheless, the data seem to indicate that thinning with removal of the tallest coniferous regeneration increased browsing on aspen. The scarcity and low height of conifers in the 3.0S treatment likely increased selection of aspen crop trees. Also, we noted that tree spacing seemed to facilitate moose fine-scale movements in treated units. For instance, frequent bark stripping was observed on aspen without being detected as a significant treatment effect. The exact reason why browsing on fir appeared to be limited following thinning with retention of tall conifers is not known. The proportion of fir that was affected in these treatments (2.5A, 3.0A and 3.5A) was four-fold lower than in the control. Retention of tall conifers may have provided more choice of food for moose in thinned units. Among other explanations, we hypothesize that the unthinned control may have been preferentially occupied by moose for its sheltered conditions (Schwab and Pitt 1991) and by snowshoe hare for its dense shrubby vegetation (Litvatis *et al.* 1985). Further observations are required to gain greater insight into browsing with regard to conifer retention, as it certainly influences availability and choice of food.

Growth

Thinning was applied to the aspen but the treatment enhanced DBH growth of both aspen and understory

conifers (Fig. 1). Contrary to our first and second hypotheses, however, this effect was not proportional to aspen spacing after 10 years. The DBH growth increase averaged 90% for aspen which is higher than the 10-year gains of 55% and 61% observed in Ontario aspen stands that were thinned respectively at 10- and 15-year-old (Rice *et al.* 2001). Although the response was detected later on conifers, their DBH increment and height growth doubled without affecting aspen DBH response, thereby confirming our third hypothesis. The height growth response of conifers was only detected after 10 years; such a delay could explain why Bokalo *et al.* (2007) found no effect of aspen spacing on white spruce height after 3–4 years in western Canada. Furthermore, the 100% decennial gain was lower than the 200–300% gains that were reported for understory balsam fir in the Saguenay-Lac-Saint-Jean region of Quebec (Prévost and Gauthier 2012). Nevertheless, this study supports the use of PCT to allow conifer ingress into openings, as has been suggested by Rice *et al.* (2001). Both spruce and fir responded well to this form of release cutting. This rejects our fourth hypothesis predicting a better response of fir than spruce, which is yet another positive outcome from a silvicultural perspective. The growth curves also indicate that both species responded well in the treatment that retained only small regeneration (3.0S; Fig. 1); this response is consistent with the ability of young conifers to respond to release (Ruel *et al.* 2000). As a whole, we conclude that thinning accelerated early development of the stratified

species mixture (Smith *et al.* 1997), thereby enhancing growth of both aspen and conifers through the implementation of an ecosystem-based silvicultural approach.

Crown development of all species was enhanced by PCT. As was the case for DBH, aspen response occurred earlier and was less pronounced than conifer response. Moreover, live crown characteristics illustrate the stratification that had been developing in thinned and control experimental units (Fig. 2). At both years 5 and 10, aspen and conifer crowns had an optimal vertical arrangement in the canopy space of thinned units. The treatment allowed the sharing of growing space in an intimate species mixture where the spatial complementarity in tree crowns enhanced light interception and use (Williams *et al.* 2017). At year 10, shorter conifer crowns in the control were indicative of overtopping, which may develop into a mature aspen-dominated stand with suppressed advance growth (e.g., MacDonald *et al.* 2004). Such stands represent an even greater challenge for maintaining coniferous species (Greene *et al.* 2002) for instance, which may require careful application of two-step shelterwood cutting (Prévost and DeBlois 2014). In the present study, we intervened at the early stage of stand development by spacing aspen saplings and taking particular care with understory conifers. Future surveys would indicate how this approach using spatial complementarity of species could influence structural stand development and further silvicultural interventions.

Thinning resulted in 80–90% immediate lowering of aspen BA (year 0), but the growth potential of residual selected crop trees should be enhanced from greater growing space on individual tree basis (Smith *et al.* 1997). Furthermore, the residual aspen BA of 1–2 m²/ha was below the levels that were suggested by Comeau (2001) to provide near-optimal understory conditions for white spruce growth (<8 m²/ha) or survival (<20 m²/ha). The residual BA of balsam fir was adversely affected by the two different measures of advanced growth protection in the 3.0-m spacing, with an 80% immediate loss following the operational approach (treatment 3.0S: <1/3 of the aspen crop tree height). This may indicate the extent to which retention of taller stems can enhance conifer site occupancy in the short-term, although the growth response of young firs has decreased the net BA loss to 65% in 10 years. Because aspen occupies the main canopy, we believe that its growth response will remain independent of understory conifers, as long as the latter remain in a lower position. Monitoring aspen development in the two 3.0-m spacings with different levels of conifer retention (3.0A vs. 3.0S) would allow us to validate this assumption. Further, all treatments should ultimately be evaluated in terms of merchantable (DBH ≥9.1 cm) BA by species, and BA and volume per stem to assess sawlog potential with regard to branching (e.g., Weiskittel *et al.* 2009), wood density and lumber strength (Zhang *et al.* 2006).

Regeneration

Aspen asexual reproduction capacity was observed after thinning in the 8-year-old stand under study. Substantial suckering and stump sprouting occurred in all treated experimental units, but most aspen stems that emerged post-thinning rapidly died out (Fig. 4). From year 5 onward, treated units contained fewer stems than the control and aspen density was

constantly lowered. This transient aspen regrowth was found to be independent of levels of spacing or advance growth protection. Nevertheless, the shade of residual aspen trees, retained conifers and other regenerated species certainly contributed to the quick death of new aspen suckers. It is also probable that widespread root connections had a confounding effect on post-thinning vegetative reproduction and decline (Baret and DesRochers 2011). For instance, root connections between cut trees and crop trees may restrict resources (water, nutrients and carbohydrates) for root suckers and stump sprouts (DesRochers and Liefers 2001). This was already suspected following thinning (Prévost and Gauthier 2012); our field observations of low-vigour aspen regrowth precisely suggest that resources provided by the existing root systems were limited.

PCT retaining all advance growth was more efficient in maintaining overall conifer regeneration. Therefore, our fifth hypothesis asserting a PCT effect on conifers was confirmed only for balsam fir in the 3.0-m spacing that retained only small advance growth (Fig. 5). We believe that fir was affected by this lowest level of retention because it far outnumbered spruce in tall conifer regeneration of the stand. Other species that occupied the understory prior to thinning regenerated in all treatments. Owing to abundant vegetative reproduction, red maple, mountain maple, striped maple and beaked hazelnut accounted for more than 20 000 stems/ha after 10 years. This agrees with the regeneration dynamics observed by Prévost and Gauthier (2012) following thinning in a comparable stand. However, red maple and beaked hazelnut were the only species to experience increases in density post-thinning and removal of tallest conifers facilitated their development (Figs. 5 and 6). Given that it is capable of rapidly capturing the available growing space (Fei and Steiner 2009), red maple increased by 120% following the removal of tall conifers, compared to 60% following their retention. Beaked hazelnut also benefited from removal of the tallest conifers, with an increase of 450% with respect to the control. This treatment greatly stimulated hazelnut vegetative reproduction, but those treatments retaining tall conifers also contained two to three times more hazelnut than the control over the 10-year period. It is likely that inherent variability of spatial distribution of this species prevented this effect from being detected statistically. Like aspen, beaked hazelnut can reproduce by both sprouting and suckering (Tappeiner 1971) which may explain the abundant recruitment of the species. In this study, red maple and beaked hazelnut quickly captured the growing space following thinning and benefited most from removal of tall conifer advance growth.

The effect of PCT on pin cherry regeneration from germination of buried seeds (Wendel 1990) needs to be interpreted cautiously. Other treatments (including the control) had mean densities of pin cherry (300–700 stems/ha) that were as low as the narrowest spacing, without being formally tested or declared statistically different from the widest spacing. A closer inspection of the data revealed that some regeneration subplots contained high numbers of pin cherry stems in one experimental unit of the 3.5-m spacing. It is possible that this widest spacing interacted with an important seed bank that was localized in this unit, which seems to be supported by the observed greater variation in the data.

Conclusions

Thinning in pure aspen stands is rightly under debate due to the self-thinning ability of this shade-intolerant species. However, aspen often overtops conifers in early successional boreal mixedwood stands. In such stratified mixtures, aspen self-thinning is not sufficient to create understory conditions for optimal growth and survival of conifers. Results from this study confirm that PCT may be viewed as a means of redistributing resources to fewer aspen stems in the upper canopy, while releasing understory conifers from suppression. The positive growth and survival responses of conifers must be considered when evaluating the overall merit of PCT in aspen-dominated stands. By favouring species mixtures and limiting stand hardwood conversion in the boreal mixedwood forest, this approach could be considered as an ecosystem-based forest management practice. Growing species in mixtures has been recently gaining interest, and modulating growth and composition of species mixtures that readily establish over vast areas could result in a low-cost, high-return silvicultural practice.

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