Modelling stand development after partial harvests: An empirically based, spatially explicit analysis for lowland black spruce

H.C. Thorpe *, M.C. Vanderwel, M.M. Fuller, S.C. Thomas, J.P. Caspersen

Faculty of Forestry, University of Toronto, 33 Willcocks St., Toronto, Ontario, M5S 3B3 Canada

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ABSTRACT

Across forest ecosystems worldwide, alternative silvicultural practices such as partial or "structural retention" harvesting are gaining increasing use as means to balance economic and ecological management goals. Recent studies have documented highly elevated rates of residual-tree mortality and growth, both of which are likely to influence post-harvest stand development. Explicit consideration of residual-tree responses to partial harvest is therefore required to make accurate growth and yield predictions. In this paper we incorporate empirically based, spatially explicit tree growth and mortality predictors into a forest simulation model in order to quantify stand dynamics following a range of simulated partial harvests. We consider lowland black spruce boreal forests and use a common strip-cutting technique, Harvest with Advance Regeneration Protection, as a reference against which to compare alternative scenarios. Predicted stand development proceeded most rapidly in scenarios with reduced skidding impacts and relatively high levels of retention, since these treatments were associated with lower residual-tree mortality rates and larger growing stocks respectively. Stand development was also influenced on a proportional basis by residual-tree growth rates, which increased with declining neighbourhood competition. Across a range of harvest scenarios with equivalent retention levels (20%), differences in residual-tree responses among treatments led to a 35-year range in projected basal area return intervals (70–105 years). Our results demonstrate that short-term responses of residual trees affect stand development rates over long (>100-year) time scales, and show that post-harvest stand recovery rates are influenced not only by the retention level but also by the specific parameters of partial harvest prescriptions, including the layout of skid trails and the spatial arrangement of residual trees. Results from this study provide essential information for evaluating partial harvests in the black spruce boreal forest and supply modelling tools for assessing alternative silvicultural treatments in other forest ecosystems.

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1. Introduction

Prediction of stand growth and yield has been a primary focus of forestry since the inception of the discipline (Assmann, 1970; Messier et al., 2003), with research generally centred on developing aspatial models to predict growth and yields in single-species, even-aged stands. Recently, as forest management goals have broadened beyond timber production, silviculture has diversified to include novel treatments such as partial or "structural retention" harvests, which aim to improve ecosystem service provision in managed stands (e.g., Franklin et al., 1997; Lindenmayer and McCarthy, 2002; Keeton, 2006). Since both habitat and timber supplies depend to a large degree on stand structure, the need for models that accurately describe stand development following partial harvests is crucial for evaluating these treatments from either

an ecological or an economic perspective (Thorpe and Thomas, 2007). However, the structural complexity of partially harvested stands and lack of appropriate models make quantitative predictions a challenge.

In even-aged stands, growth and yield predictions are most commonly made using normal yield tables, which describe relationships between stand age and timber volume for individual species across ranges of site productivity (e.g., Plonski, 1974; Oliver and Larson, 1996). Yield tables can generally be applied only to very homogeneous areas, such as monospecific (but see Penner, 2008), even-aged, and reasonably young (<150 years) stands, and are unable to produce accurate predictions of development in structurally heterogeneous stands (Groot et al., 2004). Individual-based models, in contrast, allow for a wide range of conditions within single stands and thus offer the most viable approach for modelling partially harvested stands (Coates et al., 2003; Groot et al., 2004). Many individual-based models have been developed and used for simulating forest dynamics and/or predicting growth and yields (e.g., Shugart and West, 1977; Shugart et al., 1980; Leemans, 1992; Phillips et al., 2004; reviewed in Liu and Ashton, 1995; Porte and

Bartelink, 2002). Examples include the distance-independent Forest Vegetation Simulator (FVS: Teck et al., 1996; Lacerte et al., 2006) and its regional variants (e.g., TWIGS/STEMS: Brand and Holdaway, 1989), and the spatially explicit forest simulator SORTIE (Pacala et al., 1993, 1996) and its descendants, SORTIE/BC (Coates et al., 2003) and SORTIE-ND (Murphy, 2008).

Previous studies have employed individual-based models to investigate the effects of partial harvest scenarios on forest structure (Rüger et al., 2007), regeneration (Coates et al., 2003; Temesgen et al., 2006), and habitat quality (Pausas et al., 1997). But despite recent research documenting elevated rates of post-harvest tree mortality (e.g., Scott and Mitchell, 2005; Maguire et al., 2006; Jönsson et al., 2007; Bladon et al., 2008; Thorpe et al., 2008) and large, time-lagged growth responses of mature residual trees to partial harvests (e.g., Youngblood, 1991; Latham and Tappeiner, 2002; Jones and Thomas, 2004; Thorpe et al., 2007), no study has attempted to quantify how residual-tree responses will influence long-term stand development after partial harvests. Where residual trees display high mortality rates and/or lagged growth, disregarding these responses will lead to overestimated yields, underestimated growth rates of sub-canopy trees, and inaccurately characterised forest structure and habitat quality.

In this study we incorporate new predictors of residual-tree growth and mortality responses to harvest into a spatially explicit, individual-based forest simulator model to explore stand dynamics following a variety of partial harvest scenarios in the black spruce boreal forest. Growth and mortality predictors are based on previous empirical studies of partially harvested black spruce stands (Thorpe et al., 2007, 2008). We use a strip-cutting technique commonly employed in the eastern Canadian boreal forest as a reference prescription against which to evaluate simulated alternative partial harvest scenarios at the stand (5-ha) level. Using simulation results, we address the following questions. (1) How are short-term growth and mortality dynamics influenced by the partial harvest prescription? (2) How does elevated post-harvest mortality impact stand development over short and long time scales? (3) How are basal area return interval estimates affected by the partial harvest prescription?

2. Methods

2.1. Study site

The model used in this study was developed and parameterised using data collected in partially harvested lowland black spruce stands in northeastern Ontario, Canada. Field sites were located near Cochrane, Ontario, in the northern clay belt region of the boreal forest (Rowe, 1972), where flat topography, poorly drained organic soils, and nearly monospecific stands of black spruce (*Picea mariana* (Mill.) B.S.P.) dominate. The climate is cold, with a mean annual temperature of 0.6 °C and average annual precipitation of 880 mm (Environment Canada, 2002). Study sites were treated with Harvest with Advance Regeneration Protection (HARP), a silvicultural prescription developed for uneven-aged black spruce stands to protect small merchantable stems and regeneration. HARP-treated stands are characterised by alternating clearcut strips 5–7 m wide, where harvest equipment travels, and partial cut strips 5–9 m wide, in which ~12 cm diameter limit cutting is carried out.

2.2. Model development

To investigate how responses of residual trees influence post-harvest stand development, we linked together spatially explicit neighbourhood models of post-harvest growth and mortality and simulated short- and long-term stand dynamic responses to partial harvest treatments. Short-term (10-year) simulations were conducted to assess the relative importance of residual-tree growth and mortality responses across a range of partial harvest treatments, and long-term (120-year) simulations were carried out to obtain basal area return interval estimates for each treatment. In the following sections, we describe the model, its behaviours, the initialization procedure, and the partial harvest scenarios we explored.

2.2.1. Modelling platform

We employed SORTIE-ND, a spatially explicit, individual-based forest simulator, as the modelling platform for the simulations conducted in this study. However, with the exception of recruitment, all submodels were written (in C/C++) and parameterised specifically for this study. SORTIE-ND is a descendant of SORTIE, a light-driven succession model originally developed for hardwood forests in the northeastern United States (Pacala et al., 1993, 1996) that was later re-parameterised for British Columbia forests and modified to permit harvesting (SORTIE/BC: Coates et al., 2003). SORTIE-ND ("neighbourhood dynamics") is the most recent, and first open-source, version of the model.

2.2.2. Mortality

In a previous study (Thorpe et al., 2008), we used a chronosequence approach and dendrochronological techniques to quantify mortality rates before, during and after partial harvesting in lowland black spruce stands. We documented highly elevated rates of post-harvest mortality. On average, >13% of residual trees died in the first decade after harvest, with mortality split nearly equally between windthrown and standing dead trees. Both for windthrow and standing death, skid trail proximity was the most important predictor of mortality risk, and predicted 10-year cumulative mortality rates ranged from <3 to >35% of residual trees across the observed range of skid trail proximity (Thorpe et al., 2008). Skid trail proximity values were obtained by tallying the number of stumps located in skid trails that were found within 7.35 m (a neighbourhood radius parameter, estimated by maximum likelihood analysis) of a residual tree. Other factors that influenced post-harvest mortality risk were neighbourhood basal area, tree size, and time since harvest. Crowded residual trees were at higher risk of standing death, while windthrow risk increased with exposure and tree size. Both windthrow and standing death risk declined with increasing time since harvest.

The mortality submodel used in this study implements our empirical results (Thorpe et al., 2008). Mortality occurs at a constant rate prior to harvest and affects trees independently of their growth rates or spatial arrangements. After harvest, residual-tree mortality is elevated above background rates and is influenced by skid trail proximity, neighbourhood basal area, tree size, and time since harvest. All mortality parameters used in the simulations were estimated in Thorpe et al. (2008) except for the background mortality rate for the long-term simulations. Since mortality generally occurs episodically (Lussier et al., 2002), the relatively low background mortality rate we found (0.28% per year) is unlikely to persist over the period considered in the long-term simulations. We addressed this by implementing a 1% background mortality rate for the 120-year simulations, the average mortality rate documented in two previous studies of black spruce (Lussier et al., 2002; Aakala et al., 2007).

2.2.3. Growth

We used the growth data described in Thorpe et al. (2007) in combination with spatial neighbourhood information to develop and parameterise a model to predict radial growth as a function of tree size, neighbourhood competition, and time since harvest (described in detail in Appendix A). Growth is predicted as a func-

tion of tree size and neighbourhood competition, with smaller trees expected to grow faster at low levels of competition but display steeper growth declines with increasing competition. Neighbourhood competition is estimated as basal area within 5 m of a target tree and is calculated separately before and after harvest. For pre-harvest growth rates, stumps are included in BA calculations, while after harvest, the only neighbours are residual trees. Many previous studies have found time-lagged growth responses to harvest (Latham and Tappeiner, 2002; Jones and Thomas, 2004; Thorpe et al., 2007). We implemented time-lagged growth in the model by including a parameter that determines the rate at which growth increases from pre- to post-harvest rates. Equations and parameters employed in the growth submodel are detailed in Appendix A.

2.2.4. Recruitment

For the long-term simulations, we implemented recruitment as a single cohort using a pre-existing SORTIE-ND submodel that allows specification of the size and density of recruiting trees in addition to the timestep in which recruitment is initiated. In each harvest scenario, we initiated 2.2-cm dbh trees in year 30 after harvest, according to data from yield tables for site class 3 spruce (Plonski, 1974). Recruiting trees were distributed across the entire simulated stand at 4-m spacing, consistent with Ontario's standard for full stocking (Groot and Adams, 2005). Recruitment was not considered in the 10-year simulations.

2.2.5. Harvest

We developed a partial harvest submodel, based on the HARP prescription, that includes three adjustable parameters: skid trail width (m), leave strip width (m), and diameter limit (cm). All trees in the skid trails are harvested, while only trees larger than the diameter limit are removed from the leave strips. For each residual tree, the harvest submodel outputs its diameter, spatial location, and skid trail proximity. The skid trail proximity, a measure of the intensity of skidding, is estimated as a tally of the number of stumps located in skid trails found within 7.35 m of each residual tree (see Thorpe et al., 2008). Although less intuitive than a distance to skid trail measure, this proxy for skid trail proximity allows trees to be influenced by more than one skid trail; for example, in scenarios with 3-m-wide leave strips, skid trail proximity values include stumps from skid trails on either side of each residual tree.

2.3. Partial harvest scenarios

The harvest scenarios considered in this study were assessed using HARP as a reference prescription. Although the structure of HARP-treated stands varies, it was useful to determine an average HARP prescription against which alternate treatments could be compared. A treatment of 6-m-wide skid trails, 8-m-wide leave strips, and a 12-cm diameter limit fit the mean of the observed data (Thorpe et al., 2007, 2008) in terms of stem density, decadal basal area growth rate, and cumulative mortality rate. We refer to this treatment simply as "HARP."

To investigate the influence of the three harvest parameters—skid trail width, leave strip width, and diameter limit—on post-harvest stand development, we designed a range of partial harvest scenarios in which we varied one of the harvest parameters while the other two remained constant (Table 1A–D). We refer to these sets of scenarios by the harvest parameter under consideration; for example, the skid trail scenarios consider five contrasting skid trail widths (3, 6, 9, 12, and 15 m) while the leave strip width and diameter limit are held constant, at 8 m and 12 cm respectively (Table 1A). For the diameter limit scenarios, we conducted simulations across diameter limits from 10 to 20 cm both at the average skidding intensity (skid trails 6 m, leave strips

8 m; Table 1C) and in the absence of skidding, by setting the skid trail width to zero (Table 1D). A no skidding prescription is analogous to helicopter logging, an unrealistically costly harvest method for lowland black spruce forests, but nonetheless a useful situation to consider for the purposes of this study.

In addition to exploring the effects of each harvest parameter in isolation, we conducted a set of "HARP comparison" treatments in which basal area retention levels were held constant at the HARP retention level, 3.4 m^2/ha (Table 1E). In order to quantify the influence of elevated mortality on post-harvest stand development, the first pair of scenarios compared the HARP treatment at observed mortality (Thorpe et al., 2008) and under the assumption of no post-harvest mortality. In the no post-harvest mortality simulations, mortality before and after harvest was held constant at the pre-harvest rate (0.28% per year in short-term simulations; 1% per year in long-term simulations). In the next scenario, the "patch cut", all trees were harvested from a 181-m-wide "skid trail" and no harvesting took place in a 43-m-wide "leave strip." The four other HARP comparison scenarios considered a gradient of skidding intensities from 0 to 75% (Table 1E). Retention levels in these treatments were constrained by altering the diameter limit. Thus, partial harvest intensity and skidding intensity varied in opposite directions. The specific harvest parameters for these treatments were: (1) 9.3-cm diameter limit with no skidding (0% skidding), (2) 10.5-cm diameter limit with 5-m skid trails and 15-m leave strips (25% skidding, (3) 12.7-cm diameter limit with 10-m skid trails and 10-m leave strips (50% skidding), and (4) 20.0-cm diameter limit with 15-m skid trails and 5-m leave strips (75% skidding).

2.4. Model initialization

Model runs were conducted on 5.02-ha (224 m × 224 m) stem maps that were created by stitching together 64 smaller plots of field data. For a previous study, we established 54 circular, 40-m diameter plots in partially harvested lowland black spruce stands, and measured species, diameter, and spatial position (x–y coordinates) of all stumps and residual trees ≥5 cm dbh ($n > 10,000$; Thorpe et al., 2008). For the purposes of this study, we recreated pre-harvest stand conditions by restoring stumps to live trees using an allometric equation to convert diameter at stump height (dsh) measurements to dbh (dbh = 0.89 × dsh − 0.80; $n = 50$; $r^2 = 0.97$). Black spruce comprised more than 92% of the sampled stems and was the only species considered in the simulations.

To produce a large stem map on which to conduct simulations, we (1) reduced each 40-m diameter circular field plot to a 28-m square stem map, (2) randomly selected ten of the 54 field plots to include in the large plot twice, and (3) randomly placed the 64 plots in an 8 × 8 grid. We repeated this process to produce 100 unique starting condition stem maps. The 5-ha scale was chosen to represent a homogeneous area within a harvest block and stands were simulated in a torus shape to eliminate edge effects, as is the convention in SORTIE-ND. The model initialization procedure was written in C/C++.

2.5. Simulation parameters

We carried out short-term simulations over 12 timesteps, 1 year per timestep, with harvests conducted in the second timestep. These simulations considered the fate of adult residual trees only; seedlings and saplings were disregarded and no recruitment into the adult size class (≥5 cm dbh) occurred over the simulation period. Long-term (120-year) simulations were carried out over 25 timesteps, with 5 years per timestep, and harvests took place in the first timestep. For both short- and long-term simulations, all harvest scenarios were run on each of the 100 unique stem maps.

Table 1
Simulated partial harvest scenarios and their corresponding prescriptions.

Partial harvest scenario description	Partial harvest scenario number	Partial harvest prescription		
		Diameter limit (cm)	Skid trail width (m)	Leave strip width (m)
A: *Skid trail*	1	12	3	8
	2	12	6	8
	3	12	9	8
	4	12	12	8
	5	12	15	8
B: *Leave strip*	6	12	6	15
	7	12	6	12
	8	12	6	9
	9	12	6	6
	10	12	6	3
C: *Diameter limit* (*mean skidding intensity*)	11	20	6	8
	12	17.5	6	8
	13	15	6	8
	14	12.5	6	8
	15	10	6	8
D: *Diameter limit* (*no skidding*)	16	20	0	224
	17	17.5	0	224
	18	15	0	224
	19	12.5	0	224
	20	10	0	224
E: *HARP comparisons*				
HARP	21	12	6	8
HARP no PHM	22	12	6	8
Patch cut	23	N/A	181	43
0% skid	24	9.3	0	224
25% skid	25	10.5	5	15
50% skid	26	12.7	10	10
75% skid	27	20.0	15	5

Notes: All stems are harvested from skid trails while only stems larger than the diameter limit are harvested from leave strips. N/A indicates no harvesting in leave strips.

3. Results

3.1. HARP

All simulations began with an initial density of 1645 ($\geq$5 cm dbh) black spruce stems per hectare, comprising basal areas (BA) of 17.7 m²/ha. The HARP treatment (6-m skid trails, 8-m leave strips, 12-cm diameter limit) reduced BA to 3.4 m²/ha. Over the first decade after harvest, cumulative post-harvest mortality (% stem density decrease/10 years) was 14.0%, and net decadal BA growth (growth–mortality) was 1.1 m²/ha, representing a 32% increase compared to the retention level. Results from long-term simulations project that HARP-treated stands will take 85 years to return to pre-harvest basal area.

3.2. Influence of harvest parameters

Across the skid trail scenarios, stand development increased with declining skid trail width (Fig. 1A). Rates of post-harvest mortality were similar across treatments (12.1–14.1%; Table 2A) as were decadal BA growth rates on a percent basis (Fig. 1A). Wider skid trails increased the area occupied by skid trails, but they did not substantially alter neighbourhood conditions of residual trees (competition levels or skidding proximities). Thus, differences in BA growth across these treatments were solely a result of the larger growing stocks available in the higher retention treatments associated with narrower skid trails. Projected BA return intervals ranged from 75 years in the 3-m skid trail treatment up to 105-years in the 15-m skid trail scenario (Table 2A).

In the leave strip scenarios, absolute and proportional BA growth rates increased with widening leave strips, a result of both increasing retention levels and declining post-harvest mortality rates (Fig. 1B; Table 2B). Mortality rates were relatively low in wide leave strip treatments because higher proportions of residual trees were located away from skid trails and their associated mortality risk. Although retention levels were similar across skid trail and leave strip treatments, the range of estimated BA return intervals was larger in the leave strip width treatments, from 70 years for 15-m leave strips up to 115 years in the 3-m leave strip treatment (Table 2B; Fig. 2B).

Stand development rates increased with diameter limit, but growth rates were fastest on a per-capita basis in smaller diameter limit treatments (Fig. 1C and D). Treatments that employed small diameter limits were associated with higher harvest intensities, and so residual trees in these treatments grew faster as a result of lower neighbourhood competition. Decadal rates of post-harvest mortality were similar across treatments, ranging from 12.0 to 14.4% in the average skidding scenarios and from 3.4 to 3.7% in the no skidding treatments. The faster BA development found in large diameter limit treatments was therefore solely due to their higher retention levels. Projected BA return intervals followed the same pattern, with the shortest intervals projected for the high retention (large diameter limit) scenarios. Across the range of tested diameter limits (20–10 cm), projected BA return intervals ranged from 65 to 95 years at average skidding (Table 2C) and from 25 to 65 years in the no skidding scenarios (Table 2D).

3.3. Impact of post-harvest mortality

We conducted simulations of the HARP treatment both at observed levels of post-harvest mortality and assuming no post-harvest elevation in mortality (i.e., mortality after harvest was held constant at the pre-harvest rate). Differences in cumulative mortality rates (2.7% vs. 14.0%; Table 2E) led to a decadal BA growth prediction overestimated by 55% (Fig. 2A). In the long-term simulations, the projected BA return interval in the no post-harvest
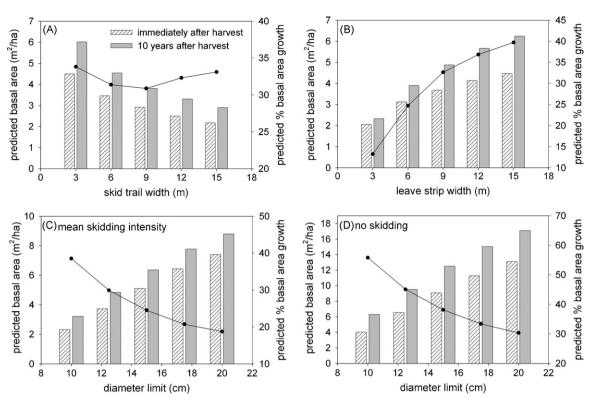
Fig. 1. Mean predicted 10-year basal area growth ($n = 100$) across a range of skid trail widths (A), leave strip widths (B), and diameter limits, with (C) and without (D) skidding. Lines represent percent basal area growth over the decade. In (A), leave strips were 8 m and the diameter limit was 12 cm; in (B), skid trails were 6 m and the diameter limit was 12 cm; in (C), skid trails were 6 m and leave strips were 8 m; and in (D), there were no skid trails. All stems in skid trails were cut, and only stems larger than the diameter limit were harvested from leave strips. Simulations considered adult trees only (≥ 5 cm dbh) and recruitment was not considered. CV was <0.05 for all scenarios.

mortality scenario was 65 years, 20 years shorter than the return interval projected for HARP under observed mortality (Table 2E). Although the magnitude of growth overestimation would vary across partial harvest scenarios, this result demonstrates that failing to incorporate realistic mortality rates into forest growth models will lead to inflated projections of stand development rates.

3.4. HARP comparisons

The final set of simulations compared the HARP treatment to a set of alternative harvest scenarios with equivalent retention levels (3.4–3.5 m²/ha). By the end of the simulated post-harvest decade, BA across these treatments ranged from 3.9 to 5.5 m²/ha, with HARP-treated stands intermediate among the scenarios (4.5 m²/ha). Both the patch cut and the 75% skidding, 20-cm diameter limit treatment showed slower BA development than HARP, while results from the HARP and the 50% skidding, 12.7-cm diameter limit treatments were nearly identical (Fig. 2C and E). The 25% skidding, 10.5-cm diameter limit and 0% skidding, 9.3-cm diameter limit treatments performed best, displaying decadal basal area growth rates 43 and 88% greater than for HARP-treated stands (Fig. 2E). Variation in decadal BA growth across these scenarios was driven largely by differences in post-harvest mortality, which ranged from 3.5% in the 0% skidding scenario to 17.8% in the 75% skidding treatment (Table 2E). BA development was also influenced by individual-tree growth rates, which increased as diameter limits decreased. The importance of residual-tree growth is apparent when comparing, for example, the HARP and patch cut scenarios. Despite higher post-harvest mortality in the HARP treatment (14.0% vs. 3.8%; Table 2E), BA at the end of the decade was higher in HARP than in the patch cut (Fig. 2C), a difference that can be attributed to the faster residual-tree growth rates found in HARP treatments, where neighbourhood competition was lower.

Projected BA return intervals followed the patterns found in the decadal simulations, with the low-skidding treatments associated with return intervals 5–15 years shorter than for HARP, while the patch cut and 75% skidding treatments were predicted to take an additional 20 years to return to pre-harvest basal areas (Table 2E; Fig. 2D and F). With the exception of the patch cut treatments, BA declined over the first timestep (5 years) after harvest in all of the HARP comparison treatments (Fig. 2D and F). In the decadal simulations, 5-year basal area declines were found only in the 75% skidding treatment (Fig. 2E). This discrepancy can be explained by the higher background rates of mortality implemented in the long-term simulations.

3.5. Influence of retention level on projected basal area return intervals

Across all harvest treatments, post-harvest stand development rates were driven primarily by retention levels, with deviations from the expected negative relationship between retention level and basal area return interval explained by differences in residual-tree responses to harvest (Fig. 3). Scenarios associated with high rates of residual-tree mortality and/or neighbourhood competition (found above the regression line) developed more slowly than average among the simulated treatments, while scenarios associated with low post-harvest mortality rates and/or reduced neighbourhood competition (found below the regression line) displayed above-average rates of post-harvest stand development.

4. Discussion

Partial harvesting has been gaining popularity in recent decades as a way to maintain biodiversity and ecological function in harvested areas. Live trees provide erosion control, appropriate

Table 2
Influence of partial harvest scenarios on predicted adult tree (>5 cm dbh) densities, decadal rates of post-harvest tree mortality and projected basal area return intervals. Within each set of scenarios, treatments are ordered from lowest to highest harvest intensity. See Table 1 for partial harvest scenario prescription details.

Partial harvest scenario description	Partial harvest scenario number[a]	Predicted per-ha live-tree density (and 95% CI) immediately after harvest	Predicted per-ha live-tree density (and 95% CI) 10 years after harvest	Predicted post-harvest mortality (%/10 years)	Projected basal area return interval (years)
A: *Skid trail*[b]					
3 m	1	846 (842, 850)	744 (740, 747)	12.2	75
6 m	2	658 (655, 661)	566 (564, 569)	14.0	85
9 m	3	550 (546, 553)	472 (469, 475)	14.1	95
12 m	4	471 (468, 473)	409 (406, 411)	13.1	100
15 m	5	410 (408, 413)	358 (356, 361)	12.6	105
B: *Leave strip*[c]					
15 m	6	843 (839, 848)	773 (769, 777)	8.3	70
12 m	7	781 (777, 784)	701 (698, 704)	10.2	75
9 m	8	694 (660, 667)	604 (600, 608)	12.9	85
6 m	9	587 (584, 590)	481 (478, 483)	18.0	95
3 m	10	387 (385, 389)	288 (286, 289)	25.7	115
C: *Diameter limit* (*mean skidding intensity*)[d]					
20 cm	11	875 (872, 879)	769 (766, 772)	12.1	65
17.5 cm	12	839 (836, 842)	732 (729, 735)	12.7	70
15 cm	13	774 (771, 778)	671 (668, 674)	13.3	75
12.5 cm	14	681 (678, 684)	586 (583, 589)	14.0	85
10 cm	15	538 (535, 541)	461 (458, 463)	14.4	95
D: *Diameter limit* (*no skidding*)[e]					
20 cm	16	1537 (1532, 1542)	1484 (1479, 1489)	3.4	25
17.5 cm	17	1469 (1464, 1473)	1415 (1411, 1420)	3.6	35
15 cm	18	1362 (1357, 1367)	1311 (1306, 1316)	3.7	50
12.5 cm	19	1192 (1186, 1197)	1146 (1142, 1155)	3.8	55
10 cm	20	933 (930, 938)	900 (896, 904)	3.6	65
E: *HARP comparisons*[f]					
HARP	21	658 (655, 661)	566 (564, 569)	14.0	85
HARP no PHM	22	658 (655, 661)	640 (637, 643)	2.7	65
Patch cut	23	311 (307, 316)	300 (295, 304)	3.8	105
0% skid	24	853 (849, 857)	823 (820, 827)	3.5	70
25% skid	25	749 (745, 752)	684 (680, 687)	8.7	80
50% skid	26	610 (607, 613)	540 (537, 543)	11.4	85
75% skid	27	404 (402, 407)	332 (330, 335)	17.8	105

[a] Partial harvest scenario numbers correspond with those presented in Table 1.
[b] Range of retention levels across treatments: 2.2–4.5 m^2/ha.
[c] Range of retention levels across treatments: 2.1–4.5 m^2/ha.
[d] Range of retention levels across treatments: 2.3–7.4 m^2/ha.
[e] Range of retention levels across treatments: 4.0–13.1 m^2/ha.
[f] Range of retention levels across treatments: 3.4–3.5 m^2/ha.

microclimates for regenerating seedlings, and habitat for animals, plants and fungi (Franklin et al., 1997), and thus the success of partial harvests depends to a large degree on survival of residual trees. Many studies have found elevated tree mortality rates following partial harvests (e.g., Scott and Mitchell, 2005; Maguire et al., 2006; Jönsson et al., 2007; Bladon et al., 2008), but to our knowledge this is the first effort to use a simulation model to quantify the impact of residual-tree responses, including post-harvest mortality, on stand development rates. Our results demonstrate that tree responses exert a strong influence on post-harvest development: even across treatments with equivalent retention levels, large disparities in stand recovery rates were projected as a result of differences in growth and mortality responses of residual trees. Thus, while discussions surrounding partial harvests have generally concerned absolute retention levels, this study shows that habitat and other ecological service provision, as well as timber production rates, will be influenced not only by *how much* of the residual forest is retained but *how* it is retained.

4.1. Model evaluation

We are confident in the results from the decadal simulations, for which the time scale considered was equivalent to the period over which we documented growth and mortality responses in the field (Thorpe et al., 2007, 2008), all model behaviours were

developed and parameterised from empirical data (Thorpe et al., 2008; Appendix A), and the starting condition maps were based on field data. Results from the simulated HARP treatment matched our field data in terms of stem density, decadal basal area growth rate, and cumulative mortality rate, and results from all other simulated harvests fell within the bounds of our empirical results on an individual-tree basis.

More uncertainty is associated with the long-term simulations, and model evaluation is made difficult by the fact that HARP is a new treatment; no long-term data (>15 years) are available. Where we were able to evaluate our results with pre-existing data, we were satisfied with the model predictions. For example, the spatial growth model (Appendix A) was developed and parameterised using data from trees ≥5 cm dbh but used in the long-term simulations to predict growth for regenerating trees (2.2–4.9 cm dbh). In our simulations, trees in the regenerating cohort first reached the adult (5 cm) size class in year 50 (Fig. 2B, D, and F), corresponding with yield table predictions for site class 3 spruce (Plonski, 1974) in which trees are expected to obtain a dbh of 5.6 cm in year 50. Finally, results from our simulations show a negative relationship between the retention level and predicted basal area return interval (Fig. 3). The intercept of the regression equation (equivalent to a 0 m^2/ha retention level) is 112.8 years, which corresponds well with the 100–120-year rotation ages expected for lowland black spruce clearcuts in northeastern Ontario.
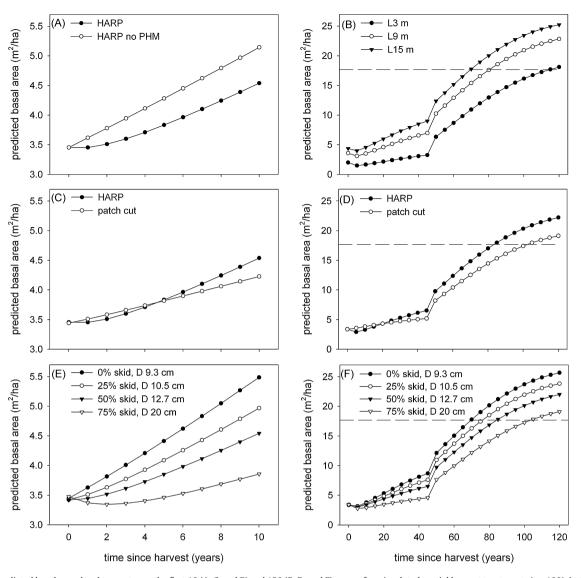
Fig. 2. Mean predicted basal area development over the first 10 (A, C, and E) and 120 (B, D, and F) years after simulated partial harvest treatments ($n = 100$). In the long-term simulations (B, D, and F), dashed lines indicate pre-harvest basal area, and BA increases in year 50 are a result of the cohort of regenerating trees reaching the adult (≥ 5 cm dbh) size class. Basal area return intervals (Table 2) are estimated for each scenario as the first timestep in which BA meets or exceeds the pre-harvest level. Prescriptions depicted include: (A) HARP (6-m skid trails, 8-m leave strips, 12-cm diameter limit), with and without elevated post-harvest mortality; (B) leave strip widths (L) ranging from 3 to 15 m across a constant diameter limit (12 cm) and skid trail width (6 m); (C and D) HARP and an equivalent retention level "patch cut" (181-m skid trail, 43-m leave strip); and (E and F) a range of HARP comparison prescriptions that include: (1) no skidding (0% skid), 9.3-cm diameter limit, (2) 5-m skid trails, 15-m leave strips (25% skid), 10.5-cm diameter limit, (3) 10-m skid trails, 10-m leave strips (50% skid), 12.7-cm diameter limit, and (4) 15-m skid trails, 5-m leave strips (75% skid), 20-cm diameter limit. CV was <0.05 for all scenarios.

4.2. Potential for further model development

The model used in this study was developed to explore how residual-tree responses to disturbance influence stand development. Here we consider lowland black spruce stand development after partial harvests, but our modelling approach could be applied in several other cases. Since structural retention silviculture is now being implemented widely, the model could be parameterised for other forest ecosystems to quantify the influence of residual-tree responses and compare differences in post-partial-harvest stand recovery rates among forest types. Moderate severity natural disturbances such as insect outbreaks have also been shown to alter demographic rates of residual trees (e.g., Taylor and MacLean, 2007) and so this modelling approach could be used to examine stand recovery after natural disturbance. Finally, our approach could be applied to look more directly at habitat supply. Outputs from the post-harvest mortality submodel, for example, could be used as input for a coarse woody debris behaviour to track the abundance of snags and logs and their decomposition rates. This would permit habitat supply quantification and comparisons over time across various harvest treatments.

In terms of growth and yield forecasting, incorporating information on tree height growth responses to harvest would greatly improve model capacity. Trees generally show faster diameter than height growth following harvest (e.g., Liu et al., 2003) and so pre- and post-harvest basal area may not be equivalent in terms of timber volume. Our basal area return intervals could therefore be underestimated compared to volume-based rotation ages.

The range of harvest scenarios explored in this study was fairly limited, particularly the spatial arrangement of retention (strips) and the harvest prescription in the leave strips (diameter limit cutting). Employing a more complex harvesting algorithm (e.g., Arii et al., 2008) would permit investigation of a broader range of partial harvest scenarios, including widely applied methods such as shelterwood and selection.
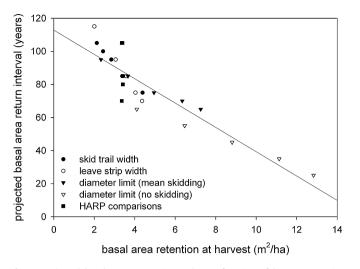
Fig. 3. Projected basal area return interval as a function of harvest retention level ($y = 112.9 - 7.35x$; $r^2 = 0.82$). Treatment groups correspond with subheadings in Table 2.

Several biological factors that influence tree growth and mortality in our study sites have not been incorporated into this modelling effort. For example, recent research suggests that partial harvesting in lowland black spruce stands may increase the rate of paludification, development of a thick, waterlogged forest floor layer that reduces stand productivity (Fenton and Bergeron, 2007). Particularly on a 120-year time scale, different partial harvest scenarios may lead to faster or slower rates of paludification and associated declines in stand development rates. Black spruce growth is also strongly influenced by age in these sites (Thorpe et al., 2007), and so residual-tree growth rates in the 120-year simulations may be overestimated for older stands. Additionally, our simplistic treatment of recruitment does not incorporate potential effects of non-tree vegetation such as Labrador tea (*Rhododendron groenlandicum*) and *Sphagnum* spp., which can outcompete black spruce seedlings on these sites; in cases where regeneration does not establish immediately after harvest, our basal area projections may be overly optimistic. Climate change impacts are also predicted to be large for the study region and will likely influence tree growth and mortality rates, especially over the long term. Thus, while results from our long-term simulations are useful for making relative comparisons among partial harvest treatments, they do not represent comprehensive projections of lowland black spruce stand development over the next century.

4.3. Forest management implications

Simulation results demonstrated that residual-tree growth and mortality responses to partial harvest exert a strong influence on post-harvest stand dynamics, both over short and long time scales. Since stand structural attributes are important predictors of habitat supply and quality (e.g., Hagan and Meehan, 2002; St-Laurent et al., 2007; Smith et al., 2008), residual-tree responses are likely to influence habitat supplies in partially harvested stands over the long term. However, it remains unclear how post-harvest mortality will influence habitat availability in partially harvested stands. Tree mortality leads to inputs of coarse woody debris, an important habitat substrate (Harmon et al., 1986), and therefore may improve the tolerability of partial harvests for forest dwelling species. Standing death in particular may increase habitat availability, since snags are often destroyed during partial harvest operations (Vanderwel et al., 2006). Windthrow mortality, in contrast, may not contribute substantially to habitat supply since it occurs soon after harvest (Thorpe et al., 2008), a time when downed woody debris is gener-

ally already abundant (Fraver et al., 2002; Keeton, 2006). While dead trees represent habitat in the form of coarse wood, they also represent a loss of growing capacity. Of the many studies that have explored the impacts of partial harvests on taxa of concern (e.g., Gitzen et al., 2007; Vanderwel et al., 2007; reviewed in Rosenvald and Lõhmus, 2008), most document enhanced persistence of late-successional species with increasing retention levels (but see Sullivan et al., 2008). Partial harvest treatments associated with rapid stand recovery rates are therefore most likely to provide high-quality habitat soon after harvest. Presumably, such treatments would also be preferable from a timber production standpoint.

Proposals to increase the utilization of partial harvests in the boreal forest are based on the notion that alternative silvicultural treatments can emulate secondary disturbances such as insect outbreaks and windstorms, or successional processes like stand break-up (Bergeron and Harvey, 1997; Harvey et al., 2002). Across the set of HARP comparisons (Fig. 2), the treatment that best resembled a natural disturbance was, arguably, the 0% skidding scenario in which all stems larger than 9.3-cm were harvested. This treatment did not include skid trails, a key structuring feature of partial harvests that are absent from naturally disturbed stands. Although natural disturbances do not systematically remove all stems above a certain diameter as did this treatment, windstorm-induced tree mortality has been shown to increase with tree diameter (e.g., Canham et al., 2001; Rich et al., 2007), and stand break-up, when a large proportion of canopy trees die within a short time period, targets large trees by definition. Among comparable harvest scenarios, the no skidding treatment was also associated with the fastest rates of residual-tree growth, the lowest rate of post-harvest mortality, and the shortest estimated BA return interval (Table 2D, Fig. 1D). This suggests that recovery after natural disturbance may proceed more rapidly than following partial harvest.

The fastest documented basal area growth occurred in the 20-cm diameter limit, no skidding treatment, for which the estimated BA return interval was 25 years (Table 2D). Results from this treatment suggest that, at least biologically, it would be feasible to conduct uneven-aged management in lowland black spruce stands, a finding that is consistent with a previous study (Groot, 2002). Such management would involve more frequent stand entries and much lower harvest intensities than are standard practice for this ecosystem. The low revenues generated from harvesting in the boreal forest may be an important factor limiting the applicability of such a management strategy (Lieffers et al., 2003).

Our simulation results project an 85-year basal area return interval for HARP-treated stands. Compared to the 100–120-year rotations expected when lowland sites are clearcut, this represents an improvement. However, results from long-term simulations indicate that simple modifications to the harvest prescription could improve stand recovery rates substantially. Employing a larger diameter limit and widening the leave strips, for example, would reduce post-harvest mortality rates, increase retention levels, and reduce basal area return intervals. Increasing retention levels generally reduces yields on a per-stand-entry basis, but this is not necessarily the case. In the leave strip scenarios, for example, the diameter limit employed was consistent across treatments, and variation in retention levels was a result of differences in collateral damage (unmerchantable trees harvested from skid trails) alone. But while each of the leave strip treatments would produce the same wood volume for the mill, predicted basal area return intervals ranged widely, from 70 to 115 years (Fig. 2B). This result shows that in addition to the retention level, the specific parameters of partial harvest prescriptions strongly influence rates of post-harvest stand recovery.

Simulation results highlighted dramatic increases in post-harvest mortality as the width of leave areas declined (Table 2B).

Across the Canadian boreal forest, low-level structural retention harvests, in which trees are retained singularly or in narrow strips, are becoming increasingly common. The capacity of these stands to provide ecological functions depends critically on residual-tree survival. If mortality rates in these treatments are very high, as our results indicate, it is unclear whether such stands will provide improved habitat or ecosystem services compared to traditional clearcuts.

Finally, although we addressed issues exclusively at the stand level in this study, the trade-off between stand and landscape scales is of particular concern to all discussions about partial harvesting. Since partial harvests are associated with a lower per-hectare timber removal rate, retrieving the same amount of fibre in a given year requires a larger area to be harvested partially than clearcut, a project associated with more active roads and their concomitant impacts on wildlife and ecosystem processes. We are unaware of any studies attempting to quantify such tradeoffs; for example, whether it is preferable from an ecological perspective to remove 50% of stand basal area over a 100-ha area, or to clearcut a 50-ha area and leave the other 50 ha unharvested. Future modelling efforts to address this question would benefit debate surrounding partial harvesting in the boreal forest.

5. Management recommendations and conclusions

Findings from this study lead to three major management recommendations. First, *distance between skid trails should be maximised*. Proximity to skid trails dramatically increases the mortality risk for residual trees in lowland black spruce sites (Thorpe et al., 2008), and thus retaining wider leave strips leads to reduced post-harvest mortality and increased retention levels (Table 2B; Fig. 2B), both of which enhance stand recovery rates. Across all treatments, stand development was hastened by higher retention levels (Fig. 3), and so we also recommend that *partial harvest treatments should maintain high levels of retention*. Increasing retention levels generally reduces harvest volume on a per-ha basis; however, minimising collateral damage by narrowing skid trails and/or maximising the distance between them leads to increased retention levels with no associated impact on timber volumes. Finally, we stress that *responses of residual trees need to be considered when planning partial harvests*. Our results show that short-term responses of residual trees have long-term consequences for post-harvest stand development. Even in scenarios with equivalent retention levels, differential responses of residual trees led to large disparities in stand development rates (e.g., Fig. 2F). It is critical for managers to consider residual-tree responses, and in particular, how to design partial harvest treatments to reduce the likelihood of residual-tree mortality.

This study demonstrates the importance of incorporating dynamic residual-tree responses into forest growth models in order to make more accurate predictions of stand development following partial harvests. We show that failing to consider post-harvest mortality leads to overestimated stand development rates, and that relatively short-term (10-year) responses of residual trees are likely to influence stand development over long time scales. Simulation results indicate that efforts to reduce post-harvest mortality, in particular maximising the distance between skid trails, will lead to enhanced rates of post-harvest stand development, and will likely improve habitat supplies and capacity for ecosystem service provision in partially harvested stands.

Appendix A. Development of a spatially explicit growth model

In a previous study (Thorpe et al., 2007), we developed an aspatial model to describe individual-tree growth responses to harvest as a function of tree age and time since harvest. In order to conduct simulations of post-harvest stand dynamics using a spatially explicit stand simulation model (SORTIE-ND), it was first necessary to develop a growth model that was spatially explicit. The model outlined below predicts tree growth as a function of size, local competition, and time since harvest.

A.1. Data description

The field and laboratory methods employed to obtain the data used in this analysis are described in detail in Thorpe et al. (2007). Data were collected in 39 circular 15- or 20-m radius plots across 13 harvest blocks representing an 11-year harvest chronosequence situated in lowland black spruce boreal stands in northeastern Ontario. In each plot, we obtained increment core samples from all live trees ≥5 cm diameter at breast height (dbh: 1.3 m) located within 10 m of the plot centre. We mapped and measured the diameter of all stems (residual trees and stumps) ≥5 cm dbh located within 15 m ($n = 26$) or 20 m ($n = 13$) of the plot centre. Stems were mapped by recording their distance and azimuth from the plot centre and converting these measurements into x and y values. These spatial data permitted us to quantify the pre- and post-harvest neighbourhood basal area for each target tree (trees from which we took an increment core sample) in the analysis.

For each target tree ($n = 944$), we calculated a pre-harvest growth rate (g_{pre}), the average ring width of the 3 growth years immediately prior to harvest, and a post-harvest growth rate (g_{post}), the mean width of the 2001, 2002, and 2003 growth rings (the most recent complete growth rings at the time of field sampling in 2004). For sites harvested in 2002, only one post-harvest growth ring was available; the g_{post} value for trees in these sites include 2003 growth data only. Each g_{post} value is associated with a time since harvest value (e.g., +1 for 2003 harvest blocks, +10 for 1992 harvest blocks).

A.2. Model description

We developed a model to predict radial growth rates of individual trees as a function of local basal area, tree size, and time since harvest. Potential radial growth rates were expected to decline with tree size:

$$MG_i = \alpha e^{-\delta dbh_i} \tag{A.1}$$

where MG_i is the maximum potential radial growth rate of individual tree i of size dbh_i and α and δ are estimated parameters. We expected that growth rates would be influenced by local competition, and that trees' sensitivity to competition would decrease as individuals increased in size. To estimate the effect of competition on radial growth, we calculated a pre- and post-harvest neighbourhood competition index (NCI) for each individual tree, based on its size and local basal area:

$$NCI_i = BA_i e^{-\omega dbh_i} \tag{A.2}$$

where BA_i is the sum of the cross-sectional area of all neighbours within 5.0 m of an individual tree i, measured in m²/ha (basal area), and ω is an estimated parameter. Each tree was associated with a pre-harvest neighbourhood BA (includes stumps and residual trees) and a post-harvest neighbourhood BA (includes residual

trees only). Growth rates were expected to decline with increasing NCI values:

$$RG_{i,pre} = MG_i e^{-\eta NCI_{i,pre}} \tag{A.3}$$

$$RG_{i,post} = MG_i e^{-\eta NCI_{i,post}} \tag{A.4}$$

where η is an estimated parameter describing the effect of NCI on tree growth. Many previous studies have found that growth response to harvest is lagged; residual trees do not respond immediately to their post-harvest growing conditions (e.g., Latham and Tappeiner, 2002; Jones and Thomas, 2004; Thorpe et al., 2007). We used an exponential function to describe the path of tree growth from $RG_{i,pre}$ to $RG_{i,post}$:

$$RG_i = RG_{i,pre} + (RG_{i,post} - RG_{i,pre})(1 - e^{-\tau tsh}) + p_i \tag{A.5}$$

where tsh is time since harvest in years, τ is an estimated parameter describing that rate at which residual trees respond to their post-harvest growing conditions, and p_i is a plot effect to account for the correlated growth of trees from the same plot.

We fit Eqs. (A.1)–(A.5) to the data (g_{pre} and g_{post}) using maximum likelihood methods and a simulated annealing algorithm. Model residuals were assumed to follow a bivariate lognormal distribution, which allowed us to account for the correlated growth of individual trees before and after harvest:

$$f(g_{pre}, g_{post}) = \frac{1}{2\pi g_{pre} g_{post} \sigma_{y_{pre}} \sigma_{y_{post}} \sqrt{1 - \rho^2}} e^{-(q/2)} \tag{A.6}$$

$$q = \frac{1}{1 - \rho^2} \left[\left(\frac{\log g_{pre} - \mu_{y_{pre}}}{\sigma_{y_{pre}}} \right)^2 - 2\rho \left(\frac{\log g_{pre} - \mu_{y_{pre}}}{\sigma_{y_{pre}}} \right) \right.$$
$$\left. \times \left(\frac{\log g_{post} - \mu_{y_{post}}}{\sigma_{y_{post}}} \right) + \left(\frac{\log g_{post} - \mu_{y_{post}}}{\sigma_{y_{post}}} \right)^2 \right]$$

where g_{pre} and g_{post} are the observed pre- and post-harvest growth rates of an individual tree and ρ is an estimated coefficient ($-1 < \rho < 1$) describing the correlation between g_{pre} and g_{post} (equations from Yue, 2002). Observed pre- (g_{pre}) and post- (g_{post}) harvest growth was lognormally distributed. The population mean and standard deviation, μ_{y_i} and σ_{y_i}, where $y_i = \log(g_i)$ and $i = $ pre, post, are given by:

$$\mu_{y_i} = \log \left(\frac{\mu_{g_i}^2}{\sqrt{\mu_{g_i}^2 + \sigma_{g_i}^2}} \right) \tag{A.7}$$

$$\sigma_{y_i} = \sqrt{\log \left(1 + \frac{\sigma_{g_i}^2}{\mu_{g_i}^2} \right)} \tag{A.8}$$

where

$$\sigma_{g_{pre}}^2 = \upsilon \mu_{g_{pre}} \tag{A.9}$$

and

$$\sigma_{g_{post}}^2 = \varsigma \mu_{g_{post}} \tag{A.10}$$

The parameters υ and ς permit $\sigma_{g_{pre}}^2$ and $\sigma_{g_{post}}^2$ to increase with $\mu_{g_{pre}}$ and $\mu_{g_{post}}$ and thus allow for heteroscedasticity. Including them in the model improved the likelihood substantially compared to models that assumed constant variances.

We compared the full model (Eqs. (A.1)–(A.5)) to alternate models that excluded the effects of tree size, neighbourhood basal area, and/or time since harvest on tree growth (δ, ω, η, and/or $\tau = 0$)

Table A.1
Maximum likelihood parameter estimates (and 95% confidence limits) of the spatial growth model (Eqs. (A.1)–(A.10)).

Parameter	MLE	
α	1.405	(1.23, 1.57)
δ	0.039	(0.03, 0.05)
ω	0.158	(0.12, 0.20)
η	0.096	(0.07, 0.13)
τ	0.351	(0.28, 0.46)
υ	0.317	(0.28, 0.36)
ζ	0.502	(0.45, 0.56)
ρ	0.582	(0.54, 0.62)

and compared them using Akaike's information criterion (AIC$_c$) corrected for small sample size ($n/K < 40$):

$$AIC_c = 2L + 2K \left(\frac{n}{n - K - 1} \right) \tag{A.11}$$

where L is the log-likelihood of the observed dataset, K is the number of parameters, and n is the sample size. To assess the relative support for each alternate model, we calculated AIC$_c$ differences (ΔAIC_c) by subtracting the best model's AIC$_c$ value (AIC$_{c-min}$) from the AIC$_c$ of alternate models (Burnham and Anderson, 2002). Finally, we computed parameter confidence limits for the best model as described in Thorpe et al. (2007).

The full model (Eqs. (A.1)–(A.5); Table A.1), which predicts radial growth rates as a function of pre- and post-harvest local basal area, tree size, and time since harvest, was selected as most parsimo-
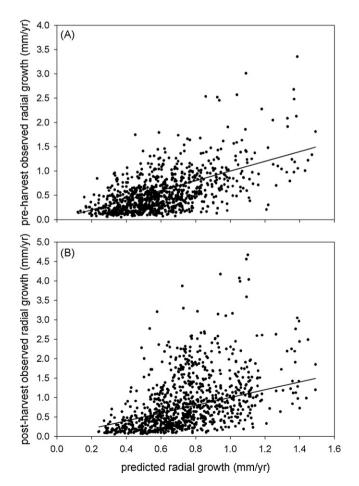

Fig. A.1. Goodness of fit of the maximum likelihood spatial growth model, which predicts radial growth rates before (A) and after (B) partial harvest. The model explained 27% of the variation in the observed data (g_{pre}, g_{post}). The line represents a 1:1 relationship between predicted and observed radial growth.
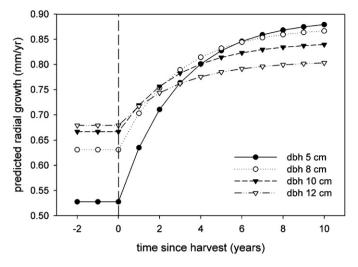
Fig. A.2. Example output from the spatial growth model. Predicted radial growth (RG) as a function of pre- and post-harvest neighbourhood basal area, time since harvest, and tree dbh. Pre- and post-harvest basal areas were held constant at 18 and 6 m²/ha respectively. Dashed vertical line indicates harvest event.

nious. No other model was associated with any support, as all $\triangle AIC_c$ values were greater than 20 (Burnham and Anderson, 2002). The best model yielded a reasonable fit to the data (Fig. A.1), explaining 27% of the variation in the observed growth data. Example model output is shown in Fig. A.2. The model is able to predict growth at the population level, but growth rates of individual trees deviate substantially from predicted, particularly in cases of rapid growth (Fig. A.1), a result that has been found in a previous study (Canham et al., 2004). Factors not included in the spatial growth model that may influence growth of black spruce trees on lowland sites include soil temperature and depth of organic matter, a proxy for site productivity. Age also has a strong influence on tree growth (Thorpe et al., 2007) but was not considered here.

In preliminary analyses, we estimated a parameter to quantify the radius over which local basal area would be calculated. We set 5 m as the upper bound, since this was the distance over which we had mapped neighbourhoods for all cored trees. In these model runs, the maximum likelihood radius parameter estimate was 5.0 m (the parameter upper bound), and so we fixed the radius parameter at 5.0 for the final analyses. In a subset of the plots ($n = 13$), we had mapped all trees within 10 m of all target trees (20 m from the plot centre). We conducted a set of analyses considering only the data from these larger plots to estimate the radius of neighbourhood influence. The maximum likelihood radius parameter estimate was 9.2 m. We performed subsequent analyses on this same subset of data in which we fixed the radius parameter at 5 m. Although this worsened the likelihood somewhat, the model R^2 changed very little, from 0.34 to 0.33. Therefore, we are confident that in using a fixed radius of 5 m in the final analysis, we captured the majority of the variation in tree growth rates attributable to differences in neighbourhood basal area.

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