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ARTICLE

Sprucing up the mixedwoods: growth response of white spruce (*Picea glauca*) to partial cutting in the eastern Canadian boreal forest[1]

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Abstract: Mixed-species stands present a number of opportunities for and challenges to forest managers. Boreal mixedwood stands in eastern Canada are often characterized by a dominant canopy of shade-intolerant aspen (*Populus tremuloides* Michx.) with more shade-tolerant conifers in the mid- to sub-canopy layers. Because the aspen and conifer components often attain optimal merchantable sizes at different moments in stand development, there is an interest in developing silvicultural practices that allow partial or total removal of aspen and favour accelerated growth of residual conifers. We tested four partial harvesting treatments in mixed aspen – white spruce (*Picea glauca* (Moench.) Voss) stands in which different proportions of aspen (0%, 50%, 65%, and 100% basal area) were removed. Ten years after treatments, 72 spruce stems representing dominant, co-dominant, and suppressed social classes were destructively sampled for stem analysis. Using linear mixed effect models, we analyzed growth as a function of treatment intensity, time since treatment, social status, pretreatment growth rate, and neighbourhood competition. Relative to control stands, radial and volume growth responses were detected only in the extreme treatment of 100% aspen removal. In relative terms, suppressed trees showed the greatest magnitude of cumulative growth increase. Compared with control trees, average annual radial and volume increments were, respectively, 23.5% and 7.1% higher for dominant trees, 67.7% and 24.1% higher for co-dominant trees, and 115.8% and 65.6% higher for suppressed trees over the 10 years after treatment. Growth response was proportional to pretreatment growth rate, and among neighbouring trees, only coniferous neighbours had a negative effect on white spruce growth. Our results suggest that in similar mixed-stand conditions, relatively heavy removal of overstory aspen accompanied by thinning of crowded conifers would result in greatest growth response of residual spruce stems.

Key words: white spruce, boreal, mixedwood, partial cutting, growth response.

Résumé : Les peuplements forestiers mixtes présentent plusieurs opportunités pour et défis aux aménagistes. Dans l'est du Canada les peuplements mixtes sont souvent dominés par le peuplier faux-tremble (*Populus tremuloides* Michx.) et une forte composante de conifères plus tolérants à l'ombre dans les strates inférieures de la canopée. Puisque les trembles et conifères atteignent souvent des dimensions marchandes optimales à des moments différents, il y a un intérêt à développer des pratiques sylvicoles qui permettent le prélèvement partiel ou total du tremble et favorisent un accroissement accéléré des conifères résiduels. Nous avons testé l'effet de la coupe partielle sur la croissance de l'épinette blanche (*Picea glauca* (Moench.) Voss) dans les peuplements mixtes où quatre intensités de prélèvement (0, 50, 65 et 100 % de la surface terrière du tremble) avaient été appliquées. Dix ans après les traitements, 72 épinettes provenant des classes sociales dominante, co-dominante et opprimée ont été abattues et des disques récoltés pour les analyses de tiges. À l'aide de modèles linéaires mixtes, la croissance a été analysée en fonction des facteurs suivants: intensité du traitement, temps depuis le traitement, statut social, taux de croissance avant traitement et compétition par les arbres voisins. Par rapport aux peuplements témoins, une augmentation de croissance a été observée seulement à la suite du traitement extrême (prélèvement du tremble = 100 %). En termes de croissance relative, les arbres opprimés ont eu la plus grande hausse de croissance cumulative. Comparativement aux arbres témoins, les taux de croissance radiale et en volume ont été supérieurs de 23,5 % et 7,1 % pour les dominants, 67,7 % et 24,1 % pour les co-dominants et 115,8 % et 65,6 % pour les arbres supprimés, au cours des 10 ans suivant les traitements. La réaction de croissance après traitement s'est avérée proportionnelle au taux de croissance avant traitement. Parmi les arbres voisins des épinettes échantillonnées, seuls les conifères avaient un effet négatif sur la croissance de ces épinettes. Nos résultats suggèrent que, dans des conditions semblables, un prélèvement relativement intensif de la strate dominante de tremble combiné à l'éclaircissement partiel des conifères favoriserait un accroissement plus important des tiges résiduelles d'épinette.

Mots-clés : épinette blanche, boréal, mixedwood, coupe partielle, réponse d'accroissement.

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Introduction

Despite the global trend of increasing roundwood procurement from single-species plantations (Jürgensen et al. 2014), since the 1970s, there has been a growing interest in the dynamics and management of forests in natural, semi-natural, and planted mixtures. This has come about as a result of a number of factors, notably (*i*) the recognition of the vulnerability of pure forest stands to biotic and environmental stresses and of the positive effect of mixtures on forest resistance to and resilience following disturbance or stress (Knoke et al. 2008), (*ii*) the potential productivity gains of mixed-species stands (Paquette and Messier 2011), and (*iii*) the higher biodiversity and habitat value of mixed forests (Felton et al. 2010). This recognition, associated with the then-emerging paradigms of close-to-nature forest management associated with the Pro Silva movement in Europe (see Bauhus et al. 2013) and natural disturbance (or dynamics) based management in North America (Franklin et al. 2002) and the southern hemisphere (Attiwill 1994), has also led to greater exploration of management practices, including the use of partial cutting, that integrate natural stand dynamics. Partial cutting is arguably more complex in mixed stands where particular growth characteristics of component species and changes in nutrient availability influence temporal dynamics of the system (Forrester 2014).

In the eastern Canadian boreal forest, early stages of development of mixedwood stands following wildfire are typically dominated by fast-growing, shade-intolerant hardwoods such as trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh) (MacDonald 1995; Bergeron 2000). Relatively shade-tolerant conifer species such as white spruce (*Picea glauca* (Moench.) Voss) and balsam fir (*Abies balsamea*) (L.) Mill.) may seed-in immediately after fire from the residual intact forest (Purdy et al. 2002) or slowly recruit in the understory in subsequent years following disturbance (Galipeau et al. 1997). Aspen and slower growing conifers do not generally attain optimal merchantable sizes at the same point in time in mixed stands because of differences in terms of regeneration dynamics, shade tolerance, and sapling and tree growth. Specifically, spruce and other conifers are often of precommercial size (<10 cm diameter at breast height (DBH; 1.3 m) in Quebec) or of small merchantable size when most aspen stems in the same stand have reached their natural or financial maturity (see Nyland 2002). When conifer stems do reach optimal size for harvesting, aspen volume has often decreased as a result of mortality from senescence (Pothier et al. 2004). As a result of these dynamics, simultaneous harvesting of the two species may yield suboptimal total stand volumes.

The removal of most or all canopy aspen in mixedwood stands should, at least temporarily, release residual conifers, including white spruce, from aspen competition. To optimize such a harvesting approach, aspen are ideally harvested before succumbing to age-related mortality and white spruce are left to occupy the freed-up growing space and exploit the greater availability of light and soil resources. Pretreatment growth rate has been shown to influence posttreatment growth (Bose et al. 2014), and vigorous, small and young trees are generally assumed to have the best potential for release partly because of the greater change in resource availability (Bevilacqua et al. 2005; Vincent et al. 2009). However, larger conifers most often exhibit the highest rates of absolute volume growth following release treatments because of their superior growing surface area (Mäkinen and Isomäki 2004; Gagné et al. 2012).

A major challenge to partial harvesting in boreal mixedwood stands is determining the optimal range of canopy opening that will inhibit competition from shrubs and regenerating aspen (if aspen is not a desired species) but allow adequate light for growth release of understory white spruce and other desired species (Comeau et al. 2005). Aspen suckering increases proportionally with harvesting intensity (Brais et al. 2004; Gradowski et al. 2010), and due to its fast growth rate, aspen has the potential to eventually overtop small white spruce trees. In addition, the complete or near-complete removal of canopy trees can negatively impact residual trees either directly through physical damage or windthrow or by causing physiological shock due to environmental stress, resulting in delayed or limited growth responses (Urban et al. 1994).

The effects of partial harvesting in mixed stands on white spruce and aspen dynamics have received considerable attention, particularly in western Canada. (For examples, see Yang (1991), Comeau et al. (2005), Stadt et al. (2007), and Huang et al. (2013).) This is less the case for the eastern Canadian boreal mixedwood forest, and to our knowledge, this is the first study in this region to asses both radial and volume growth responses of merchantable-sized white spruce stems following partial cutting in natural mixed stands. The purpose of this study was to evaluate growth rates of white spruce trees in aspen-dominated mixed stands, over a period of 10 years following a gradient of partial cutting intensities. Specifically, our objectives were to investigate the effect of treatment intensity, tree social status, pretreatment growth rate, and neighbourhood competition on posttreatment annual radial and volume growth of residual white spruce stems. We tested the following hypotheses: (*i*) trees in intermediate (50% and 65%) partial harvesting treatments have superior radial and volume growth rates compared with control stands; (*ii*) absolute growth rates are higher for dominant and co-dominant trees than for suppressed trees; (*iii*) cumulative relative growth rates are higher for suppressed trees than for co-dominant and dominant trees; and (*iv*) growth rates are negatively affected by neighbourhood competition.

Methods

Study area and site description

The study site is located in the Abitibi region of Quebec (48°14′32.2″N, 79°17′12.00′W), in the Western balsam fir – white birch biogeoclimatic subdomain (Saucier et al. 2009). The area is characterized by mesic soils, primarily Grey Luvisols originating from lacustrine clay deposits left by proglacial Lake Ojibway (Vincent and Hardy 1977). The climate is continental, with a daily average temperature of 1.7 °C and annual precipitation of 883 mm (625 mm of which falls as rain) (Rivière Kinojevis meteorological station (48°13′N, 78°52′W); http://climate.weather.gc.ca/).

The treated stands consisted of mixed aspen–conifer with mean basal area (BA, stems ≥ 5 cm DBH) of 41 $m^2 \cdot ha^{-1}$ (Table 1). Mature aspen dominated the canopy layer, with conifers generally distributed through the suppressed to co-dominant canopy layers. Mean white spruce and aspen ages were 71 and 68 years, respectively. While some old (100 to 120 years) white spruce trees were present in stands, 89% of sampled trees established within a period of 14 years, corresponding to calendar years 1937 to 1950. Aspen establishment generally occurred throughout the same time period. Basal area distribution of control stands at the time of treatments was 75% aspen (including a minor component of balsam poplar (*Populus balsamifera* L.)), 20% white spruce, 3% balsam fir, 1% black spruce (*Picea mariana* (Mill.) BSP), and 1% white birch.

Experimental design and treatments

The experimental units (EUs) were laid out based on prism inventories done prior to treatments. Partial harvesting prescriptions were applied to the EUs in the late summer of 2001 and the fall of 2002. Trees were manually harvested, limbed, and cut to length on site. Logs were hauled to roadside using narrow-tracked skidders and forwarders to minimize damage to residual trees during harvesting operations. Treatments consisted of removing different proportions of aspen to encourage the growth of residual conifer stems, primarily white spruce, and promote conifer recruitment. Treatments consisted of a no-harvest control (0% BA

Table 1. Characteristics of the 12 experimental units.

Treatment intensity class (% aspen BA removal) and replicate	Initial BA ($m^2 \cdot ha^{-1}$)	BA after treatment ($m^2 \cdot ha^{-1}$)	BA 5 years after treatment ($m^2 \cdot ha^{-1}$)	BA 10 years after treatment ($m^2 \cdot ha^{-1}$)	Stand removed (%)	Aspen removed (%)
0% (control)						
1	39.89	42.65	47.2	49.4	0	0
2	38.56	40.32	37.5	39.4	0	0
3	39.14	46.91	49.2	54.8	0	0
50% removal						
1	37.50	25.69	29.7	31.1	31	53
2	37.88	25.92	29.8	34.0	32	52
3	38.79	22.32	28.3	33.6	42	52
65% removal						
1	44.19	26.20	27.3	28.8	41	64
2	34.40	16.82	19.5	22.3	51	74
3	41.30	23.49	22.1	26.4	43	61
100% removal						
1	51.08	14.12	8.0	11.4	72	93
2	31.65	11.44	14.1	18.1	64	100
3	58.04	10.03	7.3	12.4	83	99

Note: Initial basal area (BA) values were derived from prism inventories prior to treatments based on stems ≥ 10 cm diameter at breast height (DBH), whereas posttreatment BA values (for stems ≥ 5 cm DBH) were derived from fixed radius (11.28 m) PSPs established immediately following treatments; these were remeasured at 5 and 10 years after treatment.

removal), two intermediate treatments aimed at removing 50% and 65% of aspen BA, and an extreme treatment of 100% aspen BA removal (Table 1). Each of the four experimental treatments was replicated three times for a total of 12 EUs ranging in size from ~1 to 4 ha. Immediately following treatments, a total of thirty 400 m^2 circular permanent sample plots (PSPs, radius = 11.28 m) were established: nine in each of the two intermediate treatments, six in the control, and six in the extreme treatments. Stems greater than 5 cm DBH were tagged, measured, and identified to species. PSPs established in year 0 were remeasured at 5 and 10 years after treatment.

Destructive sampling of white spruce stems

In 2012, all EUs had attained the 10-year posttreatment point. In the summer of 2012, destructive sampling was conducted for tree growth analyses. This consisted of harvesting a total of 72 residual white spruce trees from controls and partially cut stands. Live trees selected for felling had little to no external evidence of disease or loss of vigour. Two trees from each of three social status classes (dominant, co-dominant, and suppressed) were selected from each of the 12 EUs. Social status or crown class is a classification of vertical crown position of a tree relative to all other tree crowns and is generally applied to pure stands or stands composed of species with "similar regimes of height growth" (Smith et al. 1997). However, given the relative facility of measuring DBH, we used the tree diameter distribution of white spruce stems only as a proxy for height distribution in each EU (DBH vs. height for 72 sampled trees, R^2 = 0.85). Given that aspen generally occupied the dominant social class with only a minor component of spruce, assignment of social status to individuals was based exclusively on the relative size among the white spruce trees, rather than social status of all trees within stands.

Stem size distribution was calculated for each EU based on white spruce trees in the two or three PSPs located in the EU. Because crown class determination in the field can be long and imprecise and we had the DBH data, the following classification was used to select individual trees to be destructively sampled from each social status class (Bose et al. 2014): dominant trees, diameter size class ≥ 2 standard deviations (SD) of mean DBH; co-dominant trees, size class ≥ 1 SD of mean DBH; suppressed trees, size class ≤ mean DBH (we discuss this approach in the conclusion). Following felling, crown length was measured and live crown ratio for each tree was determined (Table 2).

Cross-sectional disks were collected from 11 positions along the length of the stem of each tree. The first disk was taken at stump height (0.3 m) and the second was taken from 1.3 m, breast height (BH). The remaining nine disks were sectioned from equally spaced positions relative to the length of the stem from BH to the top of the tree (Chhin et al. 2010). We determined the minimum age of canopy aspen by coring, at a height of 1 m, the stem ≥ 20 cm DBH closest to each collected white spruce stem in control and 50% and 65% BA removal EUs.

Neighbourhood characterization

At the time of felling, the neighbourhood environment of each collected white spruce tree was assessed in circular plots within a 10 m radius of each felled tree. All standing trees (≥10 cm DBH) within this radius were identified to species and measured for DBH and bole-to-bole distance to the felled white spruce tree (Canham et al. 2004; Hartmann et al. 2009).

Growth measurements

All white spruce cross-sectional disks and aspen radial cores were prepared and analyzed in the laboratory using dendroecological procedures to count and measure annual radial growth increments. Disks were visually crossdated using a microscope to identify any false or missing rings and were scanned for image analysis. Annual ring widths were measured along three radii per disk using WinDendro (Regent Instruments Canada Inc. 2009). Ring width data obtained from WinDendro were further analyzed using WinStem (Regent Instruments Canada Inc. 2004), which computed average annual radial growth increments ($mm \cdot year^{-1}$) for each disk. We used these values to reconstruct annual volume increments ($dm^3 \cdot year^{-1}$). In this paper, we focus on within-bark radial growth rates at 1.3 m and volume growth rates for the entire stem over the last 15 years of growth. Annual cumulative radial and volume growth for each year in the 10 years after treatment were used to determine relative cumulative growth (%) for each combination of social status and aspen removal treatment. Annual relative radial growth (RRG) was determined for each year by subtracting the initial radius (year prior to treatment or year 0) from the radius of each year in the posttreatment period, dividing by the initial value and multiplying by 100:

Table 2. Characteristics of white spruce trees destructively sampled in 2012 from stands subjected to partial harvesting in 2001–2002.

Treatment intensity class (% BA aspen removal) and social status	Mean DBH (min–max) (cm)	Mean tree height (min–max) (m)	Mean crown length (min–max) (m)	Mean live crown ratio	Mean crown width (min–max) (m)
0% (control)					
Dominant	34.3 (29.8–38.1)	23.5 (19.4–26.9)	16.3 (10.5–19.3)	0.69	5.9 (5.3–6.7)
Co-dominant	18.1 (16.5–19.9)	15.6 (13.0–19.8)	10.5 (9.7–11.7)	0.69	4.6 (3.3–5.6)
Suppressed	11.5 (9.0–13.8)	10.5 (7.8–12.3)	5.6 (3.4–7.5)	0.53	4.0 (3.0–5.1)
50% removal					
Dominant	30.1 (25.1–40.3)	21.7 (18.4–24.6)	15.5 (12.0–20.3)	0.71	5.6 (4.1–7.2)
Co-dominant	19.3 (13.6–24.1)	14.8 (11.3–20.4)	10.1 (6.6–14.2)	0.67	4.9 (3.5–5.8)
Suppressed	12.4 (9.7–14.3)	10.9 (10.4–11.3)	6.4 (5.3–8.6)	0.59	3.6 (3.1–4.4)
65% removal					
Dominant	38.2 (28.2–49.2)	25.4 (22.3–30.2)	20.9 (17.2–23.8)	0.83	6.9 (5.1–8.6)
Co-dominant	19.8 (18.3–20.9)	16.7 (13.4–19.9)	10.5 (7.3–13.9)	0.64	4.2 (2.9–5.8)
Suppressed	13.0 (11.2–13.8)	10.6 (9.7–12.3)	6.7 (3.1–10.1)	0.63	4.0 (2.6–4.7)
100% removal					
Dominant	36.4 (28.4–54.0)	21.7 (18.4–26.7)	16.8 (13.2–20.1)	0.78	7.6 (3.9–9.2)
Co-dominant	19.5 (17.8–20.9)	13.7 (12.4–16.0)	8.5 (5.7–10.4)	0.63	4.8 (3.9–5.7)
Suppressed	12.7 (10.3–15.5)	9.5 (6.8–12.4)	5.6 (3.2–8.5)	0.61	3.9 (2.2–4.8)

Note: BA, basal area; DBH, diameter at breast height (1.3 m); min, minimum; max, maximum.

$$\text{RRG} = \frac{(r_{yi} - r_{y0})}{r_{y0}} \times 100 \qquad (1)$$

where r_{yi} is the radius in year i and r_{y0} is the radius in year 0, prior to treatment.

These values were plotted to present relative cumulative radial growth for the 10-year posttreatment period. The same approach was used for volume growth.

We estimated pretreatment radial growth rate at 1.3 m by computing the average annual growth rate in the 5 years prior to harvesting treatments. For posttreatment growth rates, we used the annual increments for each year in the 10-year posttreatment period. Radial growth rates generally decrease following a period of rapid growth in the juvenile stage. For this reason, we determined cambial age at 1.3 m and used it to account for age effects in statistical analyses. Minimum tree age based on cambial age at 0.3 m was used to determine the age of white spruce trees in the stand.

Statistical analyses

Model selection and tree growth patterns

Growth patterns were analyzed using linear mixed effect models (Pinheiro and Bates 2000; Gelman and Hill 2007). Statistical analyses were conducted using the nlme package in R (R Core Team 2013; Pinheiro et al. 2013). Several candidate models were considered, and model selection based on Akaike's information criterion corrected for small sample sizes (AIC_c) was implemented using the AICcmodavg package (Burnham and Anderson 2002; Mazerolle 2013). For each analysis, model-averaged predictions of growth and unconditional 95% confidence intervals were computed based on the entire set of candidate models (Burnham and Anderson 2002; Mazerolle 2013).

Neighbourhood competition indices

Variants of Hegyi's (1974) neighbourhood competition index (HCI) were calculated to evaluate the influence of competition on radial and volume growth rates of collected white spruce trees. Distance-independent HCIs were calculated as a function of DBH of collected white spruce trees and neighbour trees:

$$\text{HCI}_{\text{dist indep}} = \sum_{i=1}^{n} \frac{\text{dbh}_i}{(\text{dbh}_t)} \qquad (2)$$

where dbh_i is the neighbour tree diameter at breast height (cm) and dbh_t is the collected tree diameter at breast height (cm).

Distance-dependent HCIs incorporated the bole-to-bole distance between each neighbour tree and the collected white spruce tree in the following calculation:

$$\text{HCI}_{\text{dist dep}} = \sum_{i=1}^{n} \frac{\text{dbh}_i}{(\text{dbh}_t)(\text{distance}_{it})} \qquad (3)$$

where dbh_t and dbh_i are defined as in eq. 2 and distance_{it} is the horizontal distance (m) between neighbour (i) and collected tree (t).

In total, 30 variations of HCI (see Supplementary Table S1[2]) were computed by including additional conditions, specifically neighbour tree type (broadleaf, conifer, or all species) and distance to the collected white spruce stem (≤10 m, ≤8 m, ≤6 m, ≤5 m, 5–10 m). The model selection approach was first used to determine which of the 30 HCIs best explained radial and volume growth rates of the collected white spruce stems. Each HCI was considered as a separate model, and a null model was included in the analyses. The competitive effect of neighbours was assumed to have changed through time; therefore, growth data were limited to the average of the last 3 years, specifically years 8, 9, and 10 after treatment (i.e., one observation per tree). The growth data were log-transformed to meet model assumptions of normality of residuals and homoscedasticity. For these analyses, HCI was considered as a fixed effect and EU was considered as a random effect to account for the repeated observations in each EU. The HCIs from the most parsimonious models explaining radial and volume growth were then used to build the models using additional explanatory variables in subsequent analyses for the same 3-year period.

Modelling posttreatment growth for years 8, 9, and 10 with HCI

After selecting the best HCIs explaining neighbourhood competition, nine models (see Supplementary Table S2[2]) were consid-

[2]Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2015-0489.

ered to determine the effects of partial harvesting treatments, social status, pretreatment growth rate, and HCI on average radial and volume growth rates in the last 3 years (years 8, 9, and 10 after treatment). Cambial age at 1.3 m was also included in all models (excluding the null model) when the response variable was average radial growth rate. Specific interactions between competition (HCI) and treatment intensity and between social status and treatment intensity were included in the models. These variables were considered as the fixed factors, and EU was considered as the random factor. Response variables were not transformed prior to analyses as they conformed to model assumptions.

Modelling 10-year posttreatment growth

Fifteen competing models (see Supplementary Table S3[2]), including a null model, were considered to determine the effects of partial harvesting treatments, tree social status, and pretreatment growth rates on posttreatment radial and volume growth rates for the entire 10-year posttreatment period. Treatment intensity and social status were treated as categorical variables, while pretreatment growth rate and time were treated as continuous variables. Seven of the models included the squared value of time (time^2) to account for quadratic effects; the remaining models (excluding the null model) accounted for linear effects of time only. Cambial age at 1.3 m was also included in all models (excluding the null model) when the response variable was radial growth rate. We included specific interactions to quantify changes in growth over time and determine whether growth patterns in different social statuses were similar across treatments. The above-mentioned variables were considered as fixed factors in the mixed effect models. EU and tree nested within EUs were considered as random effects. Transformations were applied to response variables to ensure that model assumptions of normality and homoscedasticity of residuals were met. A square root transformation was applied to radial growth rate and a log transformation was applied to volume growth rate.

Results

Neighborhood competition 8 to 10 years after treatment

The highest ranking HCI for radial growth in years 8 to 10 after treatments (AIC$_c$ weight 0.79) was a distance-independent model that accounted for competition by coniferous neighbours only within a 5 m radius (Table 3; for all models, see Supplementary Table S1[2]). In terms of volume growth, neighbourhood competition was best explained (AIC$_c$ weight 0.68) by a distance-dependent HCI, also accounting for competition with coniferous neighbours only, but within a 10 m radius of the sampled white spruce trees (Table 3). These respective top-ranking HCIs for spruce growth in years 8–10 were used in subsequent analyses to determine the effect of coniferous neighbourhood competition, with other variables, on the radial and volume growth rates of the white spruce trees 8–10 years after harvesting (for ranges of variable values, see Supplementary Table S4[2]).

Growth 8 to 10 years after treatment

Average annual radial growth in the last 3 years before destructive sampling was best explained by the model that accounted for the additive effects of cambial age, treatment intensity, HCI, and pretreatment growth rate (Table 4). This top model (AIC$_c$ weight 0.89) was 9.9 times more parsimonious than the second-ranking model (AIC$_c$ weight 0.09, ΔAIC$_c$ 4.58; Table 4). This same top model, excluding cambial age, was also the most parsimonious in terms of volume growth (AIC$_c$ weight 0.75), although the second-ranking model accounting for additive effects of HCI and pretreatment growth rate only was also strongly supported (ΔAIC$_c$ 2.94; Table 4).

Radial and volume growth rates differed depending on partial harvesting intensity, with white spruce trees in the 100% aspen BA removal treatment only continuing to show improved growth

Table 3. Results of model selection for linear mixed effects models based on AIC$_c$. Average annual radial growth rate (mm·year^{-1}) at 1.3 m and average annual volume growth rate along the stem (dm^3·year^{-1}) of residual white spruce trees in the last 3 years of growth (years 8–10) were analyzed as a function of the 30 variations of Hegyi's competition index (HCI). For brevity, only the most parsimonious models are shown (for all models tested, see Supplementary Table S1[2]).

Model	K	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	R^2
Radial growth at 1.3 m (mm·year^{-1})					
HCI 13*	4	111.49	0.00	0.79	0.56
HCI 22†	4	115.64	4.15	0.10	0.53
Volume growth along the stem (dm^3·year^{-1})					
HCI 22	4	140.12	0.00	0.68	0.72
HCI 13	4	141.72	1.59	0.31	0.71

Note: K, number of parameters; AIC$_c$, Akaike's information criterion corrected for small sample size; ΔAIC$_c$, AIC$_c$ relative to most parsimonious model; AIC$_c$ weight, model weight.

*Distance-independent, conifers only, within 5 m radius.

†Distant-dependent, conifers only, within 10 m radius.

rates over the control in years 8, 9, and 10 following treatment (Table 5). No differences were found between the two intermediate treatments (50% and 65%) and control stands.

The treatment effect on radial growth was independent of tree social status. In fact, models that included social status ranked relatively low. Average pretreatment growth rate was an important factor affecting growth; that is, trees with high pretreatment growth rates showed higher growth rates 7 to 10 years after treatment (Table 5).

No suppressed trees had what we considered high pretreatment growth rates (2.0 to 3.8 mm·year^{-1}). Co-dominant and dominant trees with pretreatment growth rates in this range had higher mean increments over the 10-year posttreatment period than those with lower pretreatment growth rates. Co-dominant and dominant trees younger than the median age of 52 years at time of treatment all had high pretreatment growth rates (0.95 to 3.8 mm·year^{-1}). In contrast, trees older than 52 years generally had low pretreatment growth rates (0 to 2.84 mm·year^{-1}), and older suppressed trees had very low pretreatment growth rates (0 to 0.95 mm·year^{-1}).

Neighbourhood competition, as explained by the HCIs, negatively affected both radial and volume growth rates (Table 3). The most parsimonious neighbourhood competition indices were those that accounted for competition by coniferous species only (Table 3).

Ten-year posttreatment growth

When considering both annual radial and volume growth rates as response variables, the most parsimonious models included the additive effects of treatment intensity, social status, time, time^2, pretreatment growth rate, and cambial age (for radial growth), as well as the interactions between treatment and time and treatment and time^2 (Table 6).

For radial growth, the top-ranking model was clearly the most likely, as it had all the support (AIC$_c$ weight 1.0; Table 6; for all models, see Supplementary material[2]). For volume growth, the most supported model (AIC$_c$ weight 0.68) was 2.13 times more parsimonious than the second-ranking model (Table 6), which included the same variables but excluded the quadratic effect of time (time^2).

Annual radial and volume growth rates for white spruce trees in the two intermediate partial harvesting treatments (50% and 65%) were similar to control stands. Only the extreme partial harvesting treatment of 100% aspen BA removal had a positive effect on both radial and volume growth rates of residual white spruce

Table 4. Results of model selection for linear mixed effects models based on AIC_c. Average annual radial growth rate (mm·year⁻¹) at 1.3 m and average annual within-bark volume growth rate (dm³·year⁻¹) of residual white spruce trees in the last 3 years following partial harvesting treatments were analyzed as a function of cambial age* (Age), treatment intensity† (Intensity), neighbourhood competition‡ (HCI), and pretreatment growth rate§ (Pretreat); interactions between variables are indicated by a times sign (×). For brevity, only the most parsimonious models are shown.

Model no.‖	Model	K	AIC_c	ΔAIC_c	AIC_c weight	R^2
Radial growth at 1.3 m (mm·year⁻¹)						
5	Age + Intensity + HCI + Pretreat	9	138.97	0.00	0.89	0.63
7	Age + Intensity + HCI + Pretreat + Intensity × HCI	12	143.55	4.58	0.09	0.65
Volume growth along the stem (dm³·year⁻¹)						
5	Intensity + HCI + Pretreat	8	397.66	0.00	0.75	0.89
6	HCI + Pretreat	5	400.60	2.94	0.17	0.89

Note: K, number of parameters; AIC_c, Akaike's information criterion corrected for small sample size; ΔAIC_c, AIC_c relative to most parsimonious model; AIC_c weight, model weight.

*Age: cambial age taken at 1.3 m (used to analyze radial growth only).

†Intensity: control, 50%, 65%, and 100% aspen basal area removal.

‡HCI: neighbourhood competition as determined using the most parsimonious competition index (see Table 3).

§Pretreat: the average annual radial and volume growth rate 5 years prior to treatment.

‖See Supplementary Table S2[2].

Table 5. Model-averaged estimates and their 95% confidence intervals (CI) based on model selection for linear mixed effects models. Only parameter estimates for terms that exclude 0 in the confidence interval are presented. Response variables are average annual radial growth rate (mm·year⁻¹) at 1.3 m and average annual within-bark volume growth (dm³·year⁻¹) of residual white spruce trees in the last 3 years following partial cutting treatments.

Variable	Estimate*	Lower CI	Upper CI
Radial growth at 1.3 m (mm·year⁻¹)			
Pretreatment growth rate	0.3554	0.1094	0.6014
HCI 13†	–0.0957	–0.1457	–0.0458
Cambial age	–0.0207	–0.0329	–0.0086
Intensity 4 (100% aspen BA removal)	0.8050	0.4443	1.1657
Volume growth along the stem (dm³·year⁻¹)			
Pretreatment growth rate	0.7792	0.6765	0.8818
HCI 22‡	–0.6447	–1.0369	–0.2525
Intensity 4 (100% aspen BA removal)	3.4356	1.1755	5.6956

Note: HCI, Hegyi's competition index; BA, basal area.

*Magnitude of the estimates reflects the rate of change of growth as a function of a given variable. A variable with a large negative or positive value accompanied by a confidence interval that excludes 0 has a greater effect than a variable with a wide confidence interval including 0.

†Distance-independent, conifers only, within 5 m radius.

‡Distant-dependent, conifers only, within 10 m radius.

trees in the 10 years following treatment, and this effect was consistent across all three social statuses (Table 7). Compared with trees in controls, average annual radial and volume increments in this treatment were, respectively, 23.5% and 7.1% higher for dominant trees, 67.7% and 24.1% higher for co-dominant trees, and 115.8% and 65.6% higher for suppressed trees over the 10 years after treatment. Cumulative volume growth of spruce over the posttreatment period in the 100% treatment was much higher than cumulative radial growth: volume of suppressed, co-dominant, and dominant trees increased by 373%, 147%, and 57%, respectively, compared with more modest increases of 84%, 77%, and 34% for the respective social classes in control stands.

Treatment effect was immediate, with growth rates increasing within the first 2 years following treatment. Radial growth followed a negative quadratic form, with growth rates peaking at approximately 6 years after treatment and then gradually decreasing from years 6 to 10 (Figs. 1A–1C). This pattern was apparent for all three social statuses. Volume growth followed a similar negative quadratic form, although growth rate continued to increase throughout the 10-year period (Figs. 2A–2C).

Volume growth rates were superior for dominant and co-dominant trees compared with suppressed trees (Table 7). Suppressed trees, however, exhibited the highest relative increase in cumulative radial and volume growth (Figs. 1D–1F and 2D–2F). This was apparent in all treatments including the control, but the greatest increase was observed in the 100% aspen removal treatment. Pretreatment growth rate affected both radial and volume growth (Table 7); trees with superior average growth rates in the 5 years prior to treatment continued to have superior growth rates in the posttreatment period. For radial growth, this variable was a stronger predictor of posttreatment growth rate than tree social status (Table 7).

Discussion

Partial harvesting treatments, where overstory aspen trees were removed, were successful in releasing residual merchantable-sized (≥10 cm DBH) white spruce trees. However, based on the results of this experiment, it was necessary to remove 100% of shade-intolerant broadleaved trees to significantly accelerate radial and volume growth rates of white spruce. Growth responses were best explained by treatment intensity, time since treatment, tree social status, pretreatment growth rate, and neighbourhood competition.

Neighbourhood competition

Neighbourhood competition indices are generally based on the size ratio of target and neighbour trees and assume that competition decreases with increasing distance to a neighbouring tree and decreasing neighbour size. We used a series of simple indices based on HCI because they are easily computed, yet have proved to be effective in other studies (Filipescu and Comeau 2007).

Across all treatments, average radial and volume growth in years 8, 9, and 10 after treatment were negatively influenced by neighbourhood conifer competition. Aspen is generally considered to have a competitive advantage in mixed stands on productive sites such as the ones in this study (Boivin et al. 2010). This advantage is primarily due to its prolific suckering and superior juvenile growth rate, allowing trees to attain canopy dominance and capture more resources, particularly light (Frey et al. 2003; Balandier et al. 2006). The anticipated significant competitive effect of aspen on white spruce was a fundamental assumption in the design of this partial cutting experiment. However, aspen did not exert the competitive effect on merchantable white spruce trees that we originally expected. This is potentially due to higher light transmission levels in aspen canopies related to aspen's lower leaf biomass and leaf-off seasons (Constabel and Lieffers 1996; Man and Lieffers 1999). Results concur with those of Stadt et al. (2007) and Huang et al. (2013) who, using more complex competition indices, also found that intraspecific competition

Table 6. Results of model selection for linear mixed effects models based on AIC_c. Annual radial growth rate (mm·year^{-1}) at 1.3 m and annual stem volume growth rate (dm^3·year^{-1}) for residual white spruce trees 10 years following partial harvesting treatments was analyzed as a function of cambial age* (Age), treatment intensity† (Intensity), social status‡ (SS), time§ (Time), and pretreatment growth rate‖ (Pretreat); interactions between variables are indicated by a times sign (×). For brevity, only the most parsimonious models are shown.

Model no.#	Model	K	AIC_c	ΔAIC_c	AIC_c weight	R^2
Radial growth at 1.3 m (mm·year^{-1})						
15	Age + Intensity + SS + Time + Time^2 + Pretreat + Intensity × Time + Intensity × Time^2	19	−296.63	0.00	1	0.83
Volume growth along the stem (dm^3·year^{-1})						
15	Intensity + SS + Time + Time^2 + Pretreat + Intensity × Time + Intensity × Time^2	18	523.44	0.00	0.68	0.94
22	Intensity + SS + Time + Pretreat + Intensity × Time	14	524.95	1.52	0.32	0.94

Note: *K*, number of parameters; AIC_c, Akaike's information criterion corrected for small sample size; ΔAIC_c, AIC_c relative to most parsimonious model; AIC_c weight, model weight.

*Age: cambial age taken at 1.3 m (used to analyze radial growth only).

†Intensity: control (0%), 50%, 65%, and 100% aspen basal area removal.

‡Intraspecific social status of residual white spruce trees: suppressed, co-dominant, dominant.

§Time and Time^2 were tested to determine linear and quadratic effects.

‖Pretreat: the average annual radial and volume growth rate 5 years prior to treatment.

#See Supplementary Table S3[2].

Table 7. Model-averaged estimates and their 95% confidence intervals (CI) based on model selection for linear mixed effects models. Only parameter estimates for terms that exclude 0 in the confidence interval are presented. Response variables are annual radial growth rate at 1.3 m (mm·year^{-1}) and annual volume growth rate within bark (dm^3·year^{-1}). Interactions between variables are indicated by a times sign (×). See Table 6 for variable descriptions.

Variable	Estimate*	Lower CI	Upper CI
Radial growth at 1.3 m (mm·year^{-1})			
Time	0.0275	0.0048	0.0502
Time^2	−0.0026	−0.0043	-8×10^{-4}
Pretreatment growth rate	0.3617	0.2652	0.4583
Intensity 4 (100% aspen BA removal)	0.2966	0.1311	0.4620
Intensity 4 × Time	0.1511	0.0976	0.2047
Intensity 4 × Time^2	−0.0115	−0.0162	−0.0067
Volume growth along the stem (dm^3·year^{-1})			
Time	0.0217	0.0024	0.041
SS 2 (co-dominant)	0.9391	0.6876	1.1907
SS 3 (dominant)	1.3049	0.8358	1.774
Pretreatment growth rate	0.0489	0.0300	0.0679
Intensity 4 (100% aspen BA removal)	0.3814	0.0992	0.6636
Intensity 4 × Time	0.1414	0.0050	0.2778
Intensity 4 × Time^2	−0.0111	−0.0194	−0.0029

*Magnitude of the estimates reflects the rate of change of growth as a function of a given variable. A variable with a large negative or positive value accompanied by a confidence interval that excludes 0 has a greater effect than a variable with a wide confidence interval including 0.

caused greater reductions in white spruce growth than aspen competition. In another study in young mixedwoods in Quebec, Boivin et al. (2010) found that conspecific neighbours were stronger competitors affecting balsam fir growth and that aspen was the weakest competitor among four species evaluated.

Radial growth was negatively influenced by conifer trees located anywhere within a 5 m radius to the white spruce trees regardless of actual proximity, whereas volume growth was negatively affected by conifer trees within a 10 m radius, with both DBH and proximity of neighbour trees influencing the competitive effect. Diameter growth is known to be more sensitive to competition (stand density) than height growth (Lanner 1985). Indeed, close proximity of conspecific neighbours can cause negative physical interactions between crowns and inhibit crown expansion and radial growth (Canham et al. 1994; Power et al. 2012). Once respiration demands have been met, carbon allocation is generally prioritized to height growth before diameter, and as a result, height growth is less affected by neighbour density and thinning prescriptions (Wagner 2000). This suggests that conifer-specific neighbourhood competition within the immediate vicinity of the white spruce trees influences diameter growth, less so height and volume growth (von Oheimb et al. 2011).

Treatment intensity

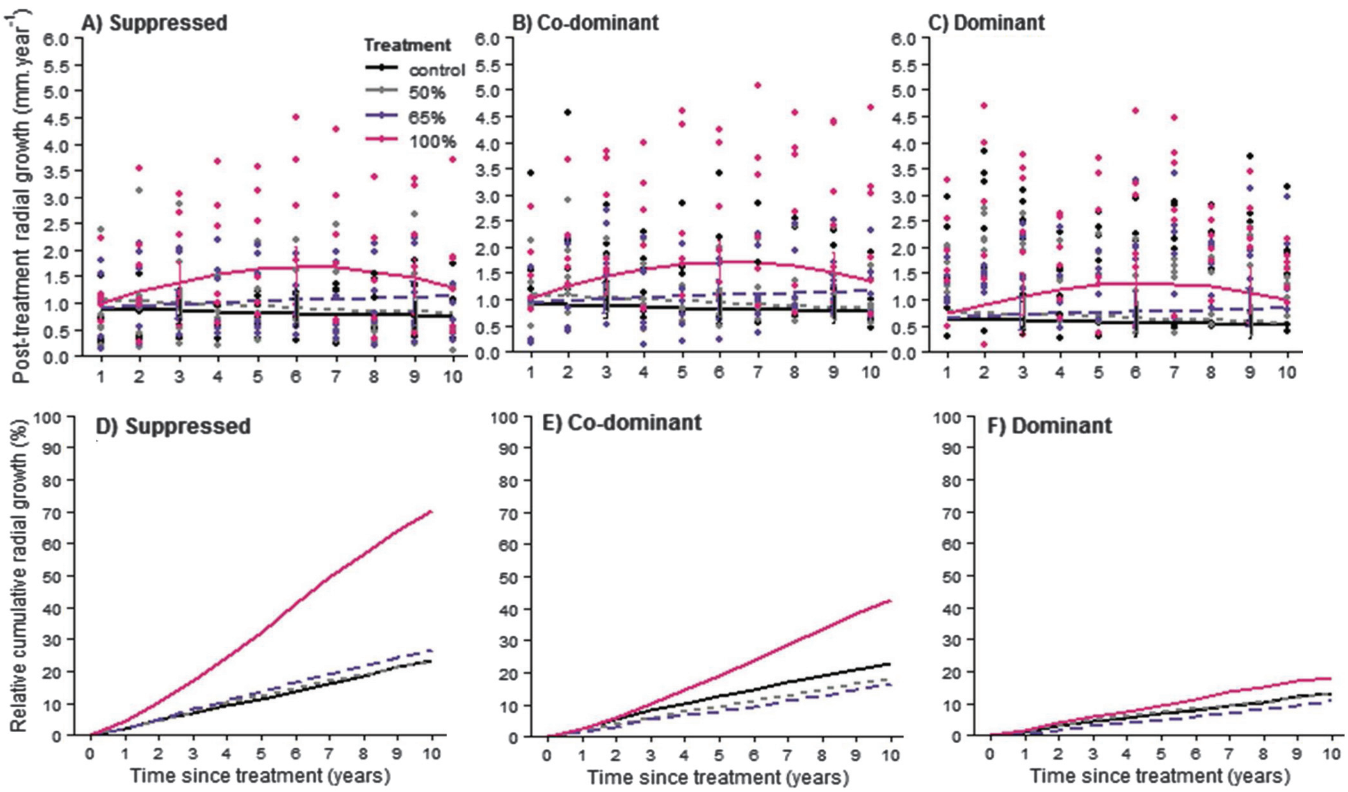
We predicted that intermediate treatments (50% and 65% aspen BA removal) would induce the greatest growth response in the residual white spruce trees by producing optimal light environments for spruce while tempering aspen recruitment (Beaudet et al. 2011). Our predictions were based on assumptions that the extreme cutting treatment could induce a growth shock in residual spruce (Urban et al. 1994; Vincent et al. 2009) and maximize competition for soil resources from a prolifically regenerating aspen cohort (Gradowski et al. 2010). However, this was not the case.

White spruce is a moderately shade-tolerant species. Physiological traits such as low photosynthetic compensation and saturation points allow the species to fix carbon more efficiently than aspen at low light levels. Nonetheless, competition for light is considered as one of the most limiting factors affecting white spruce growth (Lieffers et al. 2002; Comeau et al. 2005). While light requirements may change through tree development (Claveau et al. 2002), an optimal cutting intensity was expected to be between 45% and 65% stand BA removal (Prévost and Pothier 2003; Beaudet et al. 2011). The two intermediate treatments, aimed at 50% and 65% aspen BA removal, translated into relatively low total stand BA removals, specifically 31%–42% and 41%–51%, respectively (Table 1). Although light transmittance was not measured in the present study, we speculate that changes in light availability induced by the intermediate harvesting intensities were not enough to increase white spruce growth relative to that in controls. Moreover, due to differences in initial stand BA, both posttreatment residual BA and the proportion of broadleaf and conifer species were relatively similar in the two intermediate treatments (Table 1).

In effect, white spruce trees displayed significant increases in radial and volume growth rates only in the extreme partial cutting treatment where 100% aspen BA harvesting translated into 64%–83% removal of total stand BA. These findings are consistent with similar studies on white spruce release following partial harvesting and thinning treatments (Man and Greenway 2004; Gagné et al. 2012).

Other studies under somewhat different conditions have shown similar results. For example, in Manitoba and Saskatchewan, Yang (1989, 1991) reported that white spruce diameter and volume increased by 28% and 81%, respectively, following light thinning (44% stand BA) and 50% and 260% following moderate thinning (60% stand BA) in mixedwood stands. When subjected to complete aspen removal, white spruce diameter increment improved 50%–177% while volume increment improved 24%–304% compared

Fig. 1. Posttreatment radial growth (A, B, C) and relative cumulative radial growth (D, E, F) of white spruce presented as a function of time since treatment for suppressed, co-dominant, and dominant trees, respectively. In A–C, lines represent model-averaged predicted values and points represent observed values. Therefore, a value of 0.75 representing the minimum pretreatment growth rate of dominant trees and a value of 50.75 representing mean cambial age of all trees were used to make predictions.



with control trees over a period of 35 years. More recently, working in strip cuts in 77-year-old mixed aspen – white spruce stands in Alberta, Grover et al. (2014) found that annual diameter and volume growth increments were, respectively, 152% and 83% higher for released white spruce compared with controls.

The fact that spruce growth following the two intermediate treatments of our study did not differ from that of spruce in controls provides some contradictory evidence of aspen as a weak growth competitor for white spruce. The best models explaining radial and volume growth of residual spruce over the 10-year posttreatment period included treatment intensity among other explanatory variables. The increase in spruce growth only after total aspen removal would suggest that aspen continues to have an important (rather than minimal) competitive effect even after intermediate treatments. However, the models did include treatment intensity. Analyses of the neighbourhood competition indices also indicate that radial and volume growth of residual white spruce 8 to 10 years following partial cutting are only influenced by neighbouring conifers.

Time since treatment

Growth responses to the 100% partial harvesting prescription were apparent within the first 2 years following treatment. The lack of thinning shock and absence of an extended time lag in growth response was somewhat surprising because these effects have been observed for white spruce (Urban et al. 1994) and other conifer species following partial harvesting (Kneeshaw et al. 2002). Environmental conditions created following harvesting apparently did not induce enough physiological stress to hinder an immediate positive growth response to the treatment.

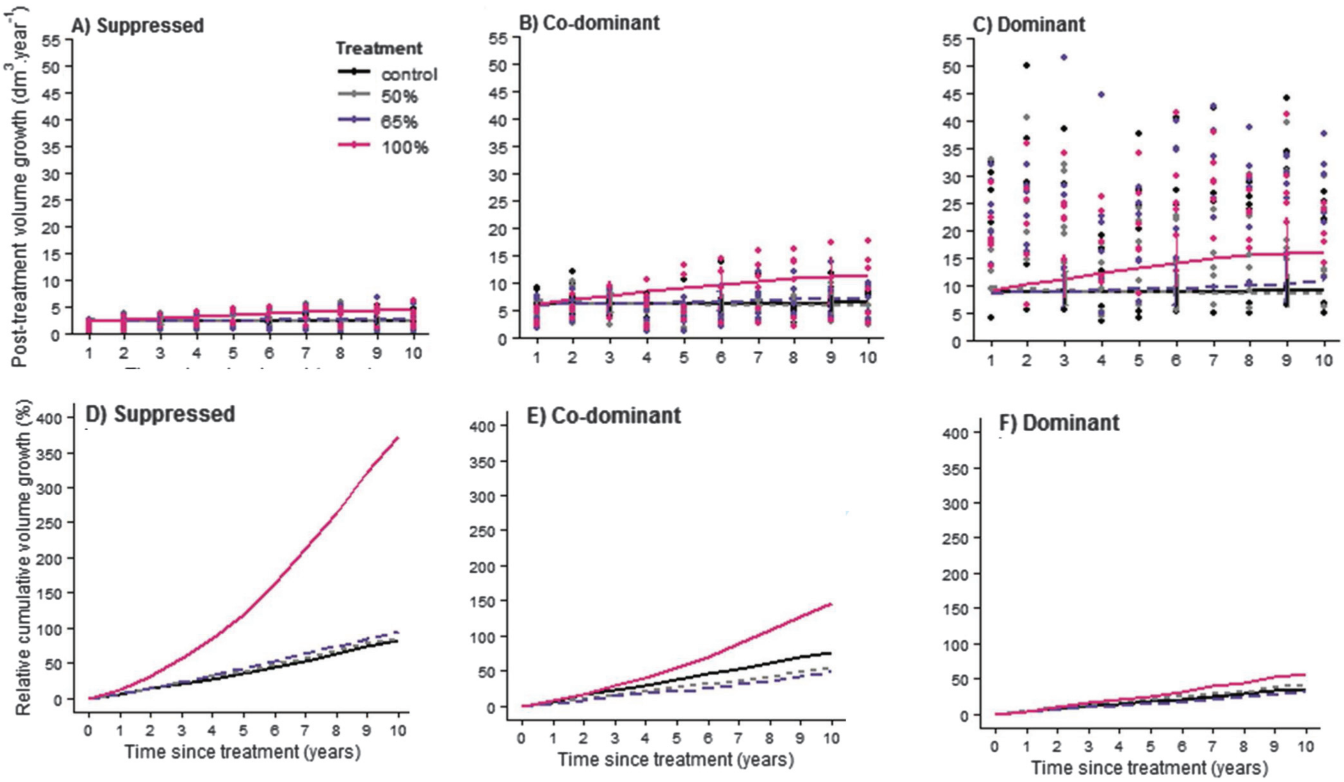
Social status, pretreatment growth rate, and cambial age

Diameter was an effective proxy for tree height, and heights of what we refer to as dominant, co-dominant, and suppressed social classes reflect three reasonably distinct height classes (DBH vs. height, $R^2 = 0.84$; see Supplementary Fig. S1[2]). However, our partitioning of trees into these three social classes based on standard deviations around mean diameters does not necessarily reflect social status (or crown class) in the classical sense of tree crown position relative to surrounding crowns in the canopy (Smith et al. 1997). Moreover, as mentioned in Methods, we considered spruce only rather than all stems (particularly aspen) present in stands. Nonetheless, while it may be more exact to refer to our three social statuses as "tallest spruce", "above-average but not tallest spruce," and "spruce of below-average height", in providing this explanation, we have preferred to use the term of social status.

We hypothesized that social status would have an effect on the magnitude of radial and volume growth responses of white spruce. Overall, radial growth was superior in the 100% aspen removal treatment compared with controls. However, we found no differences in absolute radial growth rates between the three social classes. Cambial age at the time of treatment had a direct influence on increment growth potential and affected posttreatment radial growth. Young cambium is more effective than older cambium in producing new wood cells and thicker annual rings (Vaganov et al. 2006). Radial (and diameter) growth rates decrease after maximum annual increment has been reached, so old trees generally have slower radial growth rates than younger trees of the same size (Jogiste 2000).

As expected, absolute volume growth was directly related to tree size, with the highest increments occurring in dominant trees, followed by co-dominants and finally suppressed trees. This

Fig. 2. Posttreatment volume growth (A, B, C) and relative cumulative volume growth (D, E, F) of white spruce presented as a function of time since treatment for suppressed, co-dominant, and dominant trees, respectively. In A–C, lines represent predicted values and points represent observed values. A value of 9.23 representing mean pretreatment growth rate of all trees was used to make predictions.



has been observed for white and black spruce growing in thinned plantations (Gagné et al. 2012) and natural stands in Quebec (Vincent et al. 2009) and for thinned stands of Norway spruce in Finland (Mäkinen and Isomäki 2004). By definition, larger trees have a greater height and diameter resulting in a larger cambium surface area than smaller trees. This larger surface area results in greater volume accumulation in dominant trees, even when radial growth is similar for the three social statuses.

However, in terms of relative radial and volume growth, suppressed trees showed the greatest positive response to treatments, followed by co-dominant and dominant trees. Factors at play here are related to differences in both growing conditions and growth potential of trees between the different social classes. According to Vincent et al. (2009), dominant trees are generally least affected by thinning because their relatively large crowns situated in and above the upper canopy already benefit from the highest levels of direct light exposure of all trees in a stand. While they can maintain good absolute growth rates, the relative effect of thinning on their growing environment is less than that for trees in the mid to lower canopy. Moreover, the capacity of dominant trees to respond to treatments may also be limited, particularly if they are old and (or) approaching maximum height.

In contrast, the potential change in the light environment of suppressed, intermediate, and, to a lesser extent, co-dominant trees induced by partial harvesting treatments is much greater. Although early suppression limits height growth of suppressed trees and postpones the time at which maximum growth rate is reached, it does not necessarily inhibit their growing capacity (Assmann 1970). Thus, the greater change in the light environment and the growth potential of younger, suppressed trees both contribute to explaining their superior relative growth.

Although all trees responded positively to heavy partial harvesting, growth responses were proportional to pretreatment growth rates. Less vigorous trees with slower pretreatment growth rates continue to exhibit slow but improved posttreatment growth rates. In contrast, more vigorous, younger trees continue to have the highest posttreatment growth rates. Pretreatment tree vigour has also been shown to influence posttreatment growth of trembling aspen in eastern Canada (Bose et al. 2014).

Management implications

Partial harvesting in mixed-species stands may be done for a number of reasons: conifer understory protection, enhanced growth of residual stems, or objectives related to old growth, wildlife habitat, close-to-nature management, landscape aesthetics, or social acceptability. Increasing intervention in aspen-dominated mixed stands in eastern Canada presents potential opportunities for refining harvesting practices to take advantage of differences in competitive and treatment effects, tree size, and growth potential of the component species. While large white spruce stems accrue more volume than smaller stems following partial harvesting, the relative response of suppressed and intermediate stems to these treatments is considerably greater than that of stems in co-dominant and dominant classes. Moreover, young, vigorous stems have the greatest potential for sustained positive growth increment following partial harvesting. In aspen-dominated mixedwood stands with an important spruce component in all canopy layers, positive growth of both residual spruce in the lower to mid canopy and residual aspen stems in the upper canopy can occur under specific conditions. Such conditions include a heavy, high partial cut (crown thinning) or complete removal of aspen stems, accompanied by harvesting of a portion of the largest and presumably oldest spruce and thinning of other crowded spruce (Bose et al. 2014).

Partial cutting in this study was done on an experimental scale; harvesting was relatively diffuse and done manually, using small machines to skid and forward wood to the roadside. We recognize that more large-scale partial cutting operations using bigger machines, and wider trails and corridors will produce a greater array of postharvest conditions, from intact forest to 100% stand opening, with corresponding effects on residual tree responses.

Because partial harvesting treatments can induce rapid growth responses and delay crown recession, residual trees are prone to increased stem taper. A detailed evaluation of growth allocation along the length of the stem accompanied by an assessment of wood quality properties of residual trees would provide a more complete evaluation of the success of these harvesting prescriptions.

Conclusion

Integrated mixedwood management promotes the maintenance of a naturally representative range of mixedwood stand types across forest landscapes and the efficient management of both the hardwood and softwood components in mixed stands. Results presented here demonstrate that white spruce trees are capable of accelerated growth following aspen canopy removal, but only when aspen harvesting is heavy (≈100%) and total stand basal area removal is high (64%–83%). In contrast with a number of previous studies, growth response was detectable within the first 2 years following treatment, and growth rates largely depended on cambial age and vigor prior to treatment. Longer term monitoring is required to evaluate regeneration dynamics as heavy recruitment of aspen could influence white spruce regeneration and growth in the future. Regeneration dynamics, tree mortality, and operational practices were not part of this specific study but obviously also constitute important criteria for evaluating the suitability and success of these types of partial cutting treatments. In the context of ecosystem-based management of mixedwood forests, the results of this study should contribute to the refinement of partial harvesting treatments aimed at integrating natural stand dynamics and maintaining forest productivity.

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