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Trembling aspen (*Populus tremuloides* Michx.) volume growth in the boreal mixedwood: Effect of partial harvesting, tree social status, and neighborhood competition

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ABSTRACT

Variable retention harvesting, with a focus on maintaining biological legacies on managed landscapes, has been practised in the trembling aspen (*Populus tremuloides* Michx.) dominated boreal mixedwood forests for about two decades. However, little attention has actually been given to the growth response of aspen to partial harvesting. This is the first study to report on tree-level volume growth response of aspen after partial or variable retention harvesting in the Canadian boreal forest. During the winter of 1998–1999, an uncut control, clearcut and two partial harvesting treatments – 1/3 partial cut (1/3PC, 33% BA removal using low thin); 2/3 partial cut (2/3PC, 61% BA removal using high thin) – were applied in 75 year old aspen-dominated mixedwood stands in a complete randomized block design. Twelve years after treatment application, 27 dominant and 27 co-dominant trees were collected from unharvested controls and the two partial cut treatments for stem analysis. Annual volume increment (AVI) of individual stems was analyzed as a function of treatment, tree social status, pre-treatment growth, time since treatment application (1–12 years) and neighborhood competition. The latter was estimated using a variety of neighborhood competition indices (NCI). There was no evidence of initial growth stagnation after partial harvesting applications. Only the most severe treatment of partial harvesting (2/3 PC) resulted in an increase in volume increment relative to trees in control stands. Annual increase in volume in the 2/3 partial cut was 25.6% higher than controls over 12 years. AVI of dominant trees was higher by 16.2 $dm^3\,yr^{-1}$ than that of co-dominants and was proportional to pre-treatment volume growth. No interaction between treatment and social status or pre-treatment growth was observed. The overall results indicate that competition for resources in these stands is essentially size symmetrical. These results should contribute to the development of silviculture prescriptions that aim to maintain both stand productivity and biological legacies.

1. Introduction

Variable retention harvesting, with a focus on maintaining biological legacies on managed landscapes, has been practised in the aspen-dominated boreal mixedwood forest for about two decades (Lieffers et al., 1996; Bose et al., 2014). Depending on the amount and configuration of tree retention, this system ostensibly emulates primary natural disturbances such as high intensity wildfires (less retention) or secondary disturbances such as insect outbreaks or individual or group mortality (more retention) (Thorpe and Thomas, 2007). In the boreal mixedwood, the southern-most swath of forest that extends across the boreal forest biome of Canada, partial harvesting has been proposed where intolerant hardwoods, especially trembling aspen (*Populus tremuloides* Michx.), reach maturity before more shade-tolerant softwood species (Lieffers et al., 1996; Bergeron and Harvey, 1997).While attractive from an ecosystem management viewpoint, from a timber supply and economic perspective, partial harvesting practices need to be evaluated over more than the short term (Ruel et al., 2013) and can be considered successful if residual trees respond well in terms of growth and survival (Coates, 1997; Thorpe et al., 2007).

In the last 15 years, a number of experiments have been set up across the boreal mixedwood forest to test the ecological feasibility of forest ecosystem management (FEM) (e.g., Brais et al., 2004; MacDonald et al., 2004; Solarik et al., 2010). While a number of studies have examined stand-level responses to partial harvesting

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(e.g., Man et al., 2008a; Gradowski et al., 2010; Brais et al., 2013), fewer have focused on how residual aspen trees respond individually to partial harvesting (Bladon et al., 2007; Solarik et al., 2012) and these have mainly focussed on aspen mortality in response to variable retention. Some other studies have evaluated tree-level growth responses in the continuous conifer boreal region, such as black spruce (*Picea mariana* (Mill.) responses to harvesting with advanced regeneration protection (Thorpe et al., 2007) and to commercial thinning (Goudiaby et al., 2012). We have found no studies quantifying the volume growth response of mature aspen trees to partial harvesting.

By removing trees from different canopy layers, partial harvesting affects light availability, and thereby competition among residual trees (Hartmann et al., 2009). Individual tree-level growth responses to partial harvesting have been shown to depend on tree age (Thorpe et al., 2007), size (Jones and Thomas, 2004), physiological traits (Jones et al., 2009; Anning and McCarthy, 2013b), and pre-harvest growth rate (Thorpe et al., 2007). Immediately following harvesting treatments, it is also expected that tree growth response will depend on acclimation to evolving growing conditions including availability of light and soil resources, post-harvest social status, and neighborhood competition (Thorpe et al., 2007; Hartmann et al., 2009; Anning and McCarthy, 2013a). Several studies have documented an initial (2–5 years) growth stagnation in residual trees immediately following harvesting (Jones and Thomas, 2004; Thorpe et al., 2007; Goudiaby et al., 2012) probably due to the sudden change in the stand's microclimatic condition (Bose et al., 2014). Kneeshaw et al. (2002) suggested, that larger trees may be more prone to initial growth stagnation due to the presence of higher non-photosynthetic biomass requiring higher maintenance costs and higher allocation to root growth for mechanical support.

The SAFE project ("Sylviculture et Aménagement Forestier Ecosystémique") (Brais et al., 2004; Brais et al., 2013) is a series of experiments undertaken in Northwestern Quebec, Canada to assess the feasibility of FEM silvicultural practices for this region. The first phase of the SAFE project was established in post-fire, naturally regenerated aspen-dominated stands (Brais et al., 2004; Harvey and Brais, 2007) that were submitted to four levels of harvesting, including two intensities of partial harvesting, in 1998.

The objective of the study is to evaluate the effects of partial harvesting on the annual volume increment of residual trees of trembling aspen over a 12-year period following harvesting. We specifically investigated the effects of partial harvesting treatment and tree social status on volume increment of residual trees. Because stand conditions evolve in response to harvesting (Harvey and Brais, 2007; Bose et al., accepted for publication), we also considered pre-treatment volume growth and neighborhood competition as possible explanatory factors for volume increment during last 3 year period (10–12 years following treatments). Accordingly, we tested the following hypotheses: (i) tree volume increment would increase with increasing intensities of partial harvesting (Thorpe et al., 2007), but decrease with increasing neighborhood competition in the longer term (Hartmann et al., 2009; Anning and McCarthy, 2013a); (ii) size-dependent competition indices are expected to better explain the annual volume increment of aspen residual trees over distance-dependent indices (Canham et al., 2006); and (iii) a growth lag is expected immediately after treatment applications followed by a linear increase in annual volume increment (Jones and Thomas, 2004; Thorpe et al., 2007). We also anticipated that the size of residual trees could affect their response in two different ways: (iv) dominant stems or stems with the highest pre-treatment volume increment would experience the strongest volume growth response following harvesting (Berntson and Wayne, 2000; Jones and Thomas, 2004) or, inversely, light-limited co-dominant trees (relative to dominants) could benefit the most from canopy opening (Walter and Maguire, 2004).

2. Methods

2.1. Study area

The study area is located in the Lake Duparquet Research and Teaching Forest (48°86′N–48°32′N, 79°19′W–79°30′W) in the Abitibi region of Northwestern Quebec. The region is part of the balsam fir-white birch bioclimatic domain (Saucier et al., 1998), and is characterized by the presence of extensive clay deposits left by proglacial Lake Ojibway (Vincent and Hardy, 1977). Soils are gray Luvisols and soil texture is that of heavy clay (>75% clay). The forest floor is a thin mor of 2–7 cm (Canada Soil Survey Committee, 1987).The climate is continental with mean annual precipitation (1991–2010) of 847 mm, of which 583 mm falls as rain from April to September. Mean annual temperature is 1.95 °C with an average daily temperature of 11.9 °C from April to September (BioSIM, 2012).

The stands are even-aged (75 years old at time of treatment) and originated from a wildfire in 1923 (Dansereau and Bergeron, 1993). Before treatment application, average stand basal area was 42.1 $m^2\ ha^{-1}$ of which 92.6% was trembling aspen and 3.3% conifer species. The shrub layer was dominated by mountain maple (*Acer spicatum* Lamb.) with an average density of 1327 stems ha^{-1} (Bourgeois et al., 2004). Four harvesting treatments, including a no harvest control, two intensities of partial harvesting and a clearcut, were applied during the 1998–1999 winter. The two partial harvesting treatments were designed to remove 33% (1/3 partial cut) and 61% (2/3 partial cut) of the stand's merchantable basal area. Stands in the 1/3 removal were low thinned with primarily smaller, low-vigor aspen stems removed (1/3 partial-cut). This treatment was intended to emulate density dependent mortality (self-thinning) in stand development. Stands in the 2/3 removal were crown thinned with more vigorous co-dominant and dominant aspen stems preferentially selected (2/3 partial-cut), thus presenting a mortality analogue of stand senescence (Brais et al., 2004). Harvesting treatments were applied according to a complete randomized block design with three replications (blocks) of each treatment. Experimental units ranged from 1 to 2.5 ha. In 2001, the stands were affected by a forest tent caterpillar (FTC, *Malacosoma disstrium* Hübner) outbreak.

2.2. Data collection

Trees selected for stem analyses were harvested in the fall and winter of 2011 and summer of 2012 in control and partially harvested experimental plots. Both dominant and co-dominant residual trees were selected based on their diameter, crown size and crown's relative exposure among neighbors. Average diameter at breast height (DBH, 1.3 m) was first compiled from the most recent tree inventory (2010) in permanent sample plots for each of the three experimental blocks in order to determine size ranges for each social status. DBH size was used as a first step because of its strong correlation with tree height ($r = 0.77$). Trees were considered dominant if their DBH was ⩾2 standard deviations (SD) of the experimental block average, and co-dominants if their DBH was ⩾1 SD. In addition to diameter size, visual inspection of relative crown size and exposure among neighbors was also used to select sample trees. Specifically, trees in the dominant social class (according to DBH) had to clearly have large crowns compared to others in the canopy and crowns of "DBH co-dominants" situated close to dominants had to be smaller than those of dominants. Harvested trees were located at least 20 m from roads to minimize edge effects, from permanent sample plots and from other sampled trees. All sampled trees were free of any visible damage, decay or infection.

Table 1
Characteristics of dominant and co-dominant trembling aspen trees sampled in boreal mixedwood stands submitted to partial harvesting 12 years prior to sampling.

Treatment	Social status	DBH range (cm)	Mean DBH (cm)	Height range (m)	Mean height (m)	Live crown length (range) (m)	Mean length of live crown (m)	Crown width (range) (m)	Mean crown width (m)	Mean height at age 50 years	DBH range in 1998 (pre-treatment) (cm)	Mean DBH in 1998 (pre-treatment) (cm)
Control	Dominant	34–45.4	39.5	25.6–31.1	28.02	6.8–13.6	9.7	11.1–16.4	13.3	24.2	30.4–39.0	34.3
	Co-dominant	24–27.6	25.9	22.8–28.9	25.07	2.9–9.3	6.6	6.7–9.8	8.4	21.5	18.3–25.4	21.8
1/3 partial-cut	Dominant	32.1–47.7	39.7	24.1–28.7	26.53	7.9–11.4	10.2	11.1–15.5	13.1	22.3	26.7–38.1	32.7
	Co-dominant	20.3–25.5	22.8	19.6–26.7	23.18	3.8–10.8	6.4	7.6–11.7	8.9	20.4	18.6–23.6	21.8
2/3 partial-cut	Dominant	31.2–48.4	37.7	23.5–28.9	25.89	5.5–12.2	7.8	10.8–14.1	12.9	22.0	22.3–40.4	29.0
	Co-dominant	21.7–27.2	24.2	20.8–27.5	24.25	4.4–10.6	6.8	8–10.3	9.4	19.5	17.6–24.6	20.0

Note: All sampled trees were 87–88 years old. Crown width was calculated by adding the length of two largest branches from two opposite sides of the tree.

Three trees of each social status were selected from each experimental unit (control, 1/3 partial cut and 2/3 partial cut) within each of the 3 blocks for a total 54 trees (Table 1). To develop and compare a number of competition indices, the neighborhood around each sampled tree was characterized. All live-standing neighbor trees/ high shrubs ($\geqslant$5 cm at DBH) within a 10 m radius were identified and their DBH measured. Their distance to the center of the plot (to target tree) was also measured. Distance to the center was measured with a precision of 0.1 m using a Vertex clinometer (Haglöf, Sweden).

Sampled stems were cut at the base. Eleven cross-sectional disks were collected along the stem starting with a disk (D.1) at 0.15 m or stump height (SH) and a second disk (D.2) at 1.3 m (breast height, BH). The remaining nine disks (D.3–D.11) were collected at equally spaced positions between breast height and the top of the stem (Chhin et al., 2010).

2.3. Laboratory analyses

All disks were sanded with progressively finer grits of sandpaper (60–400 grain). Disks were examined under a microscope; pointer years (severe growth declines in 1954, 1980 and 2001) and false rings (Chhin et al., 2010) were marked and trees were aged to the year 2010. Tree rings were measured and analyzed using WinDendro version 2009 (Regent Instruments). The measurements were carried out on three radii per disk (Lopatin et al., 2008). Visual cross-dating and tree-ring measurements were further validated using pointer years and the COFECHA program (Grissino-Mayer, 2001). For each sampled stem, we corrected the number of missing or mistakenly-dated rings. The correlation coefficient with a master chronology created by COFECHA was 0.62–0.97 using all sample stems. Annual volume increments were then estimated using WinStem software (Regent Instruments).

2.4. Neighborhood competition indices

The neighborhood competition surrounding each sampled tree in 2011 was quantified using the neighborhood competition index (NCI) equation used by Hartmann et al. (2009) for Sugar maple (*Acer saccharum* Marsh.) in Quebec.

$$\mathrm{NCI} = \frac{\sum_{j=1}^{N}(\mathrm{DBH}_j)^{\alpha}/(\mathrm{dist}_{ij})^{\beta}}{1000} \tag{1}$$

where DBH_j is the DBH (in cm) of a neighbor tree j, which is located at a distance dist_{ij} (in m) from the target tree i.

The neighbor size effect on competition is defined by α, whereas β defines the slope at which the competition from neighboring trees declines with their distance to the target tree. An $\alpha = 0$ indicates that competition from neighboring trees is independent of their size, an $\alpha = 1$ indicates that competition is proportional to neighbors' diameters, and an $\alpha = 2$ indicates that neighbors' effect is proportional to their basal area (Canham et al., 2006). A $\beta = 0$ indicates the competition exerted by neighbors is independent of their distance to the target tree; a $\beta = 0.5$ indicates competition is proportional to the square-root of the distance to the target tree; a $\beta = 1$ indicates that neighbors' competitive effect decreases with distance; and a $\beta = 2$ indicates that the effect increases with the power of the distance (Coates et al., 2009). The R value is the radius within which neighbors have an effect on a target tree. Thirty-six different models of NCI were considered based on all possible combinations of three α values (0, 1, or 2), four β values (0, 0.5, 1, or 2), and three R values (6, 8, or 10 m) (Appendix A). Because trembling aspen represented 81% of neighborhood basal area of all target trees and because neighbors within 8 m of all target trees were

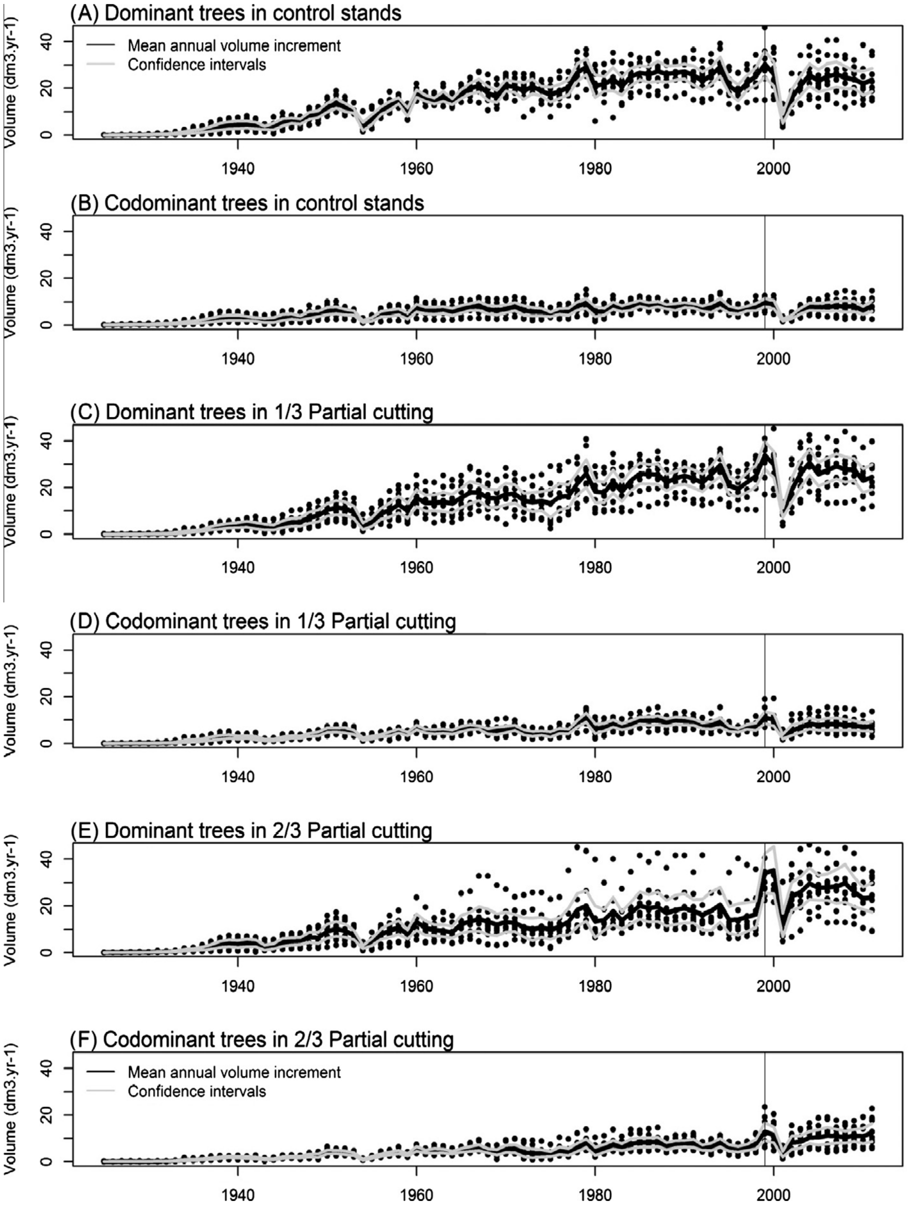

Fig. 1. Annual volume increment of sampled trees according to social status and treatments. *Note:* Vertical line indicates year of harvesting treatments.

mostly trembling aspen, we did not account for neighbor species effect in NCI estimations.

2.5. Statistical analysis

2.5.1. Selection of the NCI that best predicts annual volume increment

A model selection approach based on Akaike's Information Criterion, corrected for small samples (Burnham and Anderson, 2002; Mazerolle, 2006), was used to identify which NCI among the 36 NCI models was the most appropriate predictor of recent volume increment. Annual volume increment ($dm^3\ yr^{-1}$) of each tree was averaged over the last 3 years (2008–2010). A linear mixed model (Pinheiro and Bates, 2000) was fitted between average annual volume increment of years 2008–2010 and NCIs using the nlme package of R (Pinheiro et al., 2011; R-Development-Core-Team, 2011) with NCI treated as a fixed effect, and blocks and experimental units (EU) within blocks treated as random factors. A square-root-transformation was applied to the response variable to ensure the normality and homogeneity of the residuals of models. Model selection was implemented using the AICcmodavg package of R (Mazerolle, 2011). Along with 36 NCI models, we included a null model to test the null hypothesis of no NCI effect on annual volume increment. The best NCI model with the highest Akaike weight was retained for further analyses.

2.5.2. Factors affecting tree response to partial harvesting

We also used linear mixed models (Table 2) to assess the relationships (1) between the 1999–2010 (post-treatment) annual volume increments and harvesting treatment, tree social status and time (linear and quadratic), and (2) between the 2008–2010 average annual volume increment and harvesting treatment, NCI, tree social status and pre-treatment volume increment (average annual volume increment of last 3 years before treatment). Selected interactions were also included in models (Table 2). Additionally, a null model was included in both analyses to test the null hypothesis of no effect of explanatory variables on annual volume increment. Block, experimental unit and tree (each one nested in the former) were treated as random factors. We also accounted for the compound symmetry correlation structure between repeated (annual) measurements of individual trees. A square root transformation

Table 2
Mixed linear model analyses of annual volume increment of trembling aspen stems, 1–12 years following harvesting.

Analysis	Research questions	Response variables	Explanatory variables
1.	Best probable neighborhood competition indices	Average annual volume increment ($dm^3\ yr^{-1}$) of the last three years (2008–2010) prior to destructive sampling of stems	Variants of NCI based on α (0, 1, and 2), β (0, 0.5, 1, and 2), and R (6, 8, and 10 m)
2.	Effect of harvesting treatment, social status and time since treatment application	Annual volume increment ($dm^3\ yr^{-1}$)	Treatment, social status, time, time^2, treatment ∗ social status, partial harvesting ∗ time, and partial harvesting ∗ time^2
3.	Effect of harvesting treatment, social status, NCI, pre-treatment volume increment	Average annual volume increment ($dm^3\ yr^{-1}$) of the last three years (2008–2010) prior to destructive sampling of stems	Treatment, social status, NCI, pre-treatment volume increment, partial harvesting ∗ social status, partial harvesting ∗ NCI, partial harvesting ∗ pre-treatment volume increment

Interaction terms are specified with a ∗ (e.g., partial harvesting ∗ social status).

Table 3
Average annual and cumulative volume increment (dm^3) for the entire 12 year post partial harvesting treatment. Presented values are mean ±95% confidence intervals of $n = 9$.

Treatment	Social status	Observed cumulative volume increment 1–12 years after treatment	Observed average annual volume increment 1–12 years after treatment	Predicted average annual volume increment 1–12 years after treatment	Observed average annual volume increment for 2008–2010 years	Predicted average annual volume increment for 2008–2010 years
Control	Dominant	268.8 ± 51.6	22.4 ± 4.3	21.6 ± 4.0	23.3 ± 4.6	23.9 ± 3.7
	Co-dominant	84.1 ± 18.4	7.0 ± 1.5	6.4 ± 2.2	7.4 ± 2.1	6.9 ± 1.9
1/3 partial-cut	Dominant	309.1 ± 57.7	25.8 ± 4.8	23.8 ± 4.2	26.1 ± 5.0	24.1 ± 3.7
	Co-dominant	92.0 ± 24.6	7.7 ± 2.1	7.6 ± 2.4	7.6 ± 2.0	7.6 ± 2.0
2/3 partial-cut	Dominant	323.7 ± 74.1	27.0 ± 6.2	26.2 ± 4.4	26.3 ± 6.0	31.8 ± 5.1
	Co-dominant	120.1 ± 30.7	10.0 ± 2.6	9.0 ± 2.6	10.9 ± 2.7	10.8 ± 2.4

Table 4
Model selection based on AICc criteria of the most probable neighborhood competition indices (NCI) accounting for average (2008–2010) annual volume increment 10–12 years following partial harvesting of mixedwood stands. Of the 37 tested models, only the nine with the highest AICc weight are presented. R: limit of neighborhood radius, α and β: exponents as defined in Eq. (1), K: number of parameters, AICc: Akaike's Information Criterion corrected for small samples, ΔAICc: AICc relative to the most parsimonious model, w_i: AICc model weight.

R (m)	α	β	K	AICc	ΔAICc	AICc weight (w_i)	R^2
6	1	0	5	175.96	0.00	0.25	0.24
8	1	0	5	176.68	0.72	0.17	0.21
10	1	0	5	176.74	0.78	0.17	0.20
10	1	0.5	5	177.15	1.19	0.14	0.20
8	1	0.5	5	177.67	1.71	0.10	0.21
6	1	0.5	5	178.56	2.60	0.07	0.20
10	1	1	5	180.64	4.68	0.02	0.16
8	1	1	5	181.35	5.39	0.02	0.15
6	1	1	5	181.66	5.70	0.01	0.16

Note: Top nine models based on Akaike weight (w_i) are presented. Square root transformation was applied to response variable.

was applied to annual volume increment and to average annual volume increment to comply with the assumptions of normality and homogeneity of residuals.

We considered 13 and 15 candidate models for analysis-2 and analysis-3, respectively (Tables 5 and 6). Candidate models were compared using Akaike's Information Criterion corrected for small samples. Akaike weights were computed to assess the support in favor of each model. When the top-ranked model had an Akaike weight <0.9, we used multi-model inference to compute the model-averaged estimates of the explanatory variables and their 95% confidence intervals (Burnham and Anderson, 2002). A confidence interval excluding 0 indicated that the response variable varied with the explanatory variables of interest (Burnham and Anderson, 2002; Mazerolle, 2006). The power of the correlation (R^2) between predicted and observed values was computed as a measure of the predictive power of all candidate models.

3. Results

3.1. Annual volume increment of trees over time

Annual volume increment of sampled trees over time since stand initiation (Fig. 1) was roughly continuous from 1923 to 1980 (age 57), then remained more or less stable thereafter. Dominant trees accumulated higher volume and exhibited higher variability in annual increment than co-dominants. Strong growth anomalies (pointer years) in 1954, 1980, and in 2001 were common to all sampled trees, including those in controls. Change in annual volume increment following partial harvesting treatments in the winter 1998–1999 are visually apparent, especially in the 2/3 partial cut (Fig. 1). Cumulative volume increment (12 years) of dominants was 268.8 ± 51.6, 309.1 ± 57.7 and 323.7 ± 74.1 dm^3 yr^{-1} (mean ± 95% confidence intervals) in controls, 1/3 partial cut and 2/3 partial cut, respectively. Cumulative volume growth in co-dominants was 84.1 ± 18.4, 92.0 ± 24.6 and 120.1 ± 30.7 dm^3 yr^{-1} in controls 1/3 partial cut and 2/3 partial cut, respectively (Table 3).

3.2. Characterization of neighborhood competition 10–12 years after treatment

Of the 37 (36 + 1 null model) models of neighborhood competition indices (see Appendix A), NCIs proportional to diameters of neighboring trees ($\alpha = 1$) were among the nine indices with the highest Akaike weight and the highest R^2 (Table 4). Among these, the three most probable NCIs were independent of the distance between neighboring and target trees ($\beta = 0$). The NCI based on neighboring trees located within 6 m of the target tree ($R = 6$ m) had the highest support (Akaike weight of 0.25) and was 1.5 times more likely to the second-ranked model (Akaike weight of 0.17) (Table 4). Only the most probable NCI model was retained for further analyses.

Table 5
List of models, priori hypotheses for analysis-2 (Table 2), results of model selection and the weights of estimates with unconditional confidence intervals. Note that interaction terms are specified with a star (e.g., TREAT ∗ SS); annual volume increment (AVI), partial harvesting treatment (TREAT), time since harvesting (TIME (linear), and TIME^2 (quadratic)) and tree social status (SS).

Model No.	Candidate models	Biological hypothesis
1	AVI ~ TREAT	Positive effect of treatments
2	AVI ~ SS	Positive effect of tree social status
3	AVI ~ TREAT + SS	Positive effect of treatments with an additive effect of tree social status
4	AVI ~ TREAT + SS + TREAT ∗ SS	Positive effect of treatments, but different effect for each social status
5	AVI ~ TIME	Positive effect of time
6	AVI ~ TREAT + TIME	Positive effect of time with an additive effect of treatments
7	AVI ~ TREAT + TIME + TIME^2	Positive effect of treatments with a quadratic effect of time
8	AVI ~ TREAT + SS + TIME	Positive effect of treatments with an additive effect of tree social status and time
9	AVI ~ TREAT + SS + TIME + TIME^2	Positive effect of treatments with an additive effect of tree social status and a quadratic effect of time
10	AVI ~ TREAT + TIME + TREAT ∗ TIME	Positive effect of treatments with an additive effect of time but effect changes for each time period
11	AVI ~ TREAT + TIME + TIME^2 + TREAT ∗ TIME + TREAT ∗ TIME^2	Positive effect of treatments with a quadratic effect of time but effect changes for each time period
12	AVI ~ TREAT + SS + TIME + TIME2 + TREAT ∗ SS + TREAT ∗ TIME + TREAT ∗ TIME^2	Global model
13	AVI ~ 1	Null model

Selection of mixed linear models based on AICc for annual volume increment (AVI) of residual aspen stems 1–12 years after partial harvesting. *K*: number of parameters, AICc: Akaike's Information Criterion corrected for small sample sizes, ΔAICc: AICc relative to the most parsimonious model, w_i: AICc model weight. Only models showing AICc weights are presented below

Model No.	Candidate models	*K*	AICc	ΔAICc	AICc weight (w_i)	R^2
9	AVI ~ TREAT + SS + TIME + TIME^2	10	1417.54	0.00	0.98	0.81
8	AVI ~ TREAT + SS + TIME	9	1426.52	8.98	0.01	0.80
12	AVI ~ TREAT + SS + TIME + TIME2 + TREAT ∗ SS + TREAT ∗ TIME + TREAT ∗ TIME^2	16	1428.61	11.07	0.01	0.81

Estimates and precision (i.e., unconditional SE) of the effect of time, treatment and tree social status on annual volume increment based on model averaging

Parameter	Estimate (β)	Lower 95% CI	Upper 95% CI
Time	**0.0198**	**0.0053**	**0.0242**
Time^2	**0.008**	**0.0033**	**0.0127**
TREAT1 (1/3 partial-cut vs controls)	0.2309	−0.1616	0.6234
TREAT2 (2/3 partial-cut vs controls)	**0.4696**	**0.0771**	**0.862**
SS (Co-dominant vs dominant)	**−2.1187**	**−2.4391**	**−1.7982**

Note: No significant interactions were found to affect annual volume increment for the period of 1999–2010. Elements in bold indicate a strong effect of that explanatory variable on response variable. Only top ranked model (model-9) was used to compute the model-averaged estimates of the explanatory variables and their 95% confidence intervals as the top-ranked model had an Akaike weight >0.9.

3.3. Effect of harvesting treatment, time since harvesting and tree social status on annual volume increment

Three out of the 13 models for annual volume increment over the entire post-treatment period of 12 years had AICc weights $\geqslant$0.01 (Table 5) and all included treatment, social status and time effects. The model that included all the single factors (treatment, social status and time) and no interactions had an Akaike weight of 0.98 and was more probable than the second-ranked model (Akaike weight of 0.01) which included the same factors without the quadratic effect of time.

According to the most probable model, annual volume increment of residual trembling aspen trees increased linearly with time since partial harvesting over the 12 year period. A decrease in annual increment in 2001, resulting from defoliation by eastern tent caterpillar (*Malacosoma disstria*), accounted for the quadratic effect of time over annual volume increment. Trees in the 2/3 partial cut had a substantial increase in volume increment starting in the first growing season after treatment application (Table 5, Fig. 2A and B). Considering both dominants and co-dominants, the average annual increment in the 2/3 partial cut was 25.6% higher than in untreated control stands over the 12 year period (Table 3). No difference was found between the 1/3 partial cut and controls. The response in volume increment following harvesting was independent of tree social status, as indicated by the low Akaike weights of models that included the interaction between harvesting and social status (Model 12, Table 5). However, in all treatments including controls, annual volume increment of dominant trees was higher than that of co-dominants by an average of 16.2 $\text{dm}^3\,\text{tree}^{-1}\,\text{yr}^{-1}$ over the 12 year period (Table 3, Fig. 2A and B).

3.4. Effect of treatment, social status, NCI, and pre-treatment growth on the 2008–2010 average annual volume increment (AAVI)

Two of the 15 models for the 2008–2010 average annual volume increment (AAVI) had AICc weights >0.01 and both contained pre-treatment volume increment, tree social status and harvesting treatment as explanatory variables (Table 6). The model that included the additive effects of treatment, pre-treatment volume increment and social status had the most support (Akaike weight 0.60). This model was 1.5 times more likely than the second-ranked model (Akaike weight 0.40) which also included NCI. Because no single model had all the support of Akaike weights, we used the entire model set for inference (Table 6).

Considering both dominant and co-dominants, the 2008–2010 AAVI was higher in the 2/3 partial-cut than in the controls by an average of 11.8 $\text{dm}^3\,\text{tree}^{-1}\,\text{yr}^{-1}$ (Table 3). However, no effect of harvesting was found in the 1/3 partial cut when compared with control stands. Tree social status and pre-treatment volume increment affected AAVI (Table 6, Fig. 2C and D) with dominant trees and trees with highest pre-treatment annual volume increment (10–40 $\text{dm}^3\,\text{tree}^{-1}\,\text{yr}^{-1}$) showing the highest 2008–2010 AAVI (Fig. 2C and D). Multi-model inference produced a parameter estimate for NCI that was not significantly different from 0 (Table 6).

Table 6
List of models, priori hypotheses for analysis-3 (Table 2), results of model selection and weights of estimates with unconditional confidence intervals. Note that interaction terms are specified with a star (e.g., TREAT ∗ SS); average annual volume increment (AAVI) for the period of 2008–2010, partial harvesting treatment (TREAT), tree social status (SS), pre-treatment volume increment (PT) and neighborhood competition index (NCI).

Model No.	Candidate models	Biological hypothesis
1	AAVI ∼ TREAT	Positive effect of treatments
2	AAVI ∼ SS	Positive effect of tree social status
3	AAVI ∼ PT	Positive effect of pre-treatment growth
4	AAVI ∼ NCI	Positive effect of neighborhood competition indices
5	AAVI ∼ TREAT + SS	Positive effect of time with an additive effect of tree social status
6	AAVI ∼ TREAT + PT	Positive effect of treatments with an additive effect of pre-treatment growth
7	AAVI ∼ TREAT + NCI	Positive effect of treatments with an additive effect of neighborhood competition indices
8	AAVI ∼ TREAT + SS + PT	Positive effect of treatments with an additive effect of tree social status and pre-treatment growth
9	AAVI ∼ TREAT + SS + NCI	Positive effect of treatments with an additive effect of tree social status and neighborhood competition indices
10	AAVI ∼ TREAT + SS + PT + NCI	Positive effect of treatments with an additive effect of tree social status, pre-treatment growth and neighborhood competition indices
11	AAVI ∼ TREAT + PT + TREAT ∗ PT	Positive effect of treatments but the treatment effect change according to pre-treatment growth
12	AAVI ∼ TREAT + SS + TREAT ∗ SS	Positive effect of treatments but the treatment effect changes for each tree social status
13	AAVI ∼ TREAT + NCI + TREAT ∗ NCI	Positive effect of treatments but the treatment effect changes according to neighborhood competition indices
14	AAVI ∼ TREAT + SS + PT + NCI + TREAT ∗ SS + TREAT ∗ NCI + TREAT ∗ PT	Global model
15	AAVI ∼ 1	Null model

Selection of mixed linear models based on AICc for the average annual volume increment (AAVI) residual stems of trembling aspen 10–12 years following partial harvestings. *K*: number of parameters, AICc: Akaike's Information Criterion corrected for small sample sizes, ΔAICc: AICc relative to the most parsimonious model, w_i: AICc model weight. Only models have AICc weights presented below

Model No.	Candidate models	K	AICc	ΔAICc	AICc weight (w_i)	R^2
8	AAVI ∼ TREAT + SS + PT	8	100.56	0.00	0.60	0.85
10	AAVI ∼ TREAT + SS + PT + NCI	9	101.36	0.80	0.40	0.86

Estimates and precision (i.e., unconditional SE) of the effects of treatment, NCI, pre-treatment growth and tree social status on average annual volume increment based on model averaging

Parameter	Estimate (β)	Lower 95% CI	Upper 95% CI
TREAT1 (1/3 partial-cut vs controls)	0.1003	−0.2489	0.4494
TREAT2 (2.3 partial-cut vs controls)	**0.6308**	**0.2232**	**1.0383**
NCI (neighborhood competition index)	−1.7547	−4.1039	0.5945
PT (pre-treatment annual volume increment)	**0.0798**	**0.0536**	**0.1061**
SS2 (Co-dominant vs dominant)	**−1.0131**	**−1.4487**	**−0.5776**

Note: No significant interaction was found for average annual volume increment for years 2008–2010. Elements in bold indicate a strong effect of that explanatory variable on response variable. All models were used to compute the model-averaged estimates of the explanatory variables and their 95% confidence intervals as the top-ranked model had an Akaike weight <0.9.

4. Discussion

Annual volume increment of residual trees following partial harvesting of virtually pure and mature even-aged aspen stands is a function of partial harvesting prescription, tree social status and pre-treatment growth rate of residual trees. Crown thinning of 61% of basal area induced a long-lasting positive effect on tree growth that was independent of the neighborhood competition 10–12 years following treatment, as measured through NCI. Tree response to harvesting was proportional to growth performance prior to treatments. Despite being over 80 years old, residual aspen trees continued to grow vigorously.

4.1. Effect of partial harvesting prescription on annual volume increment

We had hypothesized that annual volume increment would increase with partial harvesting intensity. However, after partial harvesting treatments, residual trembling aspen trees showed a sizeable increase in annual volume increment only in the 2/3 partial cut. Removal of up to 33% of basal area using a low thinning had little effect on residual aspen growth. This was probably due to both the low intensity of the treatment and the fact that most stems were removed from the smaller diameter classes. These stems therefore exerted less competition for light and soil resources prior to the treatment than the residual stems that were generally larger. That is, the 1/3 partial cut (light, low thin) had little effect on resource availability for larger stems.

In the first years following partial harvesting of these stands, light availability increased with decreasing residual basal area (Brais et al., 2004). However very few differences in soil temperature and moisture or organic matter decomposition and mineralization were observed between partial cuts and control stands (Brais et al., 2004). The strong response of understory vegetation to canopy opening in the years following harvesting was attributed to the increase in light availability (Brais et al., 2004; Lapointe et al., 2007). However, light availability is generally not limiting for dominant trees; rather, trees with crowns in the mid- to lower-canopy should experience greater release after partial harvesting treatments, such as crown, selection or free thinning, because of the greater change in the light environment in these layers (Walter and Maguire, 2004). Following harvesting, canopy opening (measured at 3 m height) increased by 60% in the 1/3 partial harvesting treatment and this occurred mostly close to skid trails whereas the 180% increase in the 2/3 partial harvesting treatment reflected more openings created between trails as more trees were removed from the upper canopy (Brais et al., 2004). In the 2/3 partial cut, canopy opening was probably sufficient to increase light availability to the lower crown of residual trees. As trembling

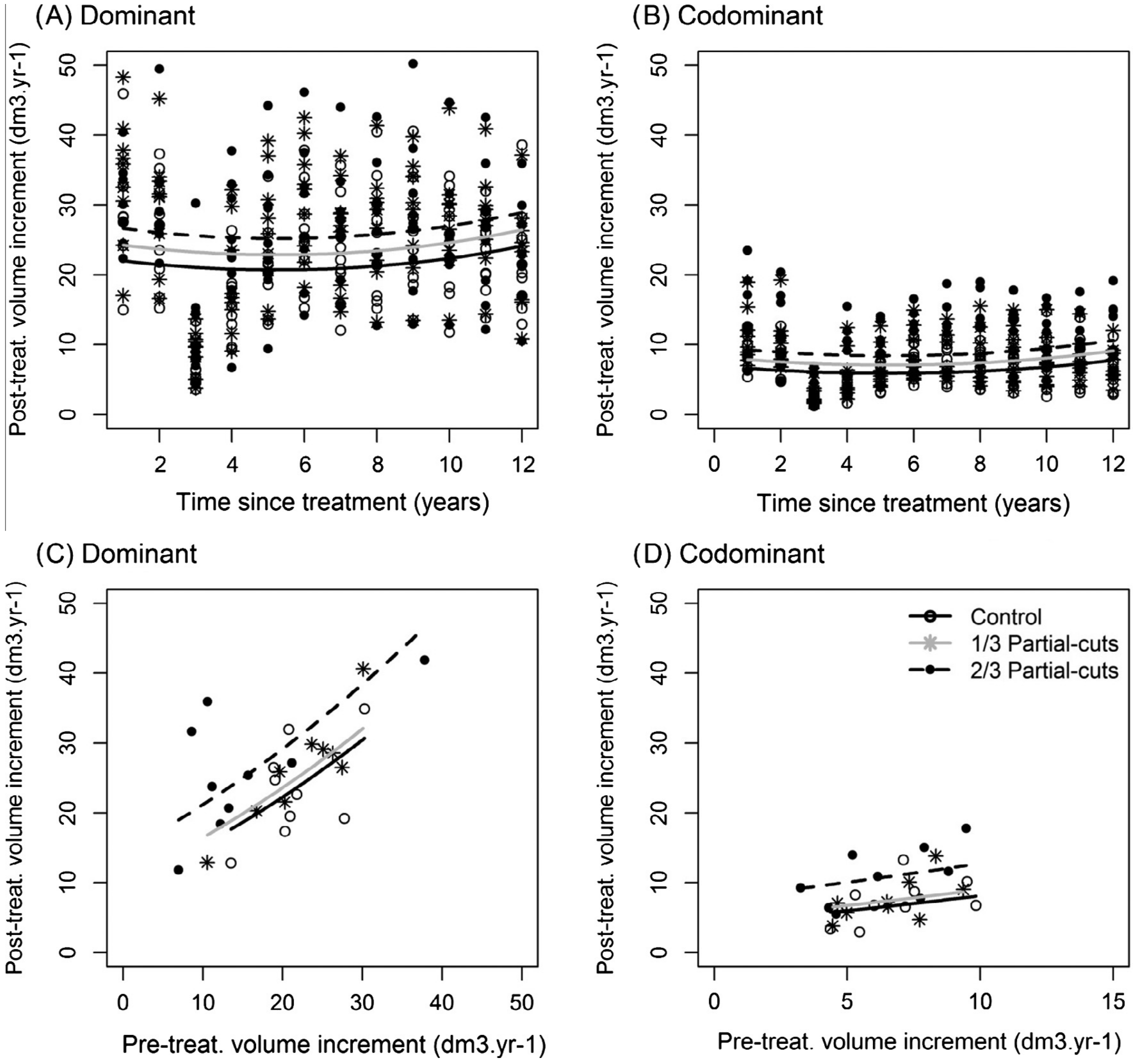

Fig. 2. Post-treatment annual volume increment of residual trembling aspen stems following partial harvesting of boreal mixedwood stands. Annual volume increment is presented as a function of time since treatment for (A) dominant and (B) co-domimant trees. Average (2008–2010) annual volume increment 10, 11 and 12 years post-treatment presented as a function of pre-treatment volume growth of (C) dominant and (D) co-dominant trees.

aspen is very shade intolerant, all trees likely benefited from this increase. Nonetheless, 12 years after harvesting, this response did not translate into any significant differences in crown dimensions within social status and between treatments (Table 1). Hence, volume growth response in partial harvesting treatments was not related to increased crown size.

Besides shade tolerance, other physiological traits of trembling aspen may explain the observed growth patterns. Trembling aspen is a nutrient demanding species (Paré et al., 2002), and because it is also a clonal species, individual stems that have suckered from a common root section or even a common parent tree can remain connected through stand development. This potentially allows transfer of carbohydrates and soil resources through a larger root network than that of an individual to connected stems. Root grafts can also contribute to maintaining a connected root network, even after some of connected trees have died (DesRochers and Lieffers, 2001; Jelínková et al., 2009). While confirming whether connections between root systems of harvested and unharvested trees improve growth response of the latter would require further testing, we could speculate that harvesting larger stems through a severe crown harvesting would provide a greater root network to exploit soil resources for residual stems. The similar, unambiguous response of dominant and co-dominant trees to partial harvesting would indicate that changes in soil resource availability were among the mechanisms underlying the increase in volume increment.

4.2. *Effect of tree social status and pre-treatment volume growth on post-treatment volume increment*

Based on stem analyses, social status of trembling aspen residual trees 12 years after treatments was consistent with their social status prior to treatment application. Dominant trees exhibited the highest increment both in absolute and relative terms (relative to pre-treatment condition) than co-dominants across time, irrespective of treatments (Tables 5 and 6). The higher volume increment by larger trees may simply reflect the greater capacity of larger crowns to capture more light for photosynthesis (Wyckoff and Clark, 2005). Metsaranta and Lieffers (2008) demonstrated that size inequality within tree populations tends to make competition asymmetric, in that larger individuals obtain a disproportionately high share of resources (Berntson and Wayne, 2000). In our study, however, response to harvesting treatments was independent of both residual stem social status and pre-treatment volume increment indicating that response to increased availability in resources was size symmetrical; that is, an individual's access to resources was proportional to its size (Schwinning and Weiner, 1998). This again raises the question regarding the role of root networks in individual tree response to changes in stand conditions.

Our results suggest that vigorous as well as less vigorous residual aspen trees will both experience increased growth following partial harvesting intensities similar to the 2/3 partial cut treatment but that the increase will be proportional to the pre-treatment growth. In even-aged aspen stands, tree social status does not tend to change following partial harvesting. That said, other studies have found size of residual stems to be a good predictor of growth following selection harvesting for a number of North American shade intolerant and tolerant species (Thorpe et al., 2007; Jones et al., 2009).

4.3. Effect of time since treatment application on annual volume increment

Our results showed an immediate increase in annual volume increment of residual trees following partial harvesting that was maintained over a 12 year period. This is in contrast with other studies (Youngblood, 1991; Thorpe et al., 2007; Jones et al., 2009; Goudiaby et al., 2012) that have shown growth stagnation initially (1–5 years) after a range of partial harvesting prescriptions and in a variety of stand types. Trembling aspen is very shade intolerant and all sampled trees were healthy at the time of treatment application. Moreover, they were in the dominant and co-dominant layers of the canopy so at least upper crowns had direct exposure to light. We presume that partial harvesting did not create unfavorable conditions, such as increased wind exposure to critical levels, to the extent of damaging or inducing stress on residual aspen trees.

Annual tree volume increment of aspen did decrease sharply in the third year following treatment applications as a result of forest tent caterpillar defoliation. This affected tree volume increment in all treatments, including controls (Fig. 1, Fig. 2A and B). Aspen trees recovered promptly from this punctual natural disturbance and maintained the rate of annual volume increment until the last monitoring year (2010). This consistent tree-level growth occurred similarly in all treatments and reflects stand-level responses and our observation that these stands are approaching but have not yet arrived at the onset of stand decline (Bose et al., accepted for publication). Man et al. (2008b) also reported near full recovery of diameter growth in surviving aspen trees following 3 years of moderate to severe tent caterpillar defoliation in similar aspen-dominated forests situated just west of our study sites. However, they observed 70% aspen mortality in the 11 years following the outbreak and higher mortality in partially cut stands than in controls. In our study, aspen stem mortality 12 years after partial harvesting was 41% in the 2/3 treatment and 19% in 1/3 treatment compared to 29% in controls (Bose et al., accepted for publication).

4.4. Effect of NCI on average annual volume increment 10–12 years following treatments

The NCI analyses were based on the tree neighborhood around our target trees that were destructively sampled (for stem analyses) in year 12 post-treatment. NCI analyses were done only for the growth period 10–12 years following treatments because we could not assume that the neighborhood remained relatively constant for a longer previous period, for example for the entire post-treatment period (i.e. that some neighborhood trees did not die or that new stems did not recruit into the ⩾5 cm DBH). In effect, compared to control treatments, cumulative aspen stem mortality over the 12 year post-treatment period was 14% higher in the 2/3 partial harvesting treatment and 10% lower in the 1/3 treatment (Bose et al., accepted for publication).

The neighborhood competition indices (see Appendix A) were based on distances of the target (sampled) tree to neighborhood trees, neighbor tree sizes, and neighborhood radius (6, 8 or 10 m). Similar to what Canham et al. (2006) observed for trembling aspen in New England, the most probable NCI index was dependent on the size of the closest neighbors (neighborhood radius=6) but independent of the actual distance between these neighbors to the target trees. However, even the most probable NCI model was a poor predictor of residual aspen volume increment 10–12 years after treatments, despite significant differences in aspen mortality observed between treatments over the 12-year period (Bose et al. accepted for publication). This is consistent with the observed constant difference in annual volume increment between trees in the 2/3 partial cuts and controls over the 12 year period.

4.5. Management implications

While recent interest in partial harvesting in the Canadian boreal mixedwood forest has largely been driven by concerns related to maintenance of biodiversity and other ecosystem services, the importance of these most productive of boreal forest ecosystems as a sustainable source of quality timber has not been lost on forest managers (LeBlanc, 2014). Reports of high residual tree mortality and growth stagnation in some situations following partial harvesting have raised questions concerning the possible negative effects of such practices on maintenance of a continuous timber supply in mixedwood regions (Thorpe and Thomas, 2007; Bose et al., 2014). Coates (1997) and Thorpe et al. (2007) emphasized that partial harvesting can only be considered as a viable silvicultural treatment if residual mortality is reasonably low and growth of residual trees is enhanced. Our results have shown a substantial tree level increase of annual volume increment after severe partial harvesting (heavy crown thinning) both for dominant and co-dominant individuals. Moreover, growth response was sustained over the entire monitoring period (12 years) except for 1 year of a tent caterpillar outbreak. Although stand-level basal area decreased slightly over this same period, due largely to mortality of small merchantable stems (Bose et al., accepted for publication), the enhanced and constant volume growth of residual trembling aspen stems following heavy partial harvesting, even in these mature stands, should provide some incentive for greater use of such practices in mixedwood management. This is particularly true if (1) treatments also promote vigorous recruitment and growth of a second cohort of desirable species (Bose et al., accepted for publication) and (2) bigger piece sizes can be expected at a later entry. Certainly from a silvicultural viewpoint, if abundant aspen recruitment and increased stand-level complexity were important objectives, a group shelterwood regime would probably enhance both better than the dispersed thinning applied in this study (Haeussler et al., 2007). Such a treatment would also have the potential effect of maintaining more large stems – key biological legacies – in the residual stand than following a severe high thinning.

That the mature (76–87 years old) aspen trees in our study responded to partial harvesting is, in itself, a somewhat surprising result. However, recent demonstration by LeBlanc (2014) of sustained growth of a portion of old, large trembling aspen trees and the development of multiple cohorts of aspen in aspen and mixed stands have important implications concerning the effects of partial harvesting and multi-cohort structure on wood supply and carbon sequestration.

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Appendix A

List of models and a priori hypotheses for analysis-1 (NCI), using equation of $\mathrm{NCI} = \frac{\sum_{j=1}^{N}(\mathrm{DBH}_j)^{\alpha}/(\mathrm{dist}_{ij})^{\beta}}{1000}$, candidate models are based on three coefficients: neighbor size effect (α), distance between neighbors to target tree (β) and the limit of neighborhood radius (R). Here response variable is average annual volume increment for the period of 2008–2010 of each tree. Note, neighbor's size is its DBH.

Model-no	Coefficients of candidate models	Biological hypothesis
1	$\alpha = 0$, $\beta = 0$ and $R = 6$	No size and distance effect; competition effect within 6 m radius
2	$\alpha = 1$, $\beta = 0$ and $R = 6$	Effect of neighbor's size but not distance; competition effect within 6 m radius
3	$\alpha = 2$, $\beta = 0$ and $R = 6$	Effect of neighbor's basal area but not distance; competition effect within 6 m radius
4	$\alpha = 0$, $\beta = 0.5$ and $R = 6$	No size but square-root of the distance effect; competition effect within 6 m radius
5	$\alpha = 1$, $\beta = 0.5$ and $R = 6$	Effect of neighbor size and square-root of the distance; competition effect within 6 m radius
6	$\alpha = 2$, $\beta = 0.5$ and $R = 6$	Effect of neighbor basal area and square-root of the distance; competition effect within 6 m radius
7	$\alpha = 0$, $\beta = 1$ and $R = 6$	No size but distance effect; competition effect within 6 m radius
8	$\alpha = 1$, $\beta = 1$ and $R = 6$	Effect of neighbor size and distance; competition effect within 6 m radius
9	$\alpha = 2$, $\beta = 1$ and $R = 6$	Effect of neighbor basal area and distance; competition effect within 6 m radius
10	$\alpha = 0$, $\beta = 2$ and $R = 6$	No size but squared distance effect; competition exists within 6 m radius
11	$\alpha = 1$, $\beta = 2$ and $R = 6$	Effect of neighbor size and squared distance; competition effect within 6 m radius
12	$\alpha = 2$, $\beta = 2$ and $R = 6$	Effect of neighbor basal area and squared distance; competition effect within 6 m radius
13	$\alpha = 0$, $\beta = 0$ and $R = 8$	No size and distance effect; competition effect within 8 m radius
14	$\alpha = 1$, $\beta = 0$ and $R = 8$	Effect of neighbor size but not distance; competition effect within 8 m radius
15	$\alpha = 2$, $\beta = 0$ and $R = 8$	Effect of neighbor basal area but not distance; competition effect within 8 m radius
16	$\alpha = 0$, $\beta = 0.5$ and $R = 8$	No size but square-root of the distance effect; competition effect within 8 m radius
17	$\alpha = 1$, $\beta = 0.5$ and $R = 8$	Effect of neighbor size and square-root of the distance; competition effect within 8 m radius
18	$\alpha = 2$, $\beta = 0.5$ and $R = 8$	Effect of neighbor basal area and square-root of the distance; competition effect within 8 m radius
19	$\alpha = 0$, $\beta = 1$ and $R = 8$	No size but distance effect; competition effect within 8 m radius
20	$\alpha = 1$, $\beta = 1$ and $R = 8$	Effect of neighbor size and distance; competition effect within 8 m radius
21	$\alpha = 2$, $\beta = 1$ and $R = 8$	Effect of neighbor basal area and distance; competition effect within 8 m radius
22	$\alpha = 0$, $\beta = 2$ and $R = 8$	No size but squared distance effect; competition effect within 8 m radius
23	$\alpha = 1$, $\beta = 2$ and $R = 8$	Effect of neighbor size and squared distance; competition effect within 8 m radius
24	$\alpha = 2$, $\beta = 2$ and $R = 8$	Effect of neighbor basal area and squared distance; competition effect within 8 m radius
25	$\alpha = 0$, $\beta = 0$ and $R = 10$	No size and distance effect; competition effect within 10 m radius
26	$\alpha = 1$, $\beta = 0$ and $R = 10$	Effect of neighbor size but not distance; competition effect within 10 m radius
27	$\alpha = 2$, $\beta = 0$ and $R = 10$	Effect of neighbor basal area but not distance; competition effect within 10 m radius
28	$\alpha = 0$, $\beta = 0.5$ and $R = 10$	No size but square-root of the distance effect; competition effect within 10 m radius
29	$\alpha = 1$, $\beta = 0.5$ and $R = 10$	Effect of neighbor size and square-root of the distance; competition effect within 10 m radius
30	$\alpha = 2$, $\beta = 0.5$ and $R = 10$	Effect of neighbor basal area and square-root of the distance; competition effect within 10 m radius
31	$\alpha = 0$, $\beta = 1$ and $R = 10$	No size but distance effect; competition effect within 10 m

Appendix A (*continued*)

Model-no	Coefficients of candidate models	Biological hypothesis
		radius
32	$\alpha = 1$, $\beta = 1$ and $R = 10$	Effect of neighbor size and distance; competition effect within 10 m radius
33	$\alpha = 2$, $\beta = 1$ and $R = 10$	Effect of neighbor basal area and distance; competition effect within 10 m radius
34	$\alpha = 0$, $\beta = 2$ and $R = 10$	No size but squared distance effect; competition effect within 10 m radius
35	$\alpha = 1$, $\beta = 2$ and $R = 10$	Effect of neighbor size and squared distance; competition effect within 10 m radius
36	$\alpha = 2$, $\beta = 2$ and $R = 10$	Effect of neighbor basal area and squared distance; competition effect within 10 m radius
37	$Y \sim 1$	Null model

References

Anning, A.K., McCarthy, B.C., 2013a. Competition, size and age affect tree growth response to fuel reduction treatments in mixed-oak forests of Ohio. For. Ecol. Manag. 307, 74–83. http://dx.doi.org/10.1016/j.foreco.2013.07.008.

Anning, A.K., McCarthy, B.C., 2013b. Long-term effects of prescribed fire and thinning on residual tree growth in mixed-oak forests of southern Ohio. Ecosystems, 1–14. http://dx.doi.org/10.1007/s10021-013-9696-6.

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

Berntson, G.M., Wayne, P.M., 2000. Characterizing the size dependence of resource acquisition within crowded plant populations. Ecology 81, 1072–1085. http://dx.doi.org/10.1890/0012-9658(2000) 081[1072:CTSDOR]2.0.CO;2.

BioSIM, 2012. Weather Databases. <ftp://ftp.cfl.forestry.ca/regniere/software/BioSIM> (accessed, October, 2013).

Bladon, K.D., Silins, U., Landhäusser, S.M., Messier, C., Lieffers, V.J., 2007. Carbon isotope discrimination and water stress in trembling aspen following variable retention harvesting. Tree Physiol. 27, 1065–1071. http://dx.doi.org/10.1093/treephys/27.7.1065.

Bose, A.K., Harvey, B.D., Brais, S., accepted for publication. Recruitment and mortality dynamics following partial cutting in aspen-dominated mixedwoods in eastern Canada. For. Ecol. Manage.

Bose, A.K., Harvey, B.D., Brais, S., Beaudet, M., Leduc, A., 2014. Constraints to partial cutting in the boreal forest of Canada in the context of natural disturbance-based management: a review. Forestry 87, 11–28. http://dx.doi.org/10.1093/forestry/cpt047.

Bourgeois, L., Messier, C., Brais, S., 2004. Mountain maple and balsam fir early response to partial and clear-cut harvesting under aspen stands of northern Quebec. Can. J. For. Res. 34, 2049–2059. http://dx.doi.org/10.1139/x04-080.

Brais, S., Harvey, B.D., Bergeron, Y., Messier, C., Greene, D., Belleau, A., Paré, D., 2004. Testing forest ecosystem management in boreal mixedwoods of northwestern Quebec: initial response of aspen stands to different levels of harvesting. Can. J. For. Res. 34, 431–446. http://dx.doi.org/10.1139/x03-144.

Brais, S., Work, T.T., Robert, É., O'Connor, C.D., Strukelj, M., Bose, A., Celentano, D., Harvey, B.D., 2013. Ecosystem responses to partial harvesting in eastern boreal mixedwood stands. Forests 4, 364–385. http://dx.doi.org/10.3390/f4020364.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springler-Verlag, New York, New York, USA.

Canada Soil Survey Committee, 1987. The Canadian System of Soil Classification, second ed. Agric. Can. Publ., pp. 1646.

Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J., 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecol. Appl. 16, 540–554. http://dx.doi.org/10.1890/1051-0761(2006) 016[0540:NAOCTC]2.0.CO;2.

Chhin, S., Hogg, E.H., Lieffers, V.J., Huang, S., 2010. Growth-climate relationships vary with height along the stem in lodgepole pine. Tree Physiol. 30, 335–345. http://dx.doi.org/10.1093/treephys/tpp120.

Coates, K.D., 1997. Windthrow damage 2 years after partial cutting at the Date Creek silvicultural systems study in the Interior Cedar-Hemlock forests of northwestern British Columbia. Can. J. For. Res. 27, 1695–1701. http://dx.doi.org/10.1139/x97-132.

Coates, K.D., Canham, C.D., LePage, P.T., 2009. Above-versus below-ground competitive effects and responses of a guild of temperate tree species. J. Ecol. 97, 118–130. http://dx.doi.org/10.1111/j.1365-2745.2008.01458.x.

Dansereau, P.-R., Bergeron, Y., 1993. Fire history in the southern boreal forest of northwestern Quebec. Can. J. For. Res. 23, 25–32. http://dx.doi.org/10.1139/x93-005.

DesRochers, A., Lieffers, V.J., 2001. The coarse-root system of mature Populus tremuloides in declining stands in Alberta. Canada. J. Veg. Sci. 12, 355–360. http://dx.doi.org/10.2307/3236849.

Goudiaby, V., Brais, S., Berninger, F., Schneider, R., 2012. Vertical patterns in specific volume increment along stems of dominant jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) after thinning. Can. J. For. Res. 42, 733–748. http://dx.doi.org/10.1139/x2012-029.

Gradowski, T., Lieffers, V.J., Landhäusser, S.M., Sidders, D., Volney, J., Spence, J.R., 2010. Regeneration of Populus nine years after variable retention harvest in boreal mixedwood forests. For. Ecol. Manag. 259, 383–389. http://dx.doi.org/10.1016/j.foreco.2009.10.033.

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. 57, 205–221.

Haeussler, S., Bergeron, Y., Brais, S., Harvey, B.D., 2007. Natural dynamics-based silviculture for maintaining plant biodiversity in Populus tremuloides-dominated boreal forests of eastern Canada. Can. J. Bot. 85, 1158–1170. http://dx.doi.org/10.1139/b07-108.

Hartmann, H., Beaudet, M., Mazerolle, M.J., Messier, C., 2009. Sugar maple (*Acer saccharum* Marsh.) growth is influenced by close conspecifics and skid trail proximity following selection harvest. For. Ecol. Manag. 258, 823–831. http://dx.doi.org/10.1016/j.foreco.2009.05.028.

Harvey, B.D., Brais, S., 2007. Partial cutting as an analogue to stem exclusion and dieback in trembling aspen (Populus tremuloides) dominated boreal mixedwoods: implications for deadwood dynamics. Can. J. For. Res. 37, 1525–1533. http://dx.doi.org/10.1139/x07-090.

Jelínková, H., Tremblay, F., DesRochers, A., 2009. Molecular and dendrochronological analysis of natural root grafting in Populus tremuloides (Salicaceae). Am. J. Bot. 96, 1500–1505.

Jones, T.A., Domke, G.M., Thomas, S.C., 2009. Canopy tree growth responses following selection harvest in seven species varying in shade tolerance. Can. J. For. Res. 39, 430–440. http://dx.doi.org/10.1139/X08-186.

Jones, T.A., Thomas, S.C., 2004. The time course of diameter increment responses to selection harvests in *Acer saccharum*. Can. J. For. Res. 34, 1525–1533. http://dx.doi.org/10.1139/x04-034.

Kneeshaw, D.D., Williams, H., Nikinmaa, E., Messier, C., 2002. Patterns of above- and below-ground response of understory conifer release 6 years after partial cutting. Can. J. For. Res. 32, 255–265. http://dx.doi.org/10.1139/x01-190.

Lapointe, B., Bradley, R., Parsons, W., Brais, S., 2007. Nutrient and light availability to white spruce seedlings in partial and clearcut harvested aspen stands. Silva Fenn. 40, 459.

LeBlanc, P.A., 2014. Incorporating multi-cohort old aspen and mixedwood dynamics into a long-term forest management plan. Forest. Chron. 90, 50–58. http://dx.doi.org/10.5558/tfc2014-010.

Lieffers, V.J., Stewart, J.D., Macmillan, R.B., Macpherson, D., Branter, K., 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. Forest. Chron. 72, 286–292. http://dx.doi.org/10.5558/tfc72286-3.

Lopatin, E., Kolstrom, T., Spiecker, H., 2008. Determination of forest growth trends in Komi Republic (northwestern Russia): combination of tree-ring analysis and remote sensing data. Boreal Environ. Res. 11, 341.

MacDonald, G.B., Cherry, M.L., Thompson, D.J., 2004. Effect of harvest intensity on development of natural regeneration and shrubs in an Ontario boreal mixedwood stand. For. Ecol. Manag. 189, 207–222. http://dx.doi.org/10.1016/j.foreco.2003.08.010.

Man, R., Kayahara, G.J., Rice, J.A., MacDonald, G.B., 2008a. Eleven-year responses of a boreal mixedwood stand to partial harvesting: light, vegetation, and regeneration dynamics. For. Ecol. Manag. 255, 697–706. http://dx.doi.org/10.1016/j.foreco.2007.09.043.

Man, R., Kayahara, G.J., Rice, J.A., MacDonald, G.B., 2008b. Response of trembling aspen to partial cutting and subsequent forest tent caterpillar defoliation in a boreal mixedwood stand in northeastern Ontario, Canada. Can. J. For. Res. 38, 1349–1356. http://dx.doi.org/10.1139/x08-005.

Mazerolle, M.J., 2006. Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. Amphibia-Reptilia 27, 169–180.

Mazerolle, M.J., 2011. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.17. <http://cran.r-project.org/web/packages/AICcmodavg/index.html>.

Metsaranta, J.M., Lieffers, V.J., 2008. Inequality of size and size increment in Pinus banksiana in relation to stand dynamics and annual growth rate. Ann. Bot. 101, 561–571. http://dx.doi.org/10.1093/aob/mcm320.

Paré, D., Rochon, P., Brais, S., 2002. Assessing the geochemical balance of managed boreal forests. Ecol. Indic. 1, 293–311. http://dx.doi.org/10.1016/S1470-160X(02)00026-2.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2011. Nlme: linear and nonlinear mixed effects models. R package version 3.1-98. <http://cran.r-project.org/web/packages/nlme/index.html> (accessed December 2011).

Pinheiro, J.C., Bates, D.M., 2000. Mixed Effects Models in S and S-PLUS. Springer Verlag.

R-Development-Core-Team, 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/> (accessed December 2011).

Ruel, J.-C., Fortin, D., Pothier, D., 2013. Partial cutting in old-growth boreal stands: an integrated experiment. Forest. Chron. 89, 360–369. http://dx.doi.org/10.5558/tfc2013-066.

Saucier, J.P., Bergeron, J.F., Grondin, P., Robitaille, A., 1998. Les régions écologiques du Québec méridional (3ie'me version): un des éléments du syste'me hiérarchique de classification écologique du territoire mis au point par le ministe're des Ressources naturelles du Québec, L'Aubelle, February–March 1998, pp. 1–12.

Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113, 447–455. http://dx.doi.org/10.1007/s004420050397.

Solarik, K.A., Lieffers, V.J., Volney, W.J.A., Pelletier, R., Spence, J.R., 2010. Seed tree density, variable retention, and stand composition influence recruitment of white spruce in boreal mixedwood forests. Can. J. For. Res. 40, 1821–1832. http://dx.doi.org/10.1139/x10-125.

Solarik, K.A., Volney, W.J.A., Lieffers, V.J., Spence, J.R., Hamann, A., 2012. Factors affecting white spruce and aspen survival after partial harvest. J. Appl. Ecol. 49, 145–154. http://dx.doi.org/10.1111/j.1365-2664.2011.02089.x.

Thorpe, H.C., Thomas, S.C., 2007. Partial harvesting in the Canadian boreal: success will depend on stand dynamic responses. Forest. Chron. 83, 319–325. http://dx.doi.org/10.5558/tfc83319-3.

Thorpe, H.C., Thomas, S.C., Caspersen, J.P., 2007. Residual-tree growth responses to partial stand harvest in the black spruce (*Picea mariana*) boreal forest. Can. J. For. Res. 37, 1563–1571. http://dx.doi.org/10.1139/x07-148.

Vincent, J.-S., Hardy, L., 1977. L'évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québécois. Géographie physique et Quaternaire 31, 357–372.

Walter, S.T., Maguire, C.C., 2004. Conifer response to three silvicultural treatments in the Oregon Coast Range foothills. Can. J. For. Res. 34, 1967–1978. http://dx.doi.org/10.1139/x04-068.

Wyckoff, P.H., Clark, J.S., 2005. Tree growth prediction using size and exposed crown area. Can. J. For. Res. 35, 13–20. http://dx.doi.org/10.1139/x04-142.

Youngblood, A.P., 1991. Radial growth after a shelterwood seed cut in a mature stand of white spruce in interior Alaska. Can. J. For. Res. 21, 410–413. http://dx.doi.org/10.1139/x91-052.