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

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2 Sprucing up the mixedwoods: Growth response of white spruce (*Picea glauca*)
3 to partial cutting in the eastern Canadian boreal forest

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28

29 Abstract

30 Mixed species stands present a number of opportunities and challenges to forest
31 managers. Boreal mixedwood stands in eastern Canada are often characterized by a
32 dominant canopy of shade intolerant aspen (*Populus tremuloides* Michx.) with more
33 shade tolerant conifers in the mid- to sub-canopy layers. Because the aspen and
34 conifer components often attain optimal merchantable sizes at different moments in
35 stand development, there is an interest in developing silvicultural practices that allow
36 partial or total removal of aspen and favour accelerated growth of residual conifers.
37 We tested four partial harvesting treatments in mixed aspen - white spruce (*Picea*
38 *glauca* (Moench.) Voss) stands in which different proportions of aspen (0, 50, 65 and
39 100% basal area) were removed. Ten years after treatments, 72 spruce stems
40 representing dominant, co-dominant, and suppressed social classes were destructively
41 sampled for stem analysis. Using linear mixed effect models, we analyzed growth as
42 a function of treatment intensity, time since treatment, social status, pre-treatment
43 growth rate, and neighbourhood competition. Relative to control stands, radial and
44 volume growth responses were detected only in the extreme treatment of 100% aspen
45 removal. In relative terms, suppressed trees showed the greatest magnitude of
46 cumulative growth increase. Compared to control trees, average annual radial and
47 volume increments were, respectively, 23.5% and 7.1% higher for dominant trees,

48 67.7% and 24.1% higher for co-dominant trees, and 115.8% and 65.6% higher for
49 suppressed trees over the 10 years post-treatment. Growth response was proportional
50 to pre-treatment growth rate and, among neighbouring trees, only coniferous
51 neighbours had a negative effect on white spruce growth. Our results suggest that, in
52 similar mixed stand conditions, relatively heavy removal of overstory aspen
53 accompanied by thinning of crowded spruce would result in greatest growth response
54 of residual spruce stems.

55

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

57 Résumé

58 Les peuplements forestiers mixtes présentent plusieurs opportunités et défis aux
59 aménagistes. Dans l'est du Canada les peuplements mixtes sont souvent dominés par
60 le peuplier faux-tremble (*Populus tremuloides* Michx.) et une forte composante de
61 conifères plus tolérants à l'ombre dans les strates inférieures de la canopée. Puisque
62 les trembles et conifères atteignent souvent des dimensions marchandes optimales à
63 des moments différents, il y a un intérêt à développer des pratiques sylvicoles qui
64 permettent le prélèvement partiel ou total du tremble et favorisent un accroissement
65 accéléré des conifères résiduels. Nous avons testé l'effet de la coupe partielle sur la
66 croissance de l'épinette blanche (*Picea glauca* (Moench.) Voss) dans les peuplements

67 mixtes où quatre intensités de prélèvement (0, 50, 65 et 100% de la surface terrière du
68 tremble) avaient été appliquées. Dix ans après les traitements, 72 épinettes provenant
69 des classes sociales dominante, co-dominante et opprimée ont été abattues et des
70 disques récoltés pour les analyses de tiges. À l'aide de modèles linéaires mixtes, la
71 croissance a été analysée en fonction des facteurs suivants: intensité du traitement,
72 temps depuis le traitement, statut social, taux de croissance avant traitement et
73 compétition par les arbres voisins. Par rapport aux peuplements témoins, une
74 augmentation de croissance a été observée seulement à la suite du traitement extrême
75 (prélèvement du tremble = 100%). En termes de croissance relative, les arbres
76 opprimés ont eu la plus grande hausse de croissance cumulative. Comparativement
77 aux arbres témoins, les taux de croissance radiale et en volume ont été supérieurs de
78 23,5% et 7,1% pour les dominants, 67,7% et 24,1% pour les co-dominants et 115,8%
79 et 65,6% pour les arbres supprimés, au cours des dix ans suivant les traitements. La
80 réaction de croissance après traitement s'est avérée proportionnelle au taux de
81 croissance avant traitement. Parmi les arbres voisins des épinettes échantillonnées,
82 seuls les conifères avaient un effet négatif sur la croissance de ces épinettes. Nos
83 résultats suggèrent que, dans des conditions semblables, un prélèvement relativement
84 intensif de la strate dominante de tremble combiné à l'éclaircissement partiel des
85 épinettes favoriserait un accroissement plus important des tiges résiduelles d'épinette.

86

87 Mots clé: épinette blanche, boréal, mixedwood, coupe partielle, réponse
88 d'accroissement
89

Draft

90 Introduction

91 Despite the global trend of increasing roundwood procurement from single-species
92 plantations, (Jürgensen et al. 2014), there has been a growing interest, since the
93 1970s, in the dynamics and management of forests in natural, semi-natural and
94 planted mixtures. This has come about as a result of a number of factors, notably 1)
95 the recognition of the vulnerability of pure forest stands to biotic and environmental
96 stresses and of the positive effect of mixtures on forest resistance to and resilience
97 following disturbance or stress (Knoke et al. 2008); 2) the potential productivity gains
98 of mixed-species stands (Paquette and Messier 2011); and 3) the higher biodiversity
99 and habitat value of mixed forests (Felton et al. 2010). This recognition, associated
100 with the then emerging paradigms of close-to-nature forest management associated
101 with the Pro Silva movement in Europe (see Bauhus et al. 2013) and natural
102 disturbance (or dynamics)-based management in North America (Franklin et al. 2002)
103 and the southern hemisphere (Attiwill 1994), has also led to greater exploration of
104 management practices, including the use of partial cutting, that integrate natural stand
105 dynamics. Partial cutting is arguably more complex in mixed stands where particular
106 growth characteristics of component species and changes in nutrient availability
107 influence temporal dynamics of the system (Forrester 2014).

108 In the eastern Canadian boreal forest, early stages of development of mixedwood
109 stands following wildfire are typically dominated by fast-growing, shade-intolerant
110 hardwoods, such as trembling aspen (*Populus tremuloides* Michx.) and white birch
111 (*Betula papyrifera* Marsh) (MacDonald 1995, Bergeron 2000). Relatively shade-
112 tolerant conifer species such as white spruce (*Picea glauca* (Moench.) Voss) and
113 balsam fir (*Abies balsamea* (L.) Mill.) may seed in immediately after fire from
114 residual intact forest (Purdy et al., 2002) or slowly recruit in the understory in
115 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, as well as sapling and tree growth. Specifically, spruce and other conifers are often of pre-commercial (< 10 cm diameter at breast height (DBH) 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. Pre-treatment growth rate has been shown to influence post-treatment 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 example, see Yang 1991; Comeau et al. 2005; Stadt et al. 2007; 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 assess 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, pre-treatment growth rate and neighbourhood competition on post-treatment 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 to control stands; (ii) absolute growth rates are higher for dominant and co-dominant trees than suppressed trees; (iii) cumulative relative growth rates are higher for suppressed trees than co-dominant and dominant trees; (iv) growth rates are negatively affected by neighbourhood competition.

165 Methods

166 *Study area and site description*

167 The study site is located in the Abitibi region of Quebec (48°14'32.2"N,
168 79°17'12.00"W), in the Western balsam fir-white birch biogeoclimatic subdomain
169 (Saucier et al. 2009). The area is characterized by mesic soils, primarily Grey
170 Luvisols originating from lacustrine clay deposits left by proglacial Lake Ojibway
171 (Vincent and Hardy 1977). The climate is continental with a daily average
172 temperature of 1.7° C and annual precipitation of 883 mm (625 mm of which falls as
173 rain) (Rivière Kinojevis meteorological station (48°13' N, 78°52' W),
174 (<http://climate.weather.gc.ca/>).

175 The treated stands consisted of mixed aspen-conifer with mean basal area (BA, stems
176 ≥ 5 cm DBH) of 41 m²·ha⁻¹ (Table 1). Mature aspen dominated the canopy layer with
177 conifers generally distributed through the suppressed to co-dominant canopy layers.
178 Mean white spruce and aspen ages were 71 and 68, respectively. While some old
179 (100 to 120 years) white spruce trees were present in stands, 89% of sampled trees
180 established within a period of 14 years, corresponding to calendar years 1937 to
181 1950. Aspen establishment generally occurred throughout the same time period.
182 Basal area distribution of control stands at the time of treatments was 75% aspen
183 (including a minor component of balsam poplar, (*Populus balsamifera* L.)), 20%
184 white spruce, 3% balsam fir, 1% black spruce (*Picea mariana* (Mill.) BSP) and 1%
185 white birch.

186 *Experimental design and treatments*

187 The experimental units were laid out based on prism inventories done prior to
188 treatments. Partial harvesting prescriptions were applied to the experimental units in
189 the late summer of 2001 and the fall of 2002. Trees were manually harvested, limbed,
190 and cut to length on site. Logs were hauled to roadside using narrow-tracked skidders
191 and forwarders in order to minimize damage to residual trees during harvesting
192 operations. Treatments consisted of removing different proportions of aspen in order
193 to encourage the growth of residual conifer stems, primarily white spruce, and
194 promote conifer recruitment. Treatments consisted of a no-harvest control (0% BA
195 removal), two intermediate treatments aimed at removing 50 and 65% of aspen BA,
196 and an extreme treatment of 100% aspen BA removal (Table 1). Each of the four
197 experimental treatments was replicated three times for a total of twelve experimental
198 units (EU) ranging in size from approximately one to four hectares. Immediately
199 following treatments, a total of thirty 400 m² circular permanent sample plots (PSPs,
200 radius=11.28 m) were established: 9 in each of the two intermediate treatments, 6 in
201 the control, and 6 in the extreme treatments. Stems greater than 5 cm in diameter at
202 breast height (DBH, 1.3 m) were tagged, measured, and identified to species. PSPs
203 established in year 0 were re-measured at 5 and 10 years post-treatment.

204 *Destructive sampling of white spruce stems*

205 In 2012, all experimental units had attained the 10 year post-treatment point. In the
206 summer of 2012, destructive sampling was conducted for tree growth analyses. This
207 consisted of harvesting a total of 72 residual white spruce trees from controls and
208 partially cut stands. Live trees selected for felling had little to no external evidence of
209 disease or loss of vigour. Two trees from each of three social status classes
210 (dominant, co-dominant, and suppressed) were selected from each of the 12 EUs.

211 Social status or crown class is a classification of vertical crown position of a tree
212 relative to all other tree crowns and is generally applied to pure stands or stands
213 composed of species with “similar regimes of height growth” (Smith et al. 1997)..
214 However, given the relative facility of measuring DBH, we used the tree diameter
215 distribution of white spruce stems only as a proxy for height distribution in each
216 experimental unit (DBH vs. height for 72 sampled trees, $R^2=0.85$). Given that aspen
217 generally occupied the dominant social class with only a minor component of spruce,
218 assignment of social status to individuals was based exclusively on the relative size
219 among the white spruce trees, rather than social status of all trees within stands.

220 Stem size distribution was calculated for each experimental unit based on white
221 spruce trees in the 2 or 3 PSPs located in the EU. Because crown class determination
222 in the field can be long and imprecise and we had the DBH data, the following
223 classification was used to select individual trees to be destructively sampled from
224 each social status class (Bose et al. 2014): dominant trees: diameter size class ≥ 2
225 standard deviations (SD) of mean DBH; co-dominant trees: size class of ≥ 1 SD of
226 mean DBH; suppressed trees: $\leq$ mean DBH. (We discuss this approach in the
227 conclusion.) Following felling, crown length was measured and live crown ratio for
228 each tree was determined (Table 2).

229 Cross sectional disks were collected from 11 positions along the length of the stem of
230 each tree. The first disk was taken at stump height (0.3 m) and the second from 1.3 m,
231 breast height (BH). The remaining 9 disks were sectioned from equally spaced
232 positions relative to the length of the stem from BH to the top of the tree (Chhin et al.
233 2010). We determined the minimum age of canopy aspen by coring, at a height of 1
234 m, the stem ≥ 20 cm DBH closest to each collected white spruce stem in control,
235 50%, and 65% BA removal experimental units.

236 *Neighbourhood characterisation*

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

242 *Growth measurements*

243 All white spruce cross sectional disks and aspen radial cores were prepared and
244 analyzed in the laboratory using dendroecological procedures to count and measure
245 annual radial growth increments. Disks were visually crossdated using a microscope
246 in order to identify any false or missing rings, and were scanned for image analysis.
247 Annual ring widths were measured along 3 radii per disk using WinDendro (Regent
248 Instruments Canada Inc. 2009). Ring width data obtained from WinDendro was
249 further analyzed using WinStem (Regent Instruments Canada Inc. 2004) which
250 computed average annual radial growth increments ($\text{mm}\cdot\text{yr}^{-1}$) for each disk. We used
251 these values to reconstruct annual volume increments ($\text{dm}^3\cdot\text{yr}^{-1}$). In this paper, we
252 focus on within-bark radial growth rates at 1.3 m and volume growth rates for the
253 entire stem over the last 15 years of growth. Annual cumulative radial and volume
254 growth for each year in the 10 years post-treatment were used to determine relative
255 cumulative growth (%) for each combination of social status and aspen removal
256 treatment. Annual relative radial growth (RRG) was determined for each year by
257 subtracting the initial radius (year prior to treatment or year 0) from the radius of each
258 year in the post-treatment period, dividing by the initial value and multiplying by
259 100:

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

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

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

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

271 Statistical analyses

272 *Model selection and tree growth patterns*

273 Growth patterns were analyzed using linear mixed effect models (Pinheiro and Bates
274 2000; Gelman and Hill 2007). Statistical analyses were conducted using the nlme
275 package in R (R Core Development Team 2012; Pinheiro et al. 2013). Several
276 candidate models were considered and model selection based on Akaike's
277 information criterion corrected for small sample sizes (AICc) was implemented using
278 the AICcmodavg package (Burnham and Anderson 2002; Mazerolle 2013). For each
279 analysis, model-averaged predictions of growth and unconditional 95% confidence
280 intervals were computed based on the entire set of candidate models (Burnham and
281 Anderson 2002; Mazerolle 2013).

282 *Neighbourhood competition indices*

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

287 (2) $HCI_{dist\ indep} = \sum_{i=1}^n \frac{dbh_i}{(dbh_t)}$

288 where, dbh_i is neighbour tree diameter at breast height (cm); dbh_t is collected tree
 289 diameter at breast height (cm).

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

292 (3) $HCI_{dist\ dep} = \sum_{i=1}^n \frac{dbh_i}{(dbh_t)(distance_{it})}$

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

295 In total, 30 variations¹ of Hegyi's HCI were computed by including additional
 296 conditions, specifically neighbour tree type (broadleaf, conifer or all species) and
 297 distance to the collected white spruce stem (≤ 10 m, ≤ 8 m, ≤ 6 m, ≤ 5 m, 5-10 m).
 298 The model selection approach was first used to determine which of the 30 HCIs best
 299 explained radial and volume growth rates of the collected white spruce stems. Each
 300 HCI was considered as a separate model and a null model was included in the
 301 analyses. The competitive effect of neighbours was assumed to have changed through
 302 time; therefore growth data was limited to the average of the last three years,
 303 specifically years 8, 9 and 10 post-treatment (i.e. 1 observation per tree). The growth
 304 data was log transformed to meet model assumptions of normality of residuals and

¹ See supplementary material (Tab S1)

305 homoscedasticity. For these analyses, HCI was considered as a fixed effect and
306 experimental unit was considered as a random effect to account for the repeated
307 observations in each experimental unit. The HCIs from the most parsimonious
308 models explaining radial and volume growth were then used to build the models
309 using additional explanatory variables in subsequent analyses for the same three year
310 period.

311

312 *Modelling years 8-9-10 post-treatment growth with HCI*

313 After selecting the best HCIs explaining neighbourhood competition, nine models²
314 were considered to determine the effects of partial harvesting treatments, social
315 status, pre-treatment growth rate and HCI on average radial and volume growth rates
316 in the last 3 years (years 8, 9 and 10 post-treatment). Cambial age at 1.3 m was also
317 included in all models (excluding the null model), when the response variable was
318 average radial growth rate. Specific interactions between competition (HCI) and
319 treatment intensity and between social status and treatment intensity were included in
320 the models. These variables were considered as the fixed factors and experimental
321 unit was considered as the random factor. Response variables were not transformed
322 prior to analyses since they conformed to model assumptions.

323 *Modelling 10-year post-treatment growth*

324 Fifteen competing models³ including a null model, were considered to determine the
325 effects of partial harvesting treatments, tree social status and pre-treatment growth
326 rates on post-treatment radial and volume growth rates for the entire 10 year post-

² See supplementary material Tab S2.

³ See supplementary material Tab S3

327 treatment period. Treatment intensity and social status were treated as categorical
328 variables while pre-treatment growth rate and time were treated as continuous
329 variables. Seven of the models included the squared value of time (time^2), to account
330 for quadratic effects while the remaining models (excluding the null model)
331 accounted for linear effects of time only. Cambial age at 1.3 m was also included in
332 all models (excluding the null model), when the response variable was radial growth
333 rate. We included specific interactions to quantify changes in growth over time and
334 determine whether growth patterns in different social statuses were similar across
335 treatments. The above-mentioned variables were considered as fixed factors in the
336 mixed effect models. Experimental unit and tree nested within experimental units
337 were considered random effects. Transformations were applied to response variables
338 to ensure that model assumptions of normality and homoscedasticity of residuals
339 were met. A square root transformation was applied to radial growth rate and a log
340 transformation was applied to volume growth rate.

341 Results

342 *Neighborhood competition 8 to 10 years after treatment*

343 The highest ranking HCI for radial growth in years 8 to 10 following treatments
344 (AICc Wt. 0.79) was a distance independent model that accounted for competition by
345 coniferous neighbours only within a 5 m radius (Table 3)⁴. In terms of volume
346 growth, neighbourhood competition was best explained (AICc Wt. 0.68) by a
347 distance dependent HCI, also accounting for competition with coniferous neighbours
348 only, but within a 10 m radius of the sampled white spruce trees (Table 3). These
349 respective top ranking HCIs for spruce growth in years 8-10 were used in subsequent
350 analyses to determine the effect of coniferous neighbourhood competition, with other

⁴ See supplementary materials, Tab S1, for all models.

variables, on the radial and volume growth rates of the white spruce trees 8 – 10 years after harvesting⁵.

Years 8-9-10 post-treatment growth

Average annual radial growth in the last 3 years before destructive sampling was best explained by the model which accounted for the additive effects of cambial age, treatment intensity, HCI and pre-treatment growth rate (Table 4). This top model (AICc Wt. 0.89) was 9.9 times more parsimonious than the second ranking model (AICc Wt. 0.09, Δ AICc 4.58, Table 4). This same top model, excluding cambial age, was also the most parsimonious in terms of volume growth (AICc Wt. 0.75), although the second ranking model accounting for additive effects of HCI and pre-treatment growth rate only was also strongly supported (Δ AICc 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 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 pre-treatment growth rate was an important factor affecting growth; that is, trees with high pre-treatment growth rates showed higher growth rates 7 to 10 years post-treatment (Table 5).

No suppressed trees had what we considered high pre-treatment growth rates (2.0 to 3.8mm·year⁻¹). Co-dominant and dominant trees with pre-treatment growth rates in

⁵ See Supplementary materials, Tab S4, for ranges of variable values.

374 this range had higher mean increments over the 10 year post-treatment period than
375 those with lower pre-treatment growth rates. Co-dominant and dominant trees
376 younger than median age of 52 at time of treatment all had high pre-treatment growth
377 rates (0.95 to $3.8 \text{ mm} \cdot \text{year}^{-1}$). In contrast, trees older than 52 generally had low pre-
378 treatment growth rates (0 to $2.84 \text{ mm} \cdot \text{year}^{-1}$) and older suppressed trees had very low
379 pre-treatment growth rates (0 to $0.95 \text{ mm} \cdot \text{year}^{-1}$).

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

384 *Ten-year post-treatment growth*

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

390 For radial growth, the top ranking model was clearly the most likely, as it had all the
391 support (AICc Wt. 1.0, Table 6; see supplementary material for all models). For
392 volume growth, the most supported model (AICc Wt. 0.68) was 2.13 times more
393 parsimonious than the second ranking model (Table 6) which included the same
394 variables but excluded the quadratic effect of time (time^2).

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

on both radial and volume growth rates of residual white spruce trees in the 10 years following treatment, and this effect was consistent across all three social statuses (Table 7). Compared to 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 post-treatment. Cumulative volume growth of spruce over the post-treatment 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 to 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 two years following treatment. Radial growth followed a negative quadratic form with growth rates peaking at approximately 6 years post-treatment, then gradually decreasing from years 6 to 10 (Fig. 1A-C). This pattern was apparent for all three social statuses. Volume growth followed a similar negative quadratic form, though growth rate continued to increase throughout the 10 year period (Fig. 2A-C).

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

423

Draft

424 Discussion

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

431 *Neighbourhood competition*

432 Neighbourhood competition indices are generally based on the size ratio of target and
433 neighbour trees and assume that competition decreases with increasing distance to a
434 neighbouring tree and decreasing neighbour size. We used a series of simple indices
435 based on Hegyi's competition index (1974) because they are easily computed, yet have
436 proved to be effective in other studies (Filipescu and Comeau 2007).

437 Across all treatments, average radial and volume growth in years 8, 9, and 10 post-
438 treatment were negatively influenced by neighbourhood conifer competition. Aspen is
439 generally considered to have a competitive advantage in mixed stands on productive
440 sites, such as the ones in this study (Boivin et al. 2010). This advantage is primarily due
441 to its prolific suckering and superior juvenile growth rate which allows trees to attain
442 canopy dominance and capture more resources, particularly light (Frey et al. 2003;
443 Balandier et al. 2006). The anticipated significant competitive effect of aspen on white
444 spruce was a fundamental assumption in the design of this partial cutting experiment.
445 However, aspen did not exert the competitive effect on merchantable white spruce trees
446 that we originally expected. This is potentially due to higher light transmission levels in
447 aspen canopies, related to aspen's lower leaf biomass, and leaf-off seasons (Constabel
448 and Lieffers 1996; Man and Lieffers 1999). Results concur with those of Stadt et al.
449 (2007) and Huang et al. (2013) who, using more complex competition indices, also found
450 that intraspecific competition caused greater reductions in white spruce growth than
451 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, and 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) This was not the case, however.

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 and Stadt 1994; 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 post-treatment 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 to 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 to 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 post-treatment 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. The NCI analyses 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 two years following treatment. The lack of thinning shock and absence of an extended time lag in growth response was somewhat surprising since 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, pre-treatment 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, $R^2 = 0.84$).⁶ 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 the 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.

⁶ See Supplementary material, Fig S1.

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 to 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 post-treatment 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 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). Larger trees by definition 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.

In terms of relative radial and volume growth, however, suppressed trees showed the greatest positive response to treatments, followed by co-dominant, and dominant trees. Factors at play here are related to differences both in 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 pre-treatment growth rates. Less vigorous trees with slower pre-treatment growth rates continue to exhibit slow but improved post-treatment growth rates. In contrast, more vigorous, younger trees continue to have the highest growth rates post-treatment. Pre-treatment tree vigour has also been shown to influence post-treatment 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 in order 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,

594 accompanied by harvesting of a portion of the largest and presumably oldest spruce, and
595 thinning of other crowded spruce (Bose et al. 2014).

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

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

607 Conclusion

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

622 partial harvesting treatments aimed at integrating natural stand dynamics and maintaining
623 forest productivity.

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1 Table 1. Characteristics of the 12 experimental units.

Treatment intensity class (% aspen BA removal) and replicate	Initial BA (m ² ·ha ⁻¹) [†]	BA post-treatment (m ² ·ha ⁻¹)	BA 5 years post-treatment (m ² ·ha ⁻¹)	BA 10 years post-treatment (m ² ·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

2 [†] Initial basal area (BA) values were derived from prism inventories prior to
3 treatments based on stems ≥ 10 cm DBH, whereas post-treatment BA values (for
4 stems ≥ 5 cm DBH) were derived from fixed radius (11.28m) PSPs established
5 immediately following treatments; these were re-measured at years 5 and 10 post-
6 treatment.

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)

Table 3. Results of model selection for linear mixed effects models based on Akaike's Information Criterion corrected for small sample size (AICc). Average annual radial growth rate ($\text{mm}\cdot\text{year}^{-1}$) at 1.3 m and average annual volume growth rate along the stem ($\text{dm}^3\cdot\text{year}^{-1}$) 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. (See supplementary material (Tab S1) for all models tested.)

Model	K	AICc	ΔAICc	AICc Wt.	R^2
<i>Radial growth at 1.3 m ($\text{mm}\cdot\text{year}^{-1}$)</i>					
HCI 13 [†]	4	111.49	0.00	0.79	0.56
HCI 2 [‡]	4	115.64	4.15	0.10	0.53
<i>Volume growth along the stem ($\text{dm}^3\cdot\text{year}^{-1}$)</i>					
HCI 22 [§]	4	140.12	0.00	0.68	0.72
HCI 13	4	141.72	1.59	0.31	0.71

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

[‡]Distant-independent, all trees, within 8 m radius.

[§]Distant-dependent, conifers only, within 10 m radius.

^{||}Distant-independent, conifers only, within 5 m radius.

Table 4. Results of model selection for linear mixed effects models based on Akaike’s Information Criterion corrected for small sample size (AICc). Average annual radial growth rate ($\text{mm}\cdot\text{year}^{-1}$) at 1.3 m and average annual within-bark volume growth rate ($\text{dm}^3\cdot\text{year}^{-1}$) of residual white spruce trees in the last 3 years following partial harvesting treatments were analyzed as a function of treatment intensity[†] (intensity), social status[‡] (ss), neighbourhood competition[§] (HCI), pre-treatment growth rate^{||} (pre-treat) and cambial age[¶] (age). Interactions between variables are specified with a colon. For brevity, only the most parsimonious models are shown.

Model number [#]	Model	K	AICc	ΔAICc	AICc Wt.	R ²
<i>Radial growth at 1.3 m ($\text{mm}\cdot\text{year}^{-1}$)</i>						
5	age + intensity + HCI + pre-treat	9	138.97	0.00	0.89	0.63
7	age + intensity + HCI + pre-treat + intensity:HCI	12	143.55	4.58	0.09	0.65
<i>Volume growth along the stem ($\text{dm}^3\cdot\text{year}^{-1}$)</i>						
5	intensity + HCI + pre-treat	8	397.66	0.00	0.75	0.89
6	HCI + pre-treat	5	400.60	2.94	0.17	0.89

K: number of parameters
AICc: Akaike’s Information Criterion corrected for small sample size
 ΔAICc : AICc relative to most parsimonious model
AICc Wt.: model weight
[†] Treatment intensity: control, 50%, 65%, 100% aspen basal area removal
[‡] Intraspecific social status of residual white spruce trees: suppressed, co-dominant, dominant
[§] Neighbourhood competition as determined using the most parsimonious competition index. See Table 3.
^{||} The average annual radial and volume growth rate 5 years prior to treatment
[¶] Cambial age taken at 1.3 m (used to analyze radial growth only)
[#] See Table S2, Supplementary material.

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

Term	Estimate [§]	Lower CI	Upper CI
<i>Radial growth at 1.3m ($\text{mm} \cdot \text{year}^{-1}$)</i>			
pre-treatment growth rate	0.3554	0.1094	0.6014
HCI13 [†]	-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
<i>Volume growth along the stem ($\text{dm}^3 \cdot \text{year}^{-1}$)</i>			
pre-treatment growth rate	0.7792	0.6765	0.8818
HCI22 [‡]	-0.6447	-1.0369	-0.2525
intensity 4 (100% aspen BA removal)	3.4356	1.1755	5.6956

[†] Neighbourhood competition index: Distance-independent, conifers only, within 5 m radius.

[‡] Neighbourhood competition index: Distant-dependent, conifers only, within 10 m radius.

[§] 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.

Table 6. Results of model selection for linear mixed effects models based on Akaike’s Information Criterion corrected for small sample size (AICc). Annual radial growth rate ($\text{mm}\cdot\text{year}^{-1}$) at 1.3 m and annual stem volume growth rate ($\text{dm}^3\cdot\text{year}^{-1}$) for residual white spruce trees 10 years following partial harvesting treatments was analyzed as a function of treatment intensity[†] (intensity), time[‡] (time), social status[§] (ss), pre-treatment growth rate^{||} (pre-treat) and cambial age[¶] (age). Interactions between variables are specified with a colon. For brevity, only the most parsimonious models are shown.

Model number	Model	K	AICc	ΔAICc	AICc Wt.	R2
	<i>Radial growth at 1.3 m ($\text{mm}\cdot\text{year}^{-1}$)</i>					
15	age + intensity + ss + time + time ² + pre-treat + intensity:time + intensity:time ²	19	-296.63	0.00	1	0.83
	<i>Volume growth along the stem ($\text{dm}^3\cdot\text{year}^{-1}$)</i>					
15	intensity + ss + time + time ² + pre-treat + intensity:time + intensity:time ²	18	523.44	0.00	0.68	0.94
22	intensity + ss + time + pre-treat + intensity:time	14	524.95	1.52	0.32	0.94

K: number of parameters

AICc: Akaike’s Information Criterion corrected for small sample size

ΔAICc : AICc relative to most parsimonious model

AICc Wt.: model weight

[†] Treatment intensity: control (0%), 50%, 65%, 100% aspen basal area removal

[‡] Time and time² were tested to determine linear and quadratic effects

[§] Intraspecific social status of residual white spruce trees: suppressed, co-dominant, dominant

^{||} Average annual radial and volume growth rate 5 years prior to treatment

[¶] Cambial age taken at 1.3 m (used to analyze radial growth only)

[#] See Table S3, Supplementary material.

Table 7. Model-averaged estimates and their 95% confidence interval (CI) based on model selection for linear mixed effects models. Only parameter estimates for terms which exclude 0 in the confidence interval are presented. Response variables are annual radial growth rate at 1.3 m ($\text{mm} \cdot \text{year}^{-1}$) and annual volume growth rate within bark ($\text{dm}^3 \cdot \text{year}^{-1}$). See Table 4 for variable descriptions.

Term	Estimate [†]	Lower CI	Upper CI
<i>Radial growth at 1.3 m ($\text{mm} \cdot \text{year}^{-1}$)</i>			
time	0.0275	0.0048	0.0502
time ²	-0.0026	-0.0043	-8e-04
pre-treatment 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
<i>Volume growth along the stem ($\text{dm}^3 \cdot \text{year}^{-1}$)</i>			
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
pre-treatment 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.

1

2 List of figures

3 Figure 1. Post-treatment radial growth (A, B C) and relative cumulative radial growth (D,
4 E, F) of white spruce presented as a function of time since treatment for suppressed, co-
5 dominant and dominant trees, respectively[†].

6 Figure 2. Post-treatment volume growth (A, B C) and relative cumulative volume growth
7 (D, E, F) of white spruce presented as a function of time since treatment for suppressed,
8 co-dominant and dominant trees, respectively[†].

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9 Figure 1

[†] Lines represent model-averaged predicted values and points represent observed values in figures A-C. Therefore, a value of 0.75 representing the minimum pre-treatment growth rate of dominant trees was used. A value of 50.75 representing mean cambial age of all trees was used to make predictions.

Figure 2

[†] Lines represent predicted values and points represent observed values in figures A-C. A value of 9.23 representing mean pre-treatment growth rate of all trees was used to make predictions.

Supplementary material for Smith, J, Harvey, BD, Koubaa, A, Brais, S, Mazerolle, MJ.

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

Draft

Figure S1 Relationship between diameter at breast height (DBH) and tree height of sampled white spruce trees in 2012.

Stem size distribution was calculated for each experimental unit based on white spruce trees in the permanent sample plots (PSPs). The following classification was used to select individual trees to be destructively sampled from each social status class: dominant trees: diameter size class ≥ 2 standard deviations (SD) of mean DBH; co-dominant trees: size class of ≥ 1 SD of mean DBH; suppressed trees $\leq$ the mean DBH.

Table S1. The 30 variations of Hegyi's neighbourhood competition index (HCI)

Model	Neighbour Tree Type	Distance Dependent	Distance to target white spruce tree
HCI1	All trees	No	0-10m
HCI 2	All trees	No	0-8m
HCI3	All trees	No	0-6m
HCI 4	All trees	No	0-5m
HCI 5	All trees	No	5-10m
HCI 6	Broadleaf	No	0-10m
HCI 7	Coniferous	No	0-10m
HCI 8	Broadleaf	No	0-8m
HCI 9	Coniferous	No	0-8m
HCI 10	Broadleaf	No	0-6m
HCI 11	Coniferous	No	0-6m
HCI 12	Broadleaf	No	0-5m
HCI 13	Coniferous	No	0-5m
HCI 14	Broadleaf	No	5-10m
HCI 15	Coniferous	No	5-10m
HCI 16	All trees	Yes	0-10m
HCI 17	All trees	Yes	0-8m
HCI 18	All trees	Yes	0-6m
HCI 19	All trees	Yes	0-5m
HCI 20	All trees	Yes	5-10m
HCI 21	Broadleaf	Yes	0-10m
HCI 22	Coniferous	Yes	0-10m
HCI 23	Broadleaf	Yes	0-8m
HCI 24	Coniferous	Yes	0-8m
HCI 25	Broadleaf	Yes	0-6m
HCI 26	Coniferous	Yes	0-6m
HCI 27	Broadleaf	Yes	0-5m
HCI 28	Coniferous	Yes	0-5m
HCI 29	Broadleaf	Yes	5-10m
HCI 30	Coniferous	Yes	5-10m

Table S2. Nine competing models used to test the effects of treatment intensity (intensity), social status (ss), pre-treatment growth rate (pre-treat), neighbourhood competition index (HCI) and cambial age¹ (age) on radial and volume growth rates of white spruce trees. Interactions between variables are specified with a colon.

Model	Biological interpretation
1. null	No effect of treatment, social status, pre-treatment growth rate or competition on average annual growth in last 3 years.
2. age + intensity + pre-treat	Growth differs depending on treatment but assumes no differences in growth between social statuses.
3. age + ss + pre-treat	Growth differs depending on tree social status but assumes no differences in growth between treatments.
4. age + HCI + pre-treat	Growth differs depending on neighbourhood competition but assumes no differences in growth between social statuses or treatments.
5. age + intensity + HCI + pre-treat	Growth differs depending on treatment and neighbourhood competition but assumes no differences in growth between social statuses.
6. age + intensity + ss + pre-treat	Growth differs depending on treatment and tree social status but assumes no differences in neighbourhood competition amongst the treatments.
7. age + intensity+ HCI + pre-treat + intensity:HCI	Growth differs depending on neighbourhood competition but assumes no differences in growth between social statuses. The effect of competition differs depending on the treatment.
8. age + intensity + ss + pre-treat + ss:intensity	Growth differs depending on social status but no difference in neighbourhood competition amongst the treatments. Growth of trees within a social status differ depending on treatment intensity.
9. age + pre-treat	Growth depends on pre-treatment growth and assumes no effect of treatment, social status or neighbourhood competition.

¹ Cambial age taken at 1.3 m (used to analyse radial growth only). That is, models 2 to 9 for volume growth do not include age.

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Table S3. Fifteen competing models used to test the effects of treatment intensity (intensity), social status (ss), time, pre-treatment growth rate (pre-treat) and cambial age¹ (age) on radial and volume growth rates of white spruce trees. Models 11 to 17 test the quadratic effect of time, models 18 to 24 test the linear effect of time. Interactions between variables are specified with a colon.

Model	Biological interpretation
10. null	No effect of treatment, social status, time or pre-treatment growth on post-treatment growth.
11. age + time + time ² + pre-treat	No effect of treatment or social status on post-treatment growth.
12. age + intensity + time + time ² + pre-treat	The effect of treatment is the same across time, no effect of social status.
13. age + intensity + ss + time + time ² + pre-treat	The effect of treatment is the same across time and assumes no differences in growth between social statuses across all treatments.
14. age + ss + time + time ² + pre-treat	There are no differences in growth between social statuses across all treatments and time.
15. age + intensity + ss + time + time ² + pre-treat + intensity:time + intensity:time ²	The effect of treatment differs across time and assumes no differences in growth between social statuses across all treatments.
16. age + intensity + ss + time + time ² + pre-treat + intensity:ss	The effect of treatment is the same across time but growth differs for trees of different social statuses depending on treatment intensity.
17. age + intensity + ss + time + time ² + pre-treat + ss:time + ss:time ²	The effect of treatment is the same across time but growth differs for trees of different social statuses across time.
18. age + time + pre-treat	No effect of treatment or social status on post-treatment growth.
19. age + intensity + time + pre-treat	The effect of treatment is the same across time periods, no effect of social status.

20. age + intensity + ss + time + pre-treat	The effect of treatment is the same across time and assumes no differences in growth between social statuses across all treatments.
21. age + ss + time + pre-treat	There are no differences in growth between social statuses across all treatments and time.
22. age + intensity + ss + time + pre-treat + intensity:time	The effect of treatment differs across time and assumes no differences in growth between social statuses across all treatments.
23. age + intensity + ss + time + pre-treat + intensity:ss	The effect of treatment is the same across time but growth rates differ for trees of different social statuses depending on treatment intensity.
24. age + intensity + ss + time + pre-treat + ss:time	The effect of treatment is the same across time but growth differs for trees of different social statuses across time.

¹ Cambial age taken at 1.3 m (used to analyse radial growth only). That is, models 11 to 24 for volume growth do not include age.

Table S4. Minimum and maximum values for several variables and two Heygi competition indices used in analyses.

Variable	Social Status	min	max
Age (years, minimum age from cambial age at 0.3m)	All spruce	52	120
	suppressed	45	77
	co-dominant	52	101
	dominant	65	120
Cambial age (years)	All spruce	12	106
	suppressed	12	55
	co-dominant	33	57
	dominant	45	106
Radial Pre5 (mm.yr ⁻¹)	All spruce	0.07	3.842
	suppressed	0,07	1,91
	co-dominant	0,218	2,99
	dominant	0,75	3,842
Volume Pre5 (dm3.yr ⁻¹)	All spruce	0.204	43.902
	suppressed	0,204	2,068
	co-dominant	1,21	9,914
	dominant	7,966	43,902
HCI13 (radial growth)	All spruce	0,94	58,22
	suppressed	4,89	58,22
	co-dominant	4,95	24,36
	dominant	0,94	14,87
HCI22 (volume growth)	All spruce	0,4	13,4
	suppressed	1,09	13,4
	co-dominant	1,3	6,87
	dominant	0,4	3,71