Residual-tree growth responses to partial stand harvest in the black spruce (*Picea mariana*) boreal forest[1]

H. C. Thorpe, S. C. Thomas, and J. P. Caspersen

Abstract: Variants of partial harvesting are gaining favour as means to balance ecosystem management and timber production objectives on managed boreal forest landscapes. Understanding how residual trees respond to these alternative silvicultural treatments is a critical step towards evaluating their potential from either a conservation or a wood supply perspective. We used dendroecological techniques combined with a chronosequence approach to quantify the temporal radial growth response pattern of residual black spruce (*Picea mariana* (Mill.) BSP) trees to partial harvest in northeastern Ontario. At its peak, 8–9 years after harvest, radial growth of residual trees had doubled. The growth pattern was characterized by a 2-year phase of no response, a subsequent period of increase 3–9 years after harvest, and a stage of declining rates 10–12 years after harvest. The magnitude of tree growth response depended strongly on tree age: peak postharvest growth was substantially higher for young trees, while old trees displayed only modest growth increases. Both the large magnitude and the time delay in postharvest growth responses have important implications for the development of more accurate quantitative tools to project future yields and, more generally, for determining whether partial harvesting is a viable management option for the boreal forest.

Résumé : Des variantes de la coupe partielle gagnent en popularité comme moyens d'atteindre un équilibre entre les objectifs d'aménagement écosystémique et de production de matière ligneuse dans les paysages aménagés de la forêt boréale. Une étape cruciale pour évaluer leur potentiel dans une perspective soit de conservation, soit d'approvisionnement en matière ligneuse, consiste à comprendre comment les arbres résiduels réagissent à ces traitements sylvicoles alternatifs. Nous avons utilisé les techniques dendroécologiques combinées à une approche impliquant une chronoséquence pour quantifier le patron de réaction de la croissance radiale dans le temps des tiges résiduelles d'épinette noire (*Picea mariana* (Mill.) BSP) à la coupe partielle dans le nord-est de l'Ontario. À son point culminant, 8 à 9 ans après la coupe, la croissance radiale des arbres résiduels avait doublé. Le patron de croissance était caractérisé par une phase de latence de 2 ans, suivie d'une période d'augmentation 3 à 9 ans après la coupe et d'un stade de taux décroissants 10 à 12 ans après la coupe. L'ampleur de la réaction en croissance des arbres dépendait étroitement de leur âge : le pic de croissance observé après la coupe était substantiellement plus prononcé chez les jeunes arbres tandis que seulement de modestes augmentations de croissance ont été observées chez les vieux arbres. Tant l'ampleur que le délai qui caractérisent la réponse en croissance après la coupe ont des conséquences importantes sur le développement d'outils quantitatifs plus justes pour prédire les rendements futurs et, de façon plus générale, pour déterminer si la coupe partielle est une option d'aménagement viable pour la forêt boréale.

[Traduit par la Rédaction]

Introduction

Interest in partial harvesting in the boreal forest biome has been increasing in recent years, primarily motivated by ecological research demonstrating important structural and compositional differences between managed and unmanaged forests at multiple scales (Bergeron 2000; Franklin et al. 2002; Seymour et al. 2002; Harper et al. 2005). Past forest management strategies have generally focussed on system simplification, for example, the conversion of natural forests to even-aged, single-species plantations, while natural disturbances produce much of the landscape variability and ecosystem complexity associated with higher biodiversity levels found in unmanaged forest regions (Kohm and Franklin 1997). Partial harvesting may reduce the stand and landscape homogeneity associated with even-aged management in the boreal forest and could thus present a means to balance ecological and timber production goals in boreal regions under forest management (Harvey et al. 2002).

The considerable gap between natural and managed forest systems has led to widespread interest in natural disturbance emulation, a management strategy aimed at generating forest ecosystems that are structurally and compositionally similar to those that arise from natural disturbances (Perera and Buse 2004). Natural disturbance emulation is based on the assumption that if these structural and compositional goals

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are met, ecosystem function and biodiversity will be maintained (Franklin 1993; Bergeron et al. 2001) and is now a management requirement in the Canadian province of Ontario (Crown Forestry Sustainability Act, R.S.O. 1994, c. 25, s. 2(3)). In the boreal forest, fire is the dominant disturbance; consequently, natural disturbance emulation was initially equated with increasing clearcut sizes to better mirror wildfire patterns (McRae et al. 2001). However, research reconstructing natural disturbance regimes has shown that fire cycles, particularly in the eastern Canadian boreal, are often much longer than current rotation ages under conventional clearcut management (Bergeron et al. 2001). Where fire cycles are long, stands escape fire well past the rotation age (80–120 years) and develop uneven-aged stand structures (Bergeron 2000). Use of short-rotation, even-aged management on these landscapes results in a disproportionate loss of old forests and their associated diversity (Bergeron et al. 1999), and the move to natural disturbance based management requires major change, either to longer rotations or to partial harvesting (Bergeron and Harvey 1997; Seymour and Hunter 1999). Partial harvesting is often considered the more attractive of these options, as it has a smaller short-term impact on wood supply (Harvey et al. 2002).

Despite the potential benefits of using partial harvesting in the boreal, there remain few empirical data to evaluate whether it is indeed a reasonable management option in this biome. Most studies have examined responses of wildlife (Lindo and Visser 2004; Deans et al. 2005; Harrison et al. 2005; Fisher and Bradbury 2006) or tree regeneration (Bourgeois et al. 2004; MacDonald et al. 2004) to partial harvest, while little research has focussed on how residual trees themselves respond. Quantifying tree responses is fundamental to evaluating partial-harvesting systems. From a wood supply, silvicultural, or wildlife perspective, partial harvesting is only likely to be deemed successful if residual trees respond well in terms of growth and survival.

When surrounding neighbours are removed, residual trees commonly display enhanced growth, but with a variable time lag following harvest. This pattern has been found in a number of species and treatments, with peak residual-tree growth occurring 6–25 years after harvest (e.g., Youngblood 1991; Groot and Hökkä 2000; Latham and Tappeiner 2002; Jones and Thomas 2004). Such positive responses may not be found in regions of the boreal where sites are low lying and poorly drained. Here, paludification, development of a thick, waterlogged forest floor layer, is a concern, as it increases with time since fire and can cause substantial declines in productivity (Fenton et al. 2005). If sites are paludified, one might expect little or no postharvest growth response.

Harvest with Advance Regeneration Protection (HARP/ Coupe avec Protection de Petites Tiges Marchandes in Québec; Tallman 1998) is a rare example of partial harvesting currently in practice on an operational scale in the boreal forest in Canada. It was developed for lowland forests before natural disturbance emulation was a management goal and implemented with the expectation that protecting soils and large advance regeneration would reduce the long (~120 year) rotations associated with clearcutting on these sites. While not explicitly designed to emulate natural disturbance, HARP is an extremely valuable case by which to evaluate the prospect of partial harvesting in the boreal forest, since it presents an operational scale of study and a relatively long period of response. This combination of factors facilitates a chronosequence approach that, in conjunction with dendroecological data, allows the decoupling of climate influences from year of harvest and permits isolation of the growth response to harvest (cf. Jones and Thomas 2004).

In this study, we quantify the temporal responses of residual black spruce (*Picea mariana* (Mill.) BSP) trees to partial harvest and address the following questions. (*i*) Does black spruce show a detectable positive growth response to partial harvesting on lowland sites? (*ii*) If so, what is the temporal pattern of this response? (*iii*) How do tree size, age, and preharvest growth rate affect this response? Quantifying these responses represents a critical step towards making growth and yield predictions and management recommendations in more complex boreal stands, with important implications for sustainability of current practices.

Materials and methods

Study site

This study was conducted near Cochrane, Ontario, in the Lake Abitibi Model Forest, a 1.2 million hectare land base in northeastern Ontario that lies within the northern clay section of the boreal region (Rowe 1972), an area known as the Clay Belt. This region is characterized by lacustrine deposits, flat topography, and poorly drained organic soils. The climate is cold, with a mean annual temperature of 0.6 °C and annual precipitation of 880 mm (Environment Canada 2002). Black spruce is the dominant tree species in 77% of stands in the Lake Abitibi Model Forest. The study area was bounded by 48°99′–49°76′N and 79°81′–80°78′W.

Harvest method

HARP was developed and first implemented in the Lake Abitibi Model Forest in the early 1990s. It is carried out in uneven-aged lowland black spruce stands, abundant across the Clay Belt, and is characterized by alternating clearcut strips (5–7 m wide) where harvesting equipment travels and partial-harvest strips (5–9 m wide) in which 10–12 cm diameter at breast height (DBH) (1.3 m) diameter-limit cutting is generally used (Tallman 1998; Deans et al. 2003). In recently cut areas in Ontario, at least six large trees per hectare are also retained to meet the province's new harvesting guidelines (Ontario Misistry of Natural Resources 2001). HARP is carried out during winter months to protect the organic soils.

Data collected during this study showed that HARP treatments reduced basal area on average by nearly 80%, from 21.25 to 4.39 $m^2 \cdot ha^{-1}$, and density of stems >5 cm DBH by 55%, from 1678 to 757$\cdot ha^{-1}$. Harvesting concentrated on large size classes: >90% of all stems >14 cm DBH were cut, while 66% of stems 5–8 cm DBH remained after harvest (Fig. 1).

Field and laboratory procedure

We employed stratified random sampling to select cutblocks (logged forest stands) across a replicated chronosequence with the following harvest dates: 1991 (n = 1), 1992

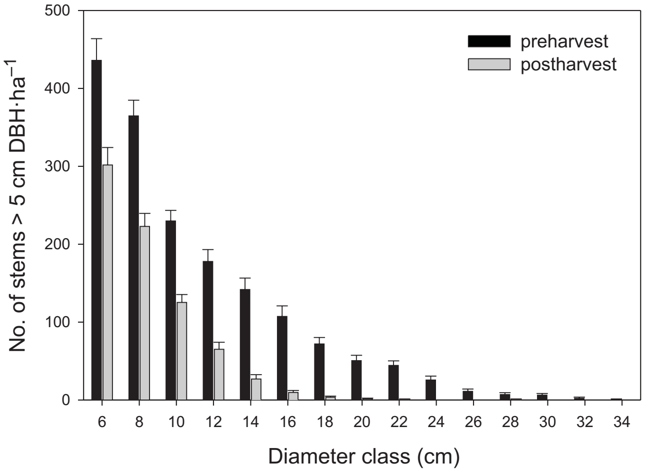


Fig. 1. Diameter frequency distributions before and after HARP. Diameters at breast height (DBH) for stumps were estimated from stump diameters (DSH) using an allometric equation created from paired sets of diameter measurements taken from stump and breast height in the field (DBH = 0.89 × DSH – 0.80; $n = 50$, $r^2 = 0.97$).

($n = 1$), 1994 ($n = 2$), 1996 ($n = 3$), 1998 ($n = 2$), 2000 ($n = 2$), and 2002 ($n = 2$). Cutblocks were selected to maximize spatial interspersion of harvest years across the landscape. All harvesting took place in the winter between the assigned cutblock year and the following year. For example, 1994 cutblocks were harvested in the winter of 1994–1995; 1995 is the first postharvest growing season. Sample size was limited in 1991 and 1992 because HARP was carried out on a trial basis only during those years. All sites were located in lowland, black spruce dominated stands. Other species included balsam fir (*Abies balsamea* (L.) Mill.), tamarack (*Larix laricina* (Du Roi) K. Koch), and balsam poplar (*Populus balsamifera* L.) but made up <3% of all stems. With the exception of two cutblocks that were previously harvested in the 1930s, preharvest stand structures were determined solely by natural disturbance histories; sites had not been cut before partial harvest (see Table 1).

During the summer of 2004, we established three circular, 10 m radius plots in each cutblock spaced 200–400 m apart to maximize block coverage. We took diameter measurements from all stumps, recently dead, and live trees >5 cm DBH within each plot. Increment core samples were obtained from each live black spruce tree at 0.3 m height to ensure pith acquisition from every stem possible. Age data should therefore be interpreted as age at 0.3 m; the tendency of black spruce to reproduce through layering on lowland sites (Stanek 1961) renders age of genetic individuals ambiguous and difficult to determine.

We mounted cores in grooved plywood holders and sanded them with increasingly higher grit sandpaper until growth rings became clear. Rings were counted and measured to within 0.001 mm using WinDendro (v. 2003*b*, Regent Instruments, Quebec). We cross-dated ring series by comparing skeleton plots with two separate master series: (*i*) an established black spruce chronology from the region (Hofgaard et al. 1999) and (*ii*) a series constructed from 60 representative cores from our data set. Ring series that showed an apparent shift in growth patterns were noted and their corresponding cores were checked for missing or false rings. Once changes were made, these series were rechecked against the masters before being included in the data set.

Statistical analysis

We calculated three measures from each tree-ring series in our data set: (*i*) tree age, (*ii*) observed preharvest radial growth rate ($\mathrm{RG}_{\mathrm{obs,\,pre}}$), the average ring width of the 3 growth years immediately prior to harvest, and (*iii*) postharvest radial growth rate ($\mathrm{RG}_{\mathrm{obs,\,post}}$), the mean width of the three most recent complete growth rings, 2001, 2002, and 2003. Sites that were harvested in 2002 had only one postharvest growth ring available; $\mathrm{RG}_{\mathrm{obs,\,post}}$ for these sites include 2003 data only. Each $\mathrm{RG}_{\mathrm{obs,\,post}}$ value was assigned a time since harvest; for example, values from 1994 cutblocks are associated with a time since harvest of +8 (see Table 1). This approach, permitted by the chronosequence method, decouples time since harvest from year of harvest and thereby distinguishes growth responses to harvest from any changes due to interannual variation in climate.

Basic growth model

To examine the postharvest response pattern of residual trees, we developed a model that predicts growth response as a function of time since harvest. Below, we describe this basic growth model as well as more complex models that include combinations of age, DBH, and preharvest growth as predictor variables. Next, we explain the methods used to estimate model parameters and confidence limits. Finally, we describe the methods used to select the model that most parsimoniously described the observed growth responses to harvest.

Following competition release, trees typically display a pattern of increased growth followed by subsequent declines towards predisturbance rates. The temporal pattern of this response can be described using the differential form of the Chapman–Richards growth function (Zeide 1993):

$$[1] \qquad I = \omega\phi\gamma\, \mathrm{e}^{-\phi t}(1 - \mathrm{e}^{-\phi t})^{\gamma - 1}$$

where I is the increase in growth above the preharvest rate, t is time since harvest, and ω, ϕ, and γ are fitted constants. We predicted postharvest radial growth by adding this growth increase I and a plot effect to the observed preharvest growth rate:

$$[2] \qquad \mathrm{RG}_{\mathrm{pred}} = \mathrm{RG}_{\mathrm{obs,\ pre}} + I + p_i$$

where $\mathrm{RG}_{\mathrm{pred}}$ is the predicted annual radial growth following harvest, $\mathrm{RG}_{\mathrm{obs,\,pre}}$ is the observed preharvest radial growth rate, I is the magnitude of the growth increase, and p_i is a fixed effect term that accounts for correlated growth of trees from the same plot.

Additional predictor variables

A number of variables may influence the magnitude of the postharvest increase in growth, particularly tree age, size, and preharvest growth rate. Younger trees are likely to display larger growth increases than old trees, while larger trees may reach faster growth rates than their smaller counterparts. Suppression may also affect individuals' ability to respond to harvest, and thus, slow preharvest growth rates may be associated with more modest growth increases.

Table 1. Description of sampling chronosequence, site disturbance histories, cutblock, plot, and core sample sizes, and corresponding years of tree-ring data used in growth analysis.

Year of HARP	No. of cutblocks (and plots)	Time of last stand-replacing fire[a]	No. of increment core samples	Calendar years in $RG_{obs, post}$[b]	Postharvest years in $RG_{obs, post}$[b] (and t[c])
1991	1 (3)	<1760	55	2001–2003	10, 11, 12 (+11)
1992	1 (3)	<1760	90	2001–2003	9, 10, 11 (+10)
1994	2 (6)	<1760 (2)	138	2001–2003	7, 8, 9 (+8)
1996	3 (9)	<1760 (2), 1800–1820[d]	195	2001–2003	5, 6, 7 (+6)
1998	2 (6)	<1760, 1760–1769[d]	154	2001–2003	3, 4, 5 (+4)
2000	2 (6)	1800–1820, 1850–1859	171	2001–2003	1, 2, 3 (+2)
2002	2 (6)	1800–1820, 1850–1859	123	2003	1 (+1)
Total	13 (39)		926		

[a] From Gauthier et al. (2002).

[b] $RG_{obs, post}$ is the per-tree average ring width calculated using the three most recent available growth rings, except for 2002 cutblocks where $RG_{obs, post}$ is represented by one ring only.

[c] t is the time since harvest associated with each $RG_{obs, post}$ value, representing the mean number of years since harvest of the tree rings used in calculating $RG_{obs, post}$.

[d] Sites developed following horse logging in the 1930s (no other cutblocks were harvested before HARP treatment).

We used these three variables to develop a set of eight nested models: a complete model that included the effect of all three variables and various reduced models that excluded one or more predictor variables (Table 2). We specified the effects of these variables by including three multipliers in an expanded form of eq. 2:

$$[3]\qquad RG_{pred} = RG_{obs,\ pre} + IADS + p_i$$

where

$$[4]\qquad A = 1 - \delta \times \text{age}$$

$$[5]\qquad D = 1 + \upsilon \times \text{DBH}$$

$$[6]\qquad S = 1 + \psi \times RG_{obs,\ pre}$$

where A, D, and S are multipliers used to specify the effects of age, diameter (size), and suppression, respectively, and δ, υ, and ψ are fitted constants. We implemented the various reduced models by setting one or more of the additional parameters (δ, υ, and ψ) to zero, thereby setting the associated multipliers A, D, and S to 1.

Estimation of parameters and their confidence limits

We fit the models to the data using maximum likelihood estimation and a simulated annealing algorithm (Hilborn and Mangel 1997). Model residuals were assumed to follow a lognormal distribution:

$$[7]\qquad f(y{:}\mu, \sigma^2) = \frac{1}{y\sqrt{2\pi\sigma^2}}\, e^{-\frac{(\log(y)-\mu)^2}{2\sigma^2}}$$

where y is the observed radial growth ($RG_{obs,\ post}$) and μ and σ^2 are the mean and variance of $\log(y)$, respectively. The mean and variance of y itself are expressed as

$$[8]\qquad u_I = e^{\mu+\frac{\sigma^2}{2}}$$

$$[9]\qquad \sigma_I^2 = e^{2\mu+2\sigma^2} - e^{2\mu+\sigma^2}$$

Since we wished to estimate the mean and variance of y, we reparameterized its distribution (eq. 7) as a function of μ_I and σ_I^2 (see Appendix A) and estimated μ_I as a function of the predictor variables (RG_{pred} in eq. 3) and σ_I^2 as a linear function of μ_I:

$$[10]\qquad \sigma_I^2 = \rho\mu_I$$

Permitting σ_I^2 to increase with μ_I, rather than remaining constant, allowed for heteroscedasticity and improved the likelihood estimates substantially.

We computed parameter confidence limits by repeatedly sampling random values to obtain 100 000 sets of parameters. We then calculated the log-likelihood of each parameter set and its deviance D from the maximum log-likelihood ($D = 2(L - L_{max})$). Sets for which the deviance exceeded the critical value of the χ^2 distribution ($\alpha = 0.05$, df = 1) were excluded. From the remaining sets, we selected the minimum and maximum parameter values as the 95% confidence limits (Hilborn and Mangel 1997).

All analyses were carried out using software written specifically for this study in the C programming language.

Model selection

We fit the eight competing models to the data as described above and compared them using Akaike's information criterion (AIC_c) corrected for small sample size ($n/K < 40$):

$$[11]\qquad AIC_c = -\,2\log(\text{likelihood}) + 2K\left(\frac{n}{n-K-1}\right)$$

where K is the number of estimated parameters in the model and n is the total number of observations. The model with the smallest AIC_c is the most parsimonious (Burnham and Anderson 2002). To assess the relative support for the alternate models, we calculated their AIC_c differences by subtracting the best model's AIC_c value ($AIC_{c\text{-}min}$) from the AIC_c of the seven other candidate models (Burnham and Anderson 2002).

Results

We sampled 2283 stems in 39 plots across 13 cutblocks including live trees, recently dead trees, and stumps to obtain pre- and postharvest diameter distributions (Fig. 1). We

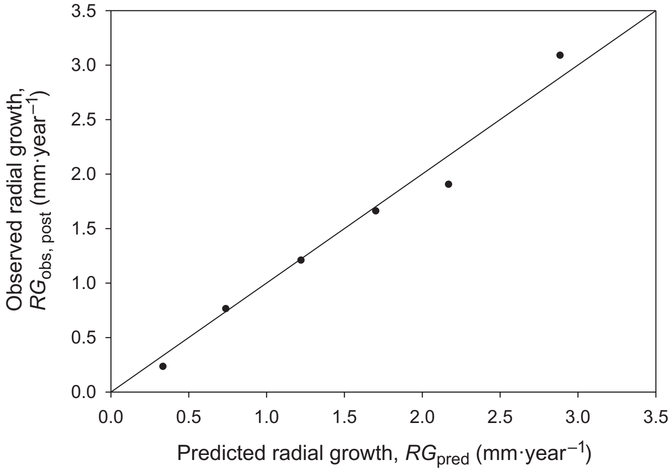
Table 2. Comparison of the eight fitted models including the predictor variables tested and associated maximum log-likelihoods, AIC_c values, and AIC_c differences (ΔAIC_c).

Model No.	Age effect (*A*)	Diameter effect (*D*)	Suppression effect (*S*)	Maximum log- likelihood	AIC_c	ΔAIC_c[a]
1	Yes	No	No	–293.92	678.13	0
2	Yes	Yes	No	–292.84	678.17	0.04
3	Yes	No	Yes	–293.31	679.11	0.98
4	Yes	Yes	Yes	–293.23	681.16	3.03
5	No	No	No	–306.14	700.37	22.24
6	No	Yes	No	–305.95	702.19	24.06
7	No	Yes	Yes	–305.81	704.11	25.98
8	No	No	Yes	–306.98	704.25	26.12

Note: The model with the lowest AIC_c is most parsimonious.

[a] ΔAIC_c is calculated as the difference between the lowest AIC_c value and the AIC_c of the candidate model being considered (Burnham and Anderson 2002).

Fig. 2. Goodness-of-fit of the maximum likelihood model (Table 2, model 1), which explained 48.6% of the variation in the observed data ($RG_{obs, post}$). Mean values of observed and predicted growth are shown for each of six classes of predicted growth (<0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0, 2.0–2.5, and >2.5 mm·year^{-1} corresponding to bin sample sizes of 217, 394, 228, 67, 11, and 9). The line represents a 1:1 relationship between predicted and observed radial growth.



were able to age 926 of the 944 increment core samples obtained from live trees; the 18 others were excluded from growth analyses.

Model selection and goodness of fit

The most parsimonious model included a term for the effect of age on residual-tree growth response to harvest (Table 2, model 1). This growth model and associated parameters yielded a good fit to the observed radial growth rates, with a 1:1 relationship between predicted and observed and symmetrically distributed residuals (Fig. 2; Table 3). The model explained 48.6% of the variation in the observed data.

Size and suppression effects

The selected best model did not include the effects of suppression or size on growth response. However, there remains substantial support for any model whose AIC_c value is within 2.0 of the minimum AIC_c (Burnham and Anderson 2002), and the models that included size (DBH) or suppression effects in addition to age (Table 2, models 2 and 3) both displayed AIC_c values within 1.0 of the $AIC_{c\text{-}min}$. Thus, a similar strength of evidence supported models 1, 2, and 3 (Table 2). However, in models 2 and 3, the parameter estimates for size and suppression were very small relative to the predictors (DBH parameter υ = 0.00056, mean DBH = 8.2 cm; suppression parameter ψ = 0.0045, mean $RG_{obs, pre}$ = 0.54 mm·year^{-1}), and therefore their inclusion in the model added only very limited predictive power. The complete model, which included age, DBH, and suppression effects, had little support, with an AIC_c difference of 3.03 (Table 2, model 4), and the four models that did not consider age effects had virtually no support, with all AIC_c differences greater than 20 (Table 2, models 5–8). Our use of a fixed, rather than random, plot effect could have resulted in overly narrow estimates of parameter confidence limits and inaccurate assessments of alternate models. However, the large magnitude of AIC_c differences between models that included age effects and those that did not (Table 2, models 1–4 versus 5–8) demonstrates the strength of this predictor and indicates that use of a more conservative approach would not have altered the study results.

Table 3. Maximum likelihood parameter estimates (and 95% confidence limits) of the most parsimonious growth model listed in Table 2 (model 1).

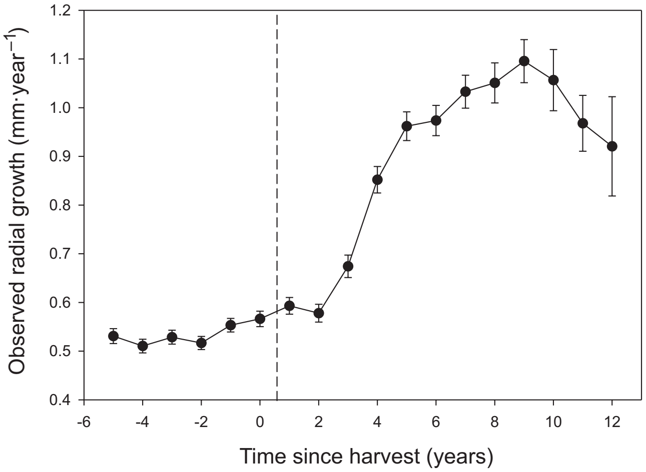
Parameter	Maximum likelihood estimate (95% confidence limit)
ω	7.52 (7.11, 8.05)
ϕ	0.226 (0.207, 0.253)
γ	6.67 (6.26, 7.36)
δ	0.0045 (0.0038, 0.0050)
ρ	0.300 (0.266, 0.334)

Growth response

Residual black spruce trees displayed a sizeable increase in growth following partial harvest. At their peak, radial growth rates were double those found before harvest. The mean observed peak was delayed, occurring 8–9 years after harvest, and the response pattern exhibited a 2-year delay period of no response followed by a 6- to 7-year period of increase after harvest (Fig. 3).

The shape of the predicted postharvest growth increase *I*, described by the Chapman–Richards function and corre-

Fig. 3. Mean (±SE) growth response of residual black spruce trees to partial harvest across all harvest years ($n = 944$). The broken vertical line indicates harvest event (displayed between years 0 and +1 because HARP is carried out during the winter months between growing seasons).

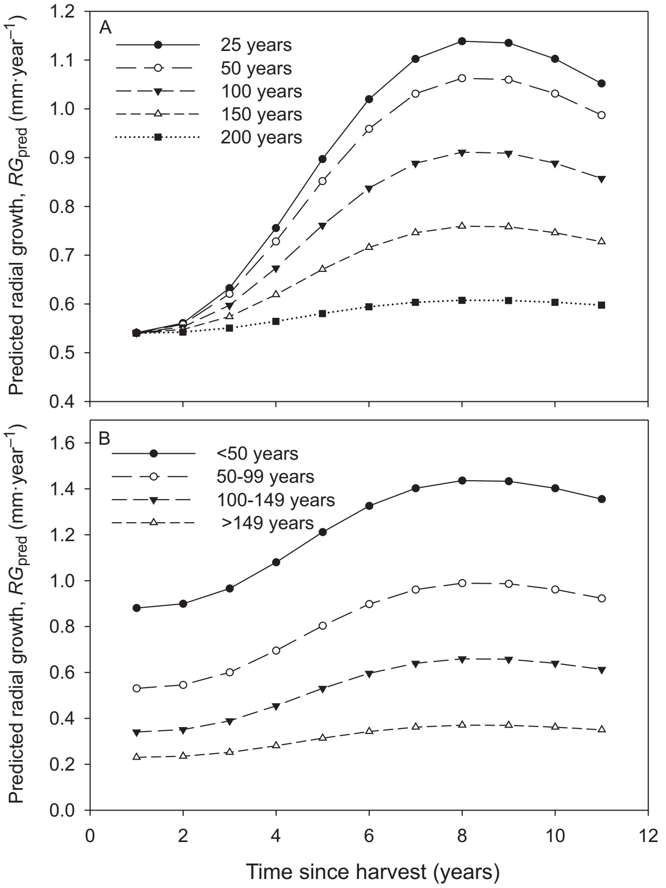


sponding parameters (eq. 1; Table 3), mirrored closely the observed pattern, with a delay period of no response predicted in the first 2 years following harvest, a subsequent increasing period up to 8–9 years after harvest, and a consequent decline (Fig. 4).

Tree age had a strong influence on the magnitude of predicted responses (Fig. 4). Older trees displayed modest growth responses compared with their younger counterparts, and very old trees (>200 years old) showed little or no positive growth response to harvest (Fig. 4). For example, 25-year-old trees were predicted to show peak radial growth increases of 0.60 mm·year^{-1}, while 175-year-old trees were expected to show growth rates elevated only 0.14 mm·year^{-1} above preharvest levels. The corresponding proportional increases varied depending on preharvest growth rate ($\mathrm{RG}_{\mathrm{obs,\,pre}}$), the intercept of the model. The average trees in our data set, 79 years old and growing 0.54 mm·year^{-1} before harvest, were expected to reach a growth peak 0.43 mm·year^{-1} above their preharvest rate, representing an 80% increase. With the same preharvest growth rate, 25-year-old trees were expected to show a 111% elevation in growth, in contrast with 175-year-olds' predicted 26% increase (Fig. 4A). Note, however, that although trees of a wide range of ages (20–193 years) displayed preharvest growth rates equal to or greater than the mean 0.54 mm·year^{-1}, the majority of old trees showed fairly slow preharvest growth rates, and most young trees were growing relatively quickly before harvest (Fig. 4B). The growth model did not quantify the extent to which preharvest growth depended on age.

In addition to time since harvest and tree age, predicted responses were affected by the plot term p_i, which accounted for up to 0.71 mm·year^{-1} differences in tree growth among plots. Estimates of p_i varied widely across plots from the same cutblock, indicating that differences in site productivity operated principally at the plot, rather than cutblock, scale.

Fig. 4. Radial growth ($\mathrm{RG}_{\mathrm{pred}}$) expressed as a function of time since harvest and tree age, as predicted by the maximum likelihood model (Table 2, model 1) (A) for a range of tree ages with equal preharvest growth rates ($\mathrm{RG}_{\mathrm{obs,\,pre}}$) and (B) for trees of varying ages and preharvest growth rates ($\mathrm{RG}_{\mathrm{obs,\,pre}}$). For Fig. 4B, values of age and preharvest growth used in the model were obtained by binning observed data by age (<50, 50–99, 100–149, and >149 years) and using each bin's mean age (39, 71, 117, and 176 years) and mean preharvest growth rate (0.88, 0.53, 0.34, and 0.23 mm·year^{-1}) to calculate predicted growth responses.



Discussion

Following partial harvest, residual black spruce trees displayed considerable increases in growth, the mean response peaking at twice the preharvest rate (mean radial growth rose from 0.54 to 1.10 mm·year^{-1}; Fig. 3). Individual growth responses were highly variable and were explained in part by differences in tree age, with younger trees expected to show the largest magnitude responses.

We presume that enhanced postharvest growth resulted from increased resources made available to residual trees after their neighbours had been removed. HARP treatments dramatically increase the light available to residual trees and likely cause soil temperatures to rise as more sunlight reaches the forest floor. In the cold, wet sites considered in this study, even small increases in soil temperature could have important implications for tree growth. Nutrient flushing following harvest may also help to explain the pattern of growth response.

Increases in radial growth did not become apparent until the third postharvest growing season (Figs. 3 and 4), a result that has been shown in other studies of residual-tree response (Youngblood 1991; Bebber et al. 2004; Jones and

Thomas 2004). We hypothesize that this pattern may be caused either by slow acclimation responses or by resource allocation to root and (or) shoot growth during the first 2 years after harvest. Evidence for the first hypothesis has been found in a sugar maple (*Acer saccharum* Marsh.) stand following selection harvest, with physiological acclimation of residual trees' lower canopy foliage requiring at least 2 years (Jones and Thomas 2007).

Between 9 and 10 years after harvest, growth rates began to decrease towards preharvest levels, perhaps a result of declining resource availability. The large increases in residual-tree growth documented here imply that competition for light and (or) declining soil temperatures could begin to limit growth of trees in the partial-cut strips of HARP-treated stands within a decade of harvest. Nutrient flushing may also be involved; the pattern of growth increase and decline could be tracking the availability of nutrients. It is important to note, however, that residual trees in the lower-competition environment of the HARP clearcut strips are unlikely to experience declining growth rates so soon after harvest. Trees in these strips were not considered in the present study since, even a decade after harvest, not a single stem met our minimum 5 cm DBH criterion.

Although they were not considered in our growth model, residual trees' spatial configurations most likely influenced their ability to respond to HARP. The combination of diameter-limit strip cuts and variable preharvest stand structures created a wide range in the spatial arrangements of residual trees: some stems remained crowded after harvest, while others were released from competition entirely. Differences in the magnitude of individual-tree growth responses not explained by tree age may be attributable to spatial variation in postharvest stand structures; such factors could account for a substantial fraction of the unexplained variation in the observed data.

Groot and Hökkä (2000) examined long-term (40-year) responses of black spruce advance regeneration to historical partial harvesting and documented approximately twofold increases in diameter growth at their peak, which occurred on average 10 years after harvest. Although the specific prescription of this horse logging treatment is unknown, it is apparent that, compared with HARP, higher densities of residual stems were retained, more large stems were left, and skid trails were substantially narrower. Further, modern harvesting equipment is often associated with forest floor rutting and soil compaction, both of which may induce the water table to rise (Lavoie et al. 2005), although winter harvesting should minimize this effect. Despite the differences in these treatments, we have documented a similar pattern and magnitude of response to partial harvest as did Groot and Hökkä (2000), but on a per residual tree, not stand-level, basis.

The pattern of gradual increase in growth following partial harvest has been found across a wide range of tree species. The time scale of this upsurge appears to vary with species and treatment, from 6 years in sugar maple selection harvests (Jones and Thomas 2004) up to 25 years in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) density reduction cuts (Latham and Tappeiner 2002). Studies of white spruce (*Picea glauca* (Moench) Voss) (Youngblood 1991), eastern white pine (*Pinus strobus* L.) (Bevilacqua et al. 2005), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (Latham and Tappeiner 2002) reported approximately twofold increases in growth following partial harvest, similar magnitudes of response to those found in the present study. In studies of sugar maple (Jones and Thomas 2004) and white pine (Bebber et al. 2004), residual trees exhibited more modest growth increases of ~60%, but these stands experienced lower harvest intensities.

A surprising result was that tree age was the best predictor of the magnitude of tree growth response (Fig. 4). Many studies have demonstrated the significance of tree size in predicting variation in growth (e.g., Canham et al. 2004; Jones and Thomas 2004) but size was not an important predictor of growth in the present study. This is likely due in part to the small range of residual-tree sizes, but tree age does appear to be a much stronger predictor of growth in this system. Other studies have shown declines in growth with tree age (e.g., Doyon et al. 1998; Seymour and Kenefic 2002), but to our knowledge, this is the first analysis to examine how patterns of growth following disturbance vary with tree age. The mechanism behind this result remains unclear, but we speculate that age-dependent increases in pathogenic fungi could be an important factor. The prevalence of these fungi, in particular root-rot fungi such as *Armillaria* spp. and *Inonotus tomentosus* (Fr.) Teng, increases with tree age in black spruce and is associated with declining growth (Whitney 1995). Such fungal infections may also affect the ability of residual trees to respond to competition reduction.

Implications for management

HARP was not originally designed to emulate natural disturbance; however, understanding how residual trees respond to this treatment is critical for evaluating partial harvests of all kinds in the boreal forest. It is expected that partial harvesting will be a viable management option only if residual trees respond with enhanced growth and high survival. We cannot comment on mortality rates here, but in terms of growth, partial harvesting appears to be a feasible silvicultural method for lowland boreal black spruce forests, particularly for relatively young stands on reasonably productive sites.

Much of the impetus behind partial cutting in the boreal has been to retain old forest associated features on managed landscapes. The largest growth responses were seen in young trees, however, implying that partial harvests are most likely to achieve a balance between maintenance of ecological services and continued timber production in stands comprising high proportions of younger stems. Old trees displayed limited growth responses (Fig. 4), suggesting that sustainable partial harvesting may not be feasible in stands, widespread across the Clay Belt, that contain large proportions of old trees. Maintaining old-growth features in such stands may require avoiding harvesting entirely.

The finding of poor growth in old trees suggests that a "crop-tree release" prescription that removed old and (or) suppressed trees and concentrated postharvest growth responses in younger, faster-growing trees would result in considerable increases in postharvest growth, and may reduce the time required for basal areas to return to preharvest levels. Enhanced growth following partial stand harvests, representing timber yields or habitat, would presumably be beneficial from both a wood supply and an ecological conservation perspective.

Overall, the finding of large but time-lagged responses of black spruce to partial harvest is an important step towards developing yield predictions for these partially harvested sites. Incorporating time-lagged growth responses into yield models will clearly improve their accuracy, since the observed growth responses are surprisingly large and the lags quite long. Our results indicate that peak growth occurs 8–9 years following HARP, but the exact pattern of the declining trend remains unquantified. A longer monitoring period is required to determine the length of time over which this growth response will persist, but it is possible that rates will remain elevated above preharvest levels for another decade or more.

Finally, an unexpected result of this study is that the strongest predictor of the postharvest growth response, tree age, is a nonstructural feature. This suggests that to predict short- to midterm responses to partial harvest accurately, preharvest sampling procedures need to broaden beyond acquisition of simple stand densities and diameter distributions.

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Appendix A

In order to reparameterize the distribution of y (eq. 7) as a function of μ_I and σ_I^2, we rearranged eqs. 8 and 9 to express μ and σ^2 as functions of μ_I and σ_I^2:

$$\text{[A1]} \qquad \mu = \log\left(\frac{\mu_I}{\sqrt{\mu_I + \sigma_I^2}}\right)$$

$$\text{[A2]} \qquad \sigma^2 = \log\left(1 + \frac{\sigma_I^2}{\mu_I^2}\right)$$

We then substituted eqs. A1 and A2 into eq. 7 to express the distribution of y as a function of μ_I and σ_I^2.