

## TREE MORTALITY FOLLOWING PARTIAL HARVESTS IS DETERMINED BY SKIDDING PROXIMITY

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**Abstract.** Recently developed structural retention harvesting strategies aim to improve habitat and ecological services provided by managed forest stands by better emulating natural disturbances. The potential for elevated mortality of residual trees following such harvests remains a critical concern for forest managers, and may present a barrier to more widespread implementation of the approach. We used a harvest chronosequence combined with dendrochronological techniques and an individual-based neighborhood analysis to examine the rate and time course of residual-tree mortality in the first decade following operational partial “structural retention” harvests in the boreal forest of Ontario, Canada. In the first year after harvest, residual-tree mortality peaked at 12.6 times the preharvest rate. Subsequently, mortality declined rapidly and approached preharvest levels within 10 years. Proximity to skid trails was the most important predictor both of windthrow and standing death, which contributed roughly equally to total postharvest mortality. Local exposure further increased windthrow risk, while crowding enhanced the risk of standing mortality. Ten years after harvest, an average of 10.5% of residual trees had died as a result of elevated postharvest mortality. Predicted cumulative elevated mortality in the first decade after harvest ranged from 2.4% to 37% of residual trees across the observed gradient of skid trail proximity, indicating that postharvest mortality will remain at or below acceptable rates only if skidding impacts are minimized. These results represent an important step toward understanding how elevated mortality may influence stand dynamics and habitat supply following moderate-severity disturbances such as partial harvests, insect outbreaks, and windstorms.

**Key words:** *alternative silviculture; black spruce; boreal forest; dendrochronology; neighborhood analyses; partial harvest; Picea mariana; structural retention; tree mortality.*

### INTRODUCTION

In recent decades, silvicultural alternatives to clear-cutting have been developed and implemented in forest regions worldwide (e.g., Franklin et al. 1997, Harvey et al. 2002, Lindenmayer and McCarthy 2002, Keeton 2006). These practices generally attempt to emulate aspects of natural disturbances and retain key structural characteristics of late-seral forests (e.g., Franklin et al. 1997). Predicated on the assumption that retaining features such as live trees and coarse woody debris will permit the maintenance of biodiversity and ecological function in managed forests, “structural retention” represents the major means through which recent advances in ecological understanding have been incorporated into modern forest management. Although early results show improved maintenance of species diversity (e.g., Lance and Phinney 2001, Deans et al. 2005, Dovčiak et al. 2006) and large growth responses of residual trees (e.g., Latham and Tappeiner 2002, Bebbler et al. 2004, Thorpe et al. 2007), the general success or failure of retention treatments has yet to be established. Evaluating these novel practices requires long-term,

detailed information on stand development following harvest, particularly on rates of postharvest tree mortality.

Disturbance is a fundamental driver of forest ecosystems, exhibiting strong influence on stand structure (Hanson and Lorimer 2007, McCarthy and Weetman 2007) and species composition (Canham et al. 2001, Papaik and Canham 2006, Rich et al. 2007). Disturbances vary widely in intensity, from catastrophic fires to gap-phase processes. Although research has traditionally focused on these extremes (Seymour et al. 2002), moderate-severity disturbances have been gaining increasing attention (e.g., Hanson and Lorimer 2007). Such disturbances, which include windstorms and insect outbreaks, are analogous to partial harvests insofar as they “retain” a substantial component of residual trees. These trees are likely to experience stress related to increased exposure, microclimatic changes (e.g., Heithacker and Halpern 2006), and reduced water availability (e.g., Liu et al. 2003), all of which may elevate tree mortality rates. If this is the case, moderate-severity disturbances might influence forest dynamics over much longer time scales than is currently assumed. Previous studies have documented higher mortality risk for trees located on gap edges compared to forest-interior trees (Young and Hubbell 1991, Lin et al. 2004), but research

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has not generally considered the potential for elevated tree mortality following intermediate-scale natural disturbances (but see Kulakowski and Veblen 2003, Taylor and MacLean 2007).

The matter of elevated tree mortality after partial harvest, in contrast, has been gaining research attention over the past decade. Reported rates of postharvest mortality span the entire possible range, from losses of <1% to 100% of residual trees (Jönsson et al. 2007, reviewed in Thorpe and Thomas 2007, Bladon et al. 2008). This variation is in large part attributable to differences in time scales and retention levels considered. Quantifying mortality risk at the level of the individual tree across gradients of retention avoids potential confounding effects of stand-level analyses (Caspersen 2006), and allows for more general conclusions regarding rates and causes of elevated mortality.

The use of neighborhood models to analyze population dynamics at the individual-tree level across ranges of small-scale, spatially explicit factors is becoming increasingly common (Canham and Uriarte 2006). Previous studies have employed neighborhood models to explore tree growth (e.g., Weiner 1984, Canham et al. 2004, Canham et al. 2006), but to our knowledge this is the first study to employ an individual-based spatial neighborhood analysis to examine postharvest tree mortality. Existing individual-based simulation models such as SORTIE-ND (*available online*)<sup>2</sup> assume that increased resource levels following disturbance always act to increase tree survivorship, and thus assume implicitly that elevated postharvest mortality does not occur. Incorporation of spatially explicit predictors of postharvest mortality into individual-based simulation models is thus essential for accurate forecasting of stand dynamics and development under alternative silvicultural scenarios.

In this study we employ dendrochronological methods and a harvest chronosequence to quantify mortality before, during, and after partial harvests, and address the following questions: (1) Does partial harvesting increase the risk of mortality for residual trees? (2) If so, what is the magnitude and time course of increased mortality? (3) How is postharvest mortality risk influenced by the size of individual trees and their proximity to skid trails, exposure to wind, and/or residual crowding?

## METHODS

### *Study area*

The clay belt is a major physiographic region that covers 125 000 km<sup>2</sup> of northern Ontario and Québec, Canada. Created by glacial lake deposits, the region is characterized by flat topography and poorly drained organic soils. Forests are dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) and understories are



FIG. 1. Partial harvesting in the black spruce boreal forest of northern Ontario, Canada. Photo courtesy of Abitibi-Bowater Incorporated, Montreal, Québec, Canada.

composed of ericaceous plants such as *Rhododendron groenlandicum* (Labrador tea), and bryophytes *Pleurozium schreberi* and *Sphagnum* species. The study area, bounded by 48°51'–50°12' N and 79°49'–80°42' W, is near Cochrane, Ontario, in the north-central portion of the clay belt, and has a mean annual temperature of 0.6°C and average annual precipitation of 880 mm, including nearly 3 m of snow (Environment Canada 2002).

Study sites were treated with Harvest with Advance Regeneration Protection (HARP), a silvicultural system developed for uneven-aged black spruce stands (Fig. 1). HARP treatments are characterized by alternating clear-cut strips (5–7 m wide) where harvest equipment travels, and partial-cut strips (5–9 m wide) in which diameter-limit cutting (generally ~12 cm) is carried out. Some larger trees are also retained within partial-cut strips to meet biodiversity guidelines (OMNR 2001), and harvesting takes place in winter to protect the organic soils.

### *Field methods*

From June to August 2005, we sampled 18 stands (hereafter “cutblocks”) that were harvested between 1995 and 2004 and represented a decade-long harvest chronosequence (including all years but 2001; HARP was not carried out in the study area during that year). We selected sites to ensure that cutblocks from the same harvest year were spatially interspersed among stands from other harvest years.

Within each cutblock we established three circular, 20 m radius plots, spaced 300–400 m apart, and measured diameter, species, and class of all dead and live stems >5 cm diameter at breast height (dbh; “breast height” is 1.3

<sup>2</sup> [www.sortie-nd.org](http://www.sortie-nd.org)

m). The five classes included: (1) live trees; (2) stumps (measured at stump height [dsh: 0.3 m] and later transformed to dbh using a regression equation developed from paired dbh and dsh measurements taken on a random subset of trees); (3) knockdowns (stems killed unintentionally by direct harvesting machinery impacts); (4) snags (stems that died standing); and (5) windthrows, including uprooted stems and stem snaps (stems that broke while alive). Stem snaps were distinguished from fallen snags based on wood structural characteristics: in contrast to fallen snags, stem snaps generally splintered at the point of breakage, maintained points of attachment, and retained bark (Senecal et al. 2004). Some trees that died standing and fell soon after may have been mistakenly classified as stem snaps. This could have led to overestimated rates of windthrow vs. standing death risk, but would not have affected overall mortality rates.

Finally, we mapped the spatial location of each stem by recording its distance and azimuth from the plot center using an Impulse 200 Laser rangefinder with Mapstar Electronic Compass Module II attachment (Laser Technology Incorporated, Centennial, Colorado, USA), and collected disk samples from all dead stems whose outermost rings had not yet decayed. This included trees that died before and after harvest; data from trees that died before harvest were used to quantify background mortality rates.

#### Laboratory methods

Disk samples were sanded with increasingly fine grit until growth rings were clearly visible. We measured tree ring widths along two radii of each disk using WinDendro v. 2003b (Regent Instruments, Québec City, Québec, Canada) and cross-dated each ring series using a local master chronology created for another study (Thorpe et al. 2007) in conjunction with the program COFECHA (Holmes 1983). An individual's year of death was classified as the year following its final year of diameter growth. We also classified each stump as either on a skid trail or in a partially cut area by plotting stem maps, delineating harvesting machinery travel corridors (hereafter "skid trails"), and manually classifying each stump.

To ensure unbiased estimates of postharvest mortality rates, we considered only the most recent five years (2001–2005) of mortality dynamics in our analysis. We were confident in our ability to cross-date all trees that died in this window. Relative to the harvest date, the span of this window differed among cutblocks in the chronosequence; for example, from +4 to +8 years since harvest in 1997 cutblocks, and from –3 to +1 years since harvest in 2004 cutblocks.

#### Statistical methods

To quantify the risk of tree mortality following partial harvest, we estimated mortality risk before, during, and after harvest using time since harvest and a set of individual-level measurements (tree size, skid trail

proximity, exposure, and crowding) as predictor variables. The following section describes the set of models we tested, the maximum likelihood methods employed to estimate their parameters, and the methods used to select the best model, calculate its parameter confidence intervals, and assess its fit.

*The basic model.*—Prior to harvest, trees die at some background rate  $\beta$ , the preharvest annual mortality risk, estimated using residual tree and stump data from partial-cut strips. In the year of harvest, individuals may be harvested (stumps), or they may be killed unintentionally by harvesting machinery (knockdowns). We expected that the risk of being cut would increase nonlinearly with tree size:

$$st_i = \mu(1 - e^{-\psi dbh_i}) \quad (1)$$

where  $st_i$  is the risk of individual  $i$  of size  $dbh_i$  being cut, and  $\mu$  and  $\psi$  are estimated parameters. The knockdown risk, in contrast, is likely to decline exponentially with dbh:

$$kd_i = \theta e^{-\chi dbh_i} \quad (2)$$

where  $kd_i$  is the risk of individual  $i$  of size  $dbh_i$  being knocked down, and  $\theta$  and  $\chi$  are estimated parameters. We expected that residual-tree mortality risk would peak immediately after harvest and then decline exponentially with time since harvest, down to some constant level:

$$W_{iy} = I_{i,w} e^{-\tau_w t} + \omega \quad (3)$$

$$S_{iy} = I_{i,s} e^{-\tau_s t} + \zeta \quad (4)$$

where  $w_{iy}$  and  $s_{iy}$  are the respective annual postharvest risks of windthrow and standing mortality for individual  $i$  in year  $y$ ,  $I_{i,w}$  and  $I_{i,s}$  are the risks of windthrow and standing death for individual  $i$  immediately after harvest, and  $\tau_w$ ,  $\tau_s$ ,  $\omega$ , and  $\zeta$  are estimated parameters. The year  $y$  is a calendar year ranging from 2001 to 2005, and time since harvest,  $t$ , is the difference between  $y$  and the year of harvest. The parameters  $\tau_w$  and  $\tau_s$  determine the rate at which windthrow or standing death risk declines with time since harvest, and  $\omega$  and  $\zeta$  are the constant postharvest rates of windthrow and standing death respectively.

The total risk of mortality for an individual  $i$  in year  $y$ ,  $p_{iy}$ , depends on the time since harvest,  $t$ :

$$p_{iy} = \begin{cases} \beta & \text{if } t < 0 \\ \beta + st_i + kd_i & \text{if } t = 0 \\ w_{iy} + s_{iy} & \text{if } t > 0. \end{cases} \quad (5)$$

We used maximum likelihood methods to estimate the parameters in Eqs. 1–5 using software written specifically for this study in the C programming language. Mortality risks before, during, and after harvest were estimated simultaneously using a simulated annealing algorithm, based on the Metropolis algorithm (Metropolis et al. 1953, Press et al. 1992), to search for parameter values that would maximize the log-likelihood ( $L$ ) of the

observed data set:

$$L = \sum_{j=1}^{54} \sum_{i=1}^{n_j} \sum_{y=2001}^{2005} [M_{iy} \ln(1 - p_{iy}) + (1 - M_{iy}) \ln(p_{iy})] \quad (6)$$

where  $n_j$  is the total number of stems in plot  $j$  and  $M_{iy}$  is a dummy variable that indicates the status (live: 1; dead: 0) of individual  $i$  in year  $y$ .

*Alternate models.*—Risk of windthrow or standing death following harvest may be influenced by a number of predictor variables not considered in the basic model. We tested for effects of tree size, skid trail proximity, exposure, and crowding on mortality risk immediately following harvest:

$$I_{i,w} = \rho_w + D_{i,w} + K_{i,w} + E_{i,w} \quad (7)$$

$$I_{i,s} = \rho_s + D_{i,s} + K_{i,s} + C_{i,s} \quad (8)$$

where  $\rho_w$  and  $\rho_s$  are estimated parameters,  $D_{i,w}$  and  $D_{i,s}$  are the effects of tree diameter on windthrow and standing death risk,  $K_{i,w}$  and  $K_{i,s}$  describe how skid trail proximity influences windthrow and standing death risk,  $E_{i,w}$  is the exposure effect on windthrow risk, and  $C_{i,s}$  represents how crowding affects standing death risk.

The effects of diameter on windthrow and standing death risk were estimated as follows:

$$D_{i,w} = \delta_w \text{dbh}_i \quad (9)$$

$$D_{i,s} = \delta_s \text{dbh}_i \quad (10)$$

where  $\delta_w$  and  $\delta_s$  are estimated (negative or positive) parameters.

Proximity to skid trails may increase both windthrow and standing death risk if skid trails are associated with harvest-related damage:

$$K_{i,w} = \kappa_w m \quad (11)$$

$$K_{i,s} = \kappa_s m \quad (12)$$

where  $m$  is the number of knockdowns and stumps located on skid trails and within  $\lambda$  meters of tree  $i$ . The parameters  $\lambda$ ,  $\kappa_w$ , and  $\kappa_s$  are estimated;  $\lambda$  quantifies the scale over which skid trails influence the mortality risk of residual trees.

We expected that windthrow risk would increase with declining postharvest neighborhood basal area, a proxy for local exposure:

$$E_{i,w} = -\eta_w \text{BA}_{i,\text{post}} \quad (13)$$

where  $\eta_w$  is an estimated parameter, and  $\text{BA}_{i,\text{post}}$  is the postharvest neighborhood basal area of individual  $i$ .  $\text{BA}_{i,\text{post}}$  is the sum of the cross-sectional area of each of the  $k$  neighboring trees,  $j$ , located within distance  $\gamma$  of tree  $i$ :

$$\text{BA}_i = \left[ \sum_{j=1}^k \pi \left( \frac{\text{dbh}}{2} \right)^2 \right] \frac{10\,000}{\pi \gamma^2} \quad (14)$$

where  $\gamma$  is an estimated parameter that quantifies the distance over which neighboring trees influence a target tree's mortality risk and dbh is in meters. For ease of interpretation,  $\text{BA}_{i,\text{post}}$  is expressed on a per hectare basis. Potential neighbors considered in  $\text{BA}_{i,\text{post}}$  calculations included live and dead residual trees.

In contrast to our hypothesis for windthrow, we expected standing death risk to increase with postharvest neighborhood basal area, a proxy for local crowding:

$$C_{i,s} = \phi_s \text{BA}_{i,\text{post}} \quad (15)$$

where  $\phi_s$  is an estimated constant.

*Model selection.*—We tested for the potential effects of size, skid trail proximity, exposure, and crowding on postharvest windthrow and standing death risk by fitting the full model to the data ( $\delta_w$ ,  $\delta_s$ ,  $\kappa_w$ ,  $\kappa_s$ ,  $\eta_w$ , and  $\phi_s \neq 0$ ) and then fitting models that excluded the effects of one or more variables ( $\delta_w$ ,  $\delta_s$ ,  $\kappa_w$ ,  $\kappa_s$ ,  $\eta_w$ , and/or  $\phi_s = 0$ ). We used Akaike's Information Criterion ( $\text{AIC}_c$ ) to select the best model:

$$\text{AIC}_c = -2L + 2K \left( \frac{n}{n - K - 1} \right) \quad (16)$$

where  $L$  is the log-likelihood of the observed data set and  $K$  is the number of estimated model parameters. The model with the lowest  $\text{AIC}_c$  is considered most parsimonious (Burnham and Anderson 2002).

*Parameter confidence limits and model fit.*—To obtain parameter confidence limits, we randomly sampled parameter values of the best model to obtain 100 000 parameter sets. We calculated the log-likelihood of each parameter set and its deviance,  $D$ , from the maximum log-likelihood ( $D = 2(L - L_{\text{max}})$ ). We excluded parameter sets whose deviance exceeded the critical value of the  $\chi^2$  distribution ( $\alpha = 0.05$ ,  $\text{df} = 1$ ), and from the remaining sets of parameters, chose the maximum and minimum values of each parameter as the 95% confidence interval (Hilborn and Mangel 1997).

We calculated the predicted probability of mortality for each individual ( $p_i$ ), using the best model and its associated maximum likelihood parameter estimates. Individuals were grouped into eight classes based on their predicted probability of mortality (0–0.025, 0.025–0.05, 0.05–0.15, 0.15–0.25, 0.25–0.4, 0.4–0.6, 0.6–0.8, 0.8–1). Within each class, we calculated the mean predicted probability of mortality and the observed proportion of dead individuals. Pairs of observed and predicted values were plotted to assess model fit.

## RESULTS

### Sample size and stand structure

We sampled 10 361 stems across 54 plots in 18 cutblocks, including 4292 live residual trees, 4683 stumps, 648 knockdowns, and 738 dead trees from which we collected a disk sample. The outermost rings of many of the disks had decayed beyond our ability to obtain an accurate year of death ( $n = 108$ ). Of the 630

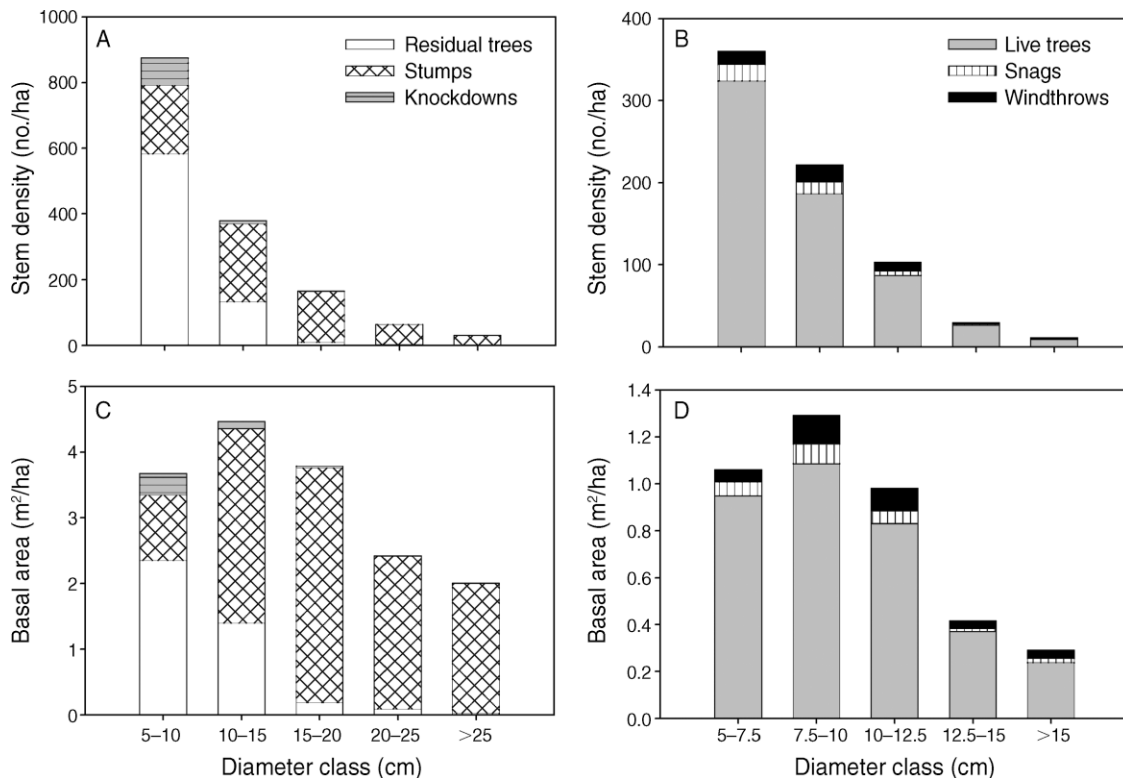


FIG. 2. Number of stems >5 cm dbh (A) before and (B) after harvest, and corresponding (C) preharvest and (D) postharvest basal area by diameter class. The 54 inventoried 0.13-ha plots included 4922 residual trees (live and dead;  $725 \pm 58$  per hectare [mean  $\pm$  SE]), 4683 stumps ( $690 \pm 44$  per hectare), and 648 knockdowns ( $95 \pm 9.8$  per hectare) >5 cm dbh. Stand basal area was composed of  $4.04 \pm 0.27$  m<sup>2</sup>/ha of residual trees,  $11.83 \pm 0.63$  m<sup>2</sup>/ha of stumps, and  $0.48 \pm 0.045$  m<sup>2</sup>/ha of knockdowns.

stems we were able to cross-date, 269 died within the 2001–2005 window and were considered in our statistical analysis. Of these dead trees, 139 had died standing, 56 were uprooted, and 74 were broken (total 130 windthrown). Black spruce made up 92% of the sampled stems. Balsam fir (*Abies balsamea* (L.) Mill.) comprised an additional 7%, while paper birch (*Betula papyrifera* Marsh.) and balsam poplar (*Populus balsamifera* L.) made up <1% of stems.

Harvesting reduced the density of stems >5 cm dbh from  $1511 \pm 87$  stems/ha (cutblock average  $\pm$  SE) to  $725 \pm 58$  stems/ha, and the basal area from  $16.35 \pm 0.62$  m<sup>2</sup>/ha to  $4.04 \pm 0.34$  m<sup>2</sup>/ha (Fig. 2). Stumps comprised the majority of the basal area,  $11.83 \pm 0.63$  m<sup>2</sup>/ha, and knockdowns contributed an additional  $0.48 \pm 0.045$  m<sup>2</sup>/ha. Harvesting was concentrated in the larger size classes: 97% of stems >15 cm dbh had been cut. Residual-tree and knockdown abundances, in contrast, peaked in the 5–10 cm size class (Fig. 2A). By the time of sampling, live trees made up  $3.47 \pm 0.31$  m<sup>2</sup>/ha of the residual basal area, while  $0.34 \pm 0.04$  m<sup>2</sup>/ha had been windthrown, and  $0.23 \pm 0.05$  m<sup>2</sup>/ha had died standing (Fig. 2D).

*Observed mortality response to harvest*

Mortality of residual trees peaked at 3.8% in the first year after harvest, a rate 12.6 times higher than the

preharvest annual rate of 0.28% (Fig. 3). Mortality declined with time, and was only 0.2% in the 10th year after harvest (Fig. 3). A decade after harvest, an average of 13.3% of residual trees had died; 6.3% had been windthrown and 7.0% had died standing. Compared to

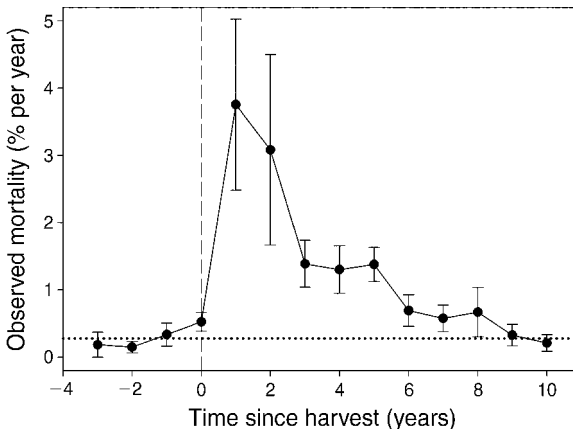


FIG. 3. Mean observed annual mortality ( $\pm$ SE) before and after partial harvest. Dashed vertical line indicates harvest event. Direct harvest (i.e., stump and knockdown) mortality is not included. Dotted line indicates estimated preharvest background mortality rate (0.28% per year).

TABLE 1. AIC<sub>c</sub> comparisons of alternate mortality models.

Model number	Effects included in windthrow risk, $I_w$	Effects included in standing death risk, $I_s$	$\Delta AIC_c$	Concordance (%)	Goodness of fit
1	$D_w + K_w + E_w$	$K_s + C_s$	0	78.9	0.961
2	$D_w + K_w + E_w$	$D_s + K_s + C_s$	1.97		
3	$K_w + E_w$	$K_s + C_s$	3.01	78.8	0.951
4	$K_w + E_w$	$D_s + K_s + C_s$	4.48		

Notes:  $D_w$  and  $D_s$  are the size effects on windthrow ( $w$ ) and standing death risk ( $s$ ) (Eqs. 9, 10),  $K_w$  and  $K_s$  are skid trail proximity effects (Eqs. 11, 12),  $E_w$  is the exposure effect (Eq. 13), and  $C_s$  is the crowding effect (Eq. 15).  $\Delta AIC_c$  is the difference between the minimum AIC<sub>c</sub>, associated with the best model, and the AIC<sub>c</sub> of any alternate model (Burnham and Anderson 2002). Models that did not include effects of skid trail proximity, exposure, and crowding had essentially no support ( $\Delta AIC_c$  values > 9.8) and are not shown. Concordance was calculated as the sum of the number of dead trees whose predicted probability of mortality was >0.5 and the number of live trees whose predicted probability of mortality was ≤0.5, divided by the total number of trees. Goodness of fit is the slope of the line between predicted probability and observed proportion of mortality, binned into eight mortality classes (0–0.025, 0.025–0.05, 0.05–0.15, 0.15–0.25, 0.25–0.4, 0.4–0.6, 0.6–0.8, 0.8–1).

the cumulative decadal mortality rate of 2.8% expected in the absence of harvest, this represents a 475% increase in mortality.

*Model selection and goodness of fit*

The most parsimonious mortality model ( $\Delta AIC_c = 0$ ) included the effects of: tree size ( $D_w$ ) on windthrow risk, skid trail proximity ( $K_w$ ,  $K_s$ ) on windthrow and standing death risk, exposure ( $E_w$ ) on windthrow risk, and crowding ( $C_s$ ) on standing death risk (Table 1, Model 1). The selected model and associated parameters (Table 2) yielded a good fit to the observed data, with a 0.96 slope between predicted and observed mortality and correct live/dead classification of 79% of all stems (Table 1, Fig. 4 and 5A, B).

*Alternate model support.*—The model that excluded all size effects had some support compared to the best model, with a  $\Delta AIC_c$  value of 3.0 (Table 1, Model 3 [Burnham and Anderson 2002]). Only two other models had  $\Delta AIC_c$  values below 5: the full model (Table 1, Model 2,  $\Delta AIC_c = 2.0$ ) and the model that included  $D_s$  but not  $D_w$  (Table 1, Model 4,  $\Delta AIC_c = 4.5$ ). While these models had some support, they did not provide any additional predictive power to their simpler forms

(Model 1 ( $\delta_s = 0$ ) and Model 3 ( $\delta_w = 0$ ,  $\delta_s = 0$ ), respectively). Models that excluded effects of skid trail proximity, exposure, and/or crowding had  $\Delta AIC_c$  values ranging from 9.8 to 42, and had essentially no support.

*Predicted mortality*

*Postharvest mortality.*—Predicted risk of windthrow peaked at 2.7% in the first year after harvest for residual trees of average size, skid trail proximity, and exposure. This risk declined with time, and had neared the estimated postharvest risk constant ( $\omega$ : 0.12% per yr; Table 2) 7–8 years after harvest. Windthrow risk increased with residual-tree size, and ranged from 2.2% to 3.3% in the first year after harvest for trees from 5 to 12.4 cm dbh, a size range representing 95% of residual trees (Fig. 5A). For trees of average skid trail proximity and crowding, the risk of standing death peaked at 1.3% in the first year after harvest (Fig. 5B). This risk declined more slowly than for windthrow and was not related to residual-tree size.

Skid trail proximity ( $K_w$ ,  $K_s$ ) was the most important predictor of postharvest mortality, both via windthrow and standing death. Skid trail proximity values ranged from 0 to 26 skid trail stumps and knockdowns (mean:

TABLE 2. Maximum likelihood parameter estimates (and 95% confidence limits) of the most parsimonious mortality model (Table 1, Model 1).

Parameter	MLE	Parameter	MLE	Associated terms
<b>Elevated postharvest mortality</b>				
$\delta_w$	0.0028 (0.0013, 0.0046)			size effect ( $D_w$ )
$\kappa_w$	0.0066 (0.0046, 0.0085)	$\kappa_s$	0.0014 (0.002, 0.0008)	skid trail effects ( $K_w$ , $K_s$ )
$\eta_w$	0.0021 (0.0014, 0.027)	$\phi_s$	0.0005 (0.0004, 0.0006)	exposure ( $E_w$ ) and crowding ( $C_s$ ) effects
$\rho_w$	0.00012 (0.000, 0.0041)	$\rho_s$	0.000 (0.000, 0.0002)	
$\tau_w$	0.629 (0.542, 0.773)	$\tau_s$	0.189 (0.156, 0.260)	
<b>Skid trail proximity and neighborhood radii (m)</b>				
$\lambda$	7.35 (7.07, 8.11)	$\gamma$	1.50 (1.38, 1.80)	
<b>Pre- and postharvest background mortality</b>				
$\beta$	0.0028 (0.0019, 0.0034)			
$\omega$	0.0012 (0.0018, 0.008)	$\zeta$	0.00004 (0.0000, 0.001)	
<b>Harvest mortality</b>				
$\mu$	4.88 (4.64, 6.12)	$\theta$	0.287 (0.237, 0.425)	harvest (stump) risk (st)
$\psi$	0.0093 (0.0072, 0.0098)	$\chi$	0.183 (0.175, 0.228)	knockdown risk (kd)

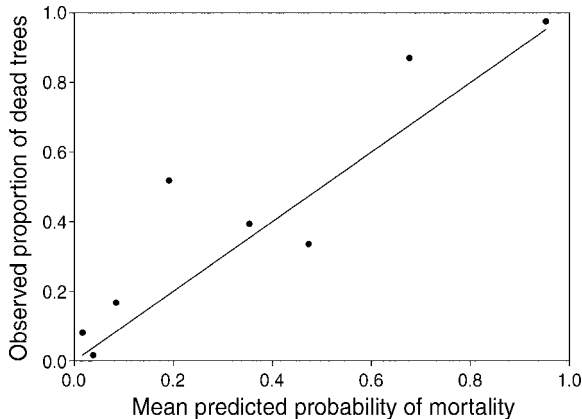


FIG. 4. Goodness of fit of the maximum likelihood model (Table 1, Model 1). The observed proportion of dead trees is plotted vs. mean values of predicted probability of mortality for each of the following eight predicted probability classes (range with number of trees in square brackets: 0–0.025 [689], 0.025–0.05 [884], 0.05–0.15 [371], 0.15–0.25 [216], 0.25–0.4 [736], 0.4–0.6 [1300], 0.6–0.8 [406], and 0.8–1 [360]). The line represents a 1:1 relationship between predicted probability and observed proportion of mortality.

7.0) located within 7.35 m of a residual tree (the skidding proximity radius  $\lambda$ ; Table 2). For residual trees of average size and postharvest neighborhood basal area, the observed range of skid trail proximities was associated with predicted windthrow rates of 0.2–9.3% and standing death rates of 0.4–3.5% in the first year after harvest (Fig. 5C, D). Although skid trail proximity had a larger immediate influence on windthrow risk, the relatively slow time course of standing death resulted in similar cumulative impacts of skidding proximity on windthrow and standing death risk over the first decade after harvest.

Windthrow risk also increased with local exposure,  $E_w$ , although this effect explained less of the observed variation in windthrow than did skid trail proximity. Postharvest neighborhood basal area ( $BA_{\text{post}}$ ), calculated within 1.5 m of each residual tree (the neighborhood radius  $\gamma$ ; Table 2), was negatively related to exposure, and ranged from 79 to 0  $\text{m}^2/\text{ha}$  (mean: 9.8  $\text{m}^2/\text{ha}$ ). This range was associated with predicted windthrow rates from 0% to 3.8% in the first year after harvest for trees of average size and skid trail proximity (Fig. 5E).

Standing death risk increased with local crowding,  $C_s$ : trees in crowded neighborhoods experienced higher postharvest standing mortality risk than those with few or no neighbors. At average skid trail proximity and peak neighborhood crowding ( $BA_{\text{post}} = 79 \text{ m}^2/\text{ha}$ ), 4.4% of residual trees were expected to die standing in the first year after harvest. More modest standing death rates of 0.8–2.4% in the first year after harvest were expected for  $BA_{\text{post}}$  values between 0 and 35  $\text{m}^2/\text{ha}$ , a range that represented the neighborhoods of 95% of residual trees (Fig. 5F).

*Background mortality.*—The estimated annual rate of mortality prior to harvest was 0.28%, a rate considerably higher than the sum of the estimated constant postharvest windthrow ( $\omega = 0.12\%$ ) and snag recruitment ( $\zeta = 0.004\%$ ) rates. This indicates that partial harvests reduce background rates of mortality, at least over the first decade after harvest.

*Harvest intensity and mortality risk.*—Cumulative elevated mortality, the combined rates of windthrow and standing death over the first decade after harvest, depended primarily on skidding proximity (Fig. 6). Across the observed range of skid trail proximities, estimated cumulative mortality ranged from 2.4% to 37%, and represented mortality rates elevated up to 12 times above background (Fig. 6A). Predicted mortality across the range of skid trail proximity was split roughly equally between snags and windthrow. In contrast, total cumulative mortality predictions varied only slightly across local retention levels ( $BA_{\text{post}}$ ), from 11.2% to 11.8%, a pattern attributed to opposite trends in the causes of standing death vs. windthrow. At high values of  $BA_{\text{post}}$ , standing death risk was highest, while windthrow risk peaked at low values of  $BA_{\text{post}}$  (Fig. 6B).

## DISCUSSION

Tree mortality plays a fundamental role in forest ecosystems, shaping their structure and composition, and contributing to the availability of light, nutrients, and habitat (Franklin et al. 1987). While models often assume that mortality risk remains constant at a given resource level (e.g., Tilman 2004), tree mortality is a highly variable process, often occurring in pulsed events, through disturbances such as windstorms and insect outbreaks. Studies have generally assumed that moderate-severity disturbances are discrete events, and have examined only a “snapshot” of postdisturbance forest structure and composition (e.g., Canham et al. 2001, Rich et al. 2007). However, if exposed residual trees experience increased risk of mortality, disturbances could alter canopy-tree dynamics over longer time scales than has generally been supposed. Little research has examined this potential phenomenon. In one study, expected increases in beetle-induced tree mortality following a windstorm were not found (Kulakowski and Veblen 2003), while another documented highly elevated windthrow rates for residual trees that survived spruce budworm outbreaks (Taylor and MacLean 2007). Further research is needed to assess the generality and magnitude of postdisturbance tree mortality in forest ecosystems.

Like residual trees in naturally disturbed forests, trees in partially cut stands are expected to be at increased risk of mortality after harvest. Our results support this hypothesis, as we documented a cumulative elevated tree mortality rate of 10.5% in the first decade after harvest, with windthrow and standing death contributing roughly equally. Windthrow rates peaked immediately following harvest and declined rapidly thereafter, while the

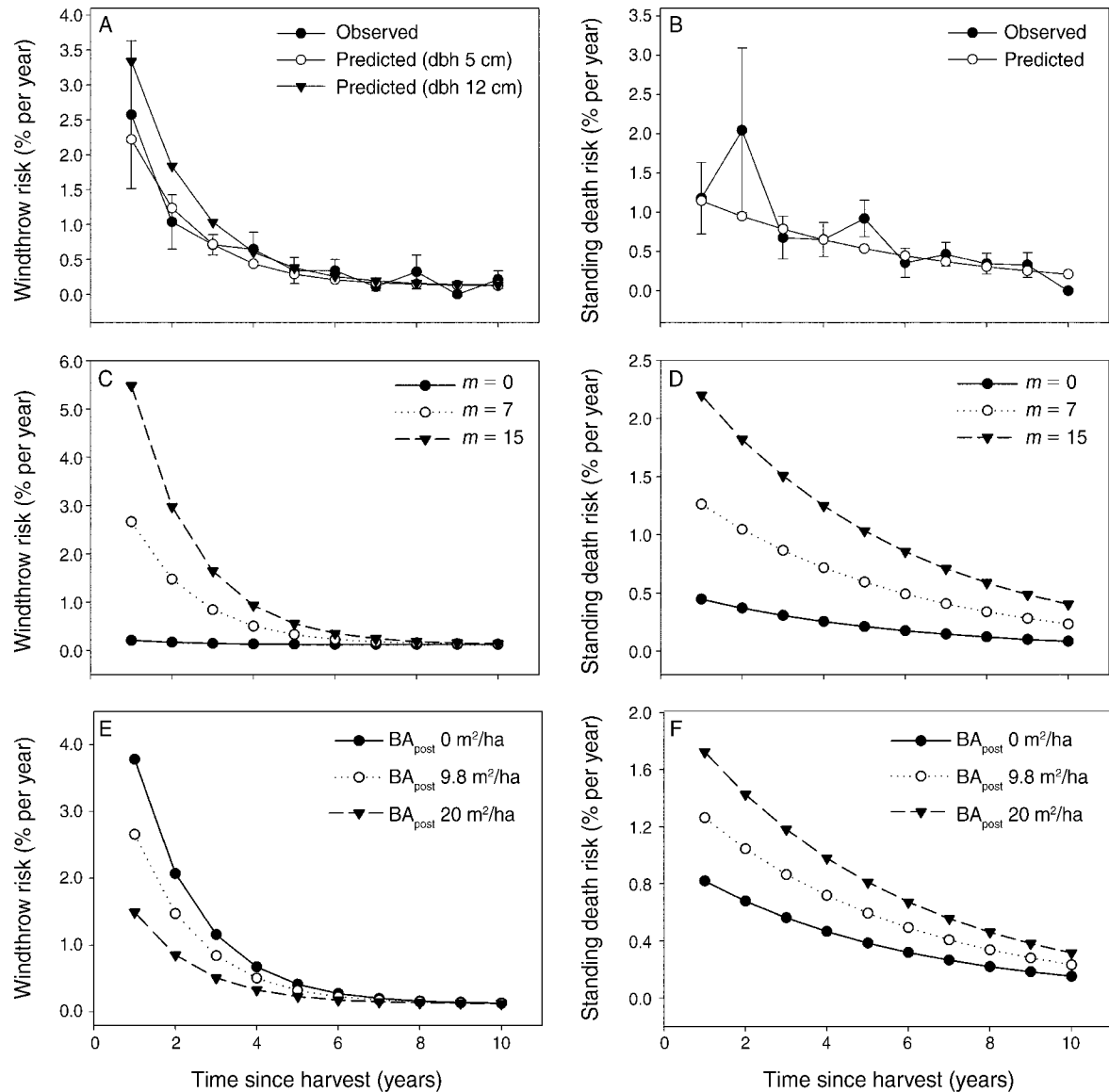


FIG. 5. Predicted risk of mortality following partial harvest. (A) Mean observed percentage of stems windthrown ( $\pm$ SE) and predicted windthrow risk at 5 and 12.4 cm dbh, (B) mean observed percentage of stems dead standing ( $\pm$ SE) and predicted standing death risk; impact of skid trail proximity on risk of (C) windthrow and (D) standing death, where  $m$  is the number of skid trail stumps and knockdowns within 7.35 m of residual trees; and effect of postharvest basal area ( $BA_{post}$ , within 1.5 m) on risk of (E) windthrow and (F) standing death. Skid trail proximity is set at its mean value ( $m = 7.0$ ) for panels A, B, E, and F;  $BA_{post}$  is set at its mean value ( $9.8 \text{ m}^2/\text{ha}$ ) for panels A–D; and dbh is set at its mean value (7.9 cm) for panels C and E.

rate of standing death displayed a more moderate peak followed by a slower postharvest decline. A recent study showed high rates of windthrow soon after harvest (0–5 years) followed by a period (5–18 years postharvest) during which standing death was the most important mode of mortality (Jönsson et al. 2007). Although much of the previous research on postharvest mortality considers windthrow only (e.g., Huggard et al. 1999, Ruel et al. 2001, Scott and Mitchell 2005), our results and those of Jönsson et al. (2007) indicate that

neglecting standing mortality will lead to substantially underestimated total losses of residual trees.

With few exceptions, prior studies of postharvest mortality have given snapshots rather than integrated mortality estimates, and have not rigorously distinguished postharvest effects from background mortality rates. Nevertheless, the mortality rate documented here is intermediate among those previously reported. Following selection harvests, low rates of mortality ( $\sim 1$ –5%) were found in temperate (Wiser et al. 2005, Caspersen 2006) and tropical (Sist and Nguyen-The

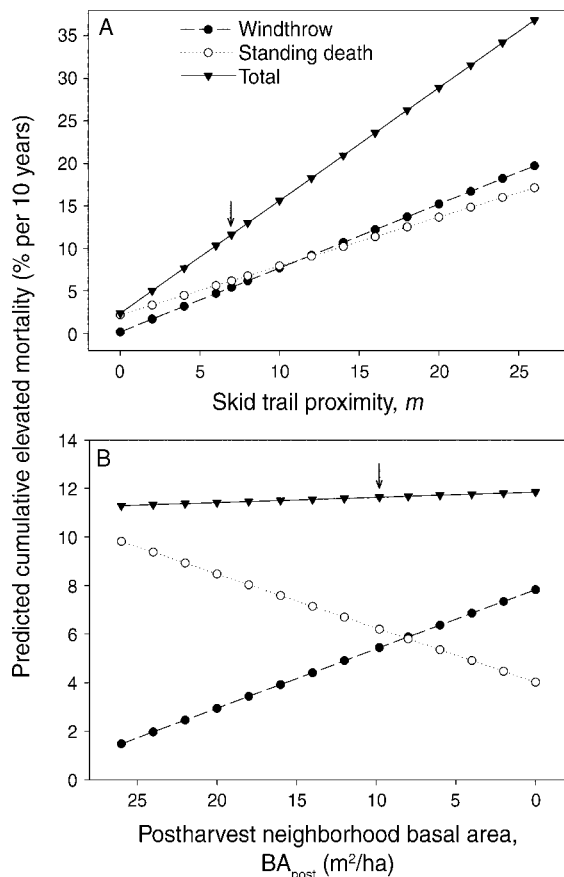


FIG. 6. Predicted cumulative elevated mortality in the first decade after partial harvest across a range of (A) skid trail proximities and (B) postharvest neighborhood basal areas, representing effects of crowding (high  $BA_{\text{post}}$ ) and exposure (low  $BA_{\text{post}}$ ). Total elevated mortality is the sum of predicted windthrow and standing death. Arrows indicate the mean observed harvest intensity. Estimates were obtained using the best model (Table 1, Model 1) and its associated parameters (Table 2) to calculate mortality from  $t = 1$  to  $t = 10$  (omitting constant postharvest mortality  $\omega$  and  $\zeta$ ). In (A),  $BA_{\text{post}}$  is set at  $9.8 \text{ m}^2/\text{ha}$  (mean observed  $BA_{\text{post}}$ ); in (B), skid trail proximity  $m$  is set at  $7.0$  (mean observed  $m$ ); and dbh is set at  $7.9 \text{ cm}$  (mean observed dbh) for A and B. Note that there was ample orthogonal variation between skid trail proximity and postharvest basal area; pairs of  $m$  and  $BA_{\text{post}}$  values considered are realistic (see *Discussion: Predictors of postharvest mortality*).

2002) forests. In studies from western North America, similarly low mortality rates have been reported in >40% retention treatments (Coates 1997, Beese and Bryant 1999, Huggard et al. 1999, Maguire et al. 2006), while high rates of windthrow (25–50%) have been found in treatments that retain <15% (Beese and Bryant 1999, Scott and Mitchell 2005). In the boreal forest, 75% retention harvests did not lead to elevated mortality in one study (Ruel et al. 2003), but windthrow rates reached 15–100% in retention patches in others (Hautala and Vanha-Majamaa 2007, Jönsson et al. 2007). A recent study of 10% retention cuts in boreal mixedwoods documented cumulative five-year mortality elevated 7.3–

35% above background levels, depending on species (aspen > poplar > birch > white spruce [Bladon et al. 2008]). Previous work on black spruce has reported losses similar to the present study (~9–20% [Ruel 1989, Ruel et al. 2001]).

The harvest treatment we considered removed nearly all trees >12 cm diameter. The small range of tree sizes retained may have influenced the rate of postharvest mortality observed. However, no general pattern between mortality risk and tree size has been established, and it is not clear whether we would have found higher or lower mortality rates had the treatment retained more large trees. A previous study found reduced postharvest mortality risk in both small and large trees (Huggard et al. 1999), while another documented decreasing postharvest mortality with increased tree size (Caspersen 2006). Studies in natural forests generally report increasing windthrow risk with tree size (e.g., Canham et al. 2001, Rich et al. 2007).

We estimated a preharvest, or background, annual mortality rate of 0.28%. This is on the low end of rates reported in the literature, which vary dramatically, both interannually and among forest types (e.g., Hennon and McClellan 2003, Senecal et al. 2004, Maguire et al. 2006, Jönsson et al. 2007). We are unaware of any published data on tree mortality rates for uneven-aged lowland black spruce stands, and thus cannot determine whether the low rate we observed is typical for these sites. However, had background mortality been 0.5% per year (a commonly reported rate), the rate of elevated mortality would still have been substantial (8.3% vs. 10.5% on a cumulative basis).

After harvest, estimated background mortality was only 0.12%, suggesting that once the postharvest mortality pulse passes, residual trees experience a period of relatively low background, or suppression-related, mortality. The only previous study to consider this also found lower background mortality after harvest (Caspersen 2006). If such reduced rates persist, they could partially offset mortality losses from the years immediately following harvest. Long-term data and very intensive sampling would be required to clarify this issue.

#### *Predictors of postharvest mortality*

Skid trail proximity was the most important determinant of windthrow and standing mortality risk. The most parsimonious predictor of skid trail effects was the number of skid trail stumps and knockdowns located within a radius of 7.35 m ( $\lambda$ ) of an individual residual tree, a distance roughly equivalent to the skid trail width. We were surprised at both the predominance of skid trail effects and their large spatial dimension, given that operations are aimed at reducing logging impacts by harvesting during winter. Proximity to skid trails is likely associated with harvest-related damage such as bark abrasion, crown damage, and/or root compaction, all of which could lead to increased risk of mortality. We

suspect that despite winter harvesting, compaction is a principal cause of postharvest mortality in this system, although its importance is likely to vary with weather conditions such as snow and frost depth.

Windthrow risk increased with declining postharvest neighborhood basal area, a finding we expected since residual trees become exposed as nearby basal area is removed. Previous studies have documented increased windthrow with harvesting intensity at the treatment level (e.g., Beese and Bryant 1999, Maguire et al. 2006, Jönsson et al. 2007). Our preliminary analyses indicated no evidence for a nonlinear trend in windthrow risk with basal area change, and we thus cannot identify a threshold rate of retention below which windthrow mortality remains negligible. The harvest method considered in this study, however, involves low rates of retention relative to other systems. Although many residual trees experienced no change in local basal area within their neighborhood radius of 1.5 m, it is unlikely that any residual tree avoided all harvest-related stress.

Postharvest neighborhood basal area also influenced standing death risk, with crowded residual trees (those with high  $BA_{\text{post}}$  values) experiencing higher risk. We conducted preliminary analyses that allowed preharvest basal area to influence standing death risk, but  $BA_{\text{post}}$  was a much better predictor. Since trees that are crowded after harvest would necessarily have been crowded before, this result suggests that previously suppressed trees, released at harvest, can respond to improved growing conditions and avoid mortality. A similar result was found in northern hardwood forests (Caspersen 2006). The effect of crowding on postharvest standing death risk also indicates that suppressed trees experience greater mortality risk after harvest than prior to it. One possible mechanism for this is wind-sway-induced cavitation of xylem vessels and subsequent effects on water transport (Liu et al. 2003, Bladon et al. 2007). This effect is expected to be more pronounced among suppressed individuals in dense stands, since they typically show high height-to-diameter ratios and low biomechanical stability (e.g., Weiner and Thomas 1992).

The estimated radius of influence for neighborhood effects ( $\gamma$ ) underlines the small scale at which neighborhood interactions operate in these black spruce stands. This neighborhood radius of 1.5 m explains the discrepancy between neighborhood- and stand-level basal areas reported. At the stand level, harvesting reduced stand basal area by 75%, from  $\sim 16$  to  $4 \text{ m}^2/\text{ha}$  (Fig. 2), while the average postharvest neighborhood basal area ( $BA_{\text{post}}$ ) was  $9.8 \text{ m}^2/\text{ha}$ . Clear-cut skid trails occupy a large proportion of the harvest area (40–50%) and represent the largest basal area reductions. These areas are largely excluded from  $BA_{\text{post}}$  calculations since only a small proportion of the clear-cut trails is located within 1.5 m of a residual tree.

Contrary to our expectations, postharvest neighborhood basal area and skid trail proximity were not strongly correlated ( $r = 0.10$ ;  $P < 0.0001$ ). While these

two predictor variables cannot be entirely independent, the low correlation coefficient between them indicates ample orthogonal variation. Residual trees with high skid trail proximities ( $m \geq 15$ ) were observed across the entire range of postharvest neighborhood basal areas,  $0\text{--}79 \text{ m}^2/\text{ha}$ , and residual trees that lost all neighbors at harvest (i.e., every tree within 1.5 m was cut) were associated with skid trail proximity values ranging from 0 to 24. Thus, a number of residual trees experienced logging damage without concomitant increases in local exposure, and many trees that were exposed by harvest did not suffer from skid trail impacts.

We documented increasing windthrow risk with size of residual trees, a finding that supports prior research on windthrow generally (e.g., Canham et al. 2001) and in black spruce, a species whose probability of windthrow increases particularly steeply with dbh (Smith et al. 1987, Rich et al. 2007). We found only a weak pattern between tree size and windthrow risk; the model that included size effects was only slightly better than the model without (Table 1, Model 1 vs. 3). This is likely a result of the small size range of residual trees retained in the harvest treatment. Contrary to our expectations, we did not find reduced risk of standing death with increasing tree size. Again, we might have detected this effect had a larger size range of trees been retained.

#### *Implications for forest ecosystem management*

The retention of live residual trees at harvest is aimed at better emulating natural forest disturbance: individual trees or forest patches commonly persist following wildfire (Franklin et al. 2002), and large proportions of canopy trees survive moderate-severity disturbances such as windstorms (Hanson and Lorimer 2007). Like residual trees in naturally disturbed forests, retained live trees in recently harvested sites are expected to provide habitat, contribute to hydrological and nutrient cycling, and reduce soil erosion (Franklin et al. 1997). Clearly, high rates of postharvest mortality will lead to reduced capacity of harvested sites to provide these ecological functions. Mortality rates exceeding 10% of residual trees have been considered an “operational failure” in some regions (Coates 1997). In the first decade following partial harvests at our study site, an average of 13.3% of residual trees died, exceeding this suggested threshold. Thus both ecological and operations objectives of structural retention harvesting may be seriously compromised in this system unless postharvest mortality is reduced.

Our analysis examined the influence of two spatial factors on postharvest mortality: neighborhood basal area and skid trail proximity. Neighborhood basal area, analogous to the rate of residual-tree retention on a local (1.5 m) scale, was not an important predictor of *total* postharvest mortality, since windthrow and standing death risk compensated for each other, peaking at exposed and crowded conditions, respectively (Fig. 6B). This result suggests that retention rates per se may not

be as important a driver of postharvest mortality as has been assumed, at least over small spatial scales. In contrast, skid trail proximity had a very strong influence on predicted total mortality. Where skidding impacts were low, postharvest mortality was negligible; at peak skidding proximity, predicted total mortality exceeded 35% of residual trees (Fig. 6A). Our results indicate that, at the mean observed postharvest basal area, decreasing skid trail coverage by half (from the mean  $m = 7.0$  to  $m = 3.5$ ) would reduce cumulative mortality in the first decade after harvest by 40%. Skid trail coverage could be reduced by widening partial-cut strips and using smaller harvesting machinery (see Groot 2002). Further research is required to determine the extent to which skidding proximity influences postharvest mortality in other forest ecosystems.

Our finding of large mortality responses to harvest that depend both on time and proximity to the disturbance represents an important step toward developing accurate predictions of stand dynamics in structural retention silviculture. Residual trees also show large growth responses to harvest (e.g., Latham and Tappeiner 2002, Bebbler et al. 2004, Thorpe et al. 2007), and thus spatially explicit, individual-based simulation models that incorporate dynamic growth and mortality responses of residual trees are required to explore the implications of partial harvest scenarios. More generally, these models are needed to evaluate the potential of novel silvicultural approaches to address biodiversity and timber production concerns over the long term. Such models will also be useful for understanding natural forest dynamics, since mortality patterns analogous to those following structural retention harvests have been documented after intermediate-scale disturbances such as insect outbreaks in natural forests (Taylor and McLean 2007). However, skid trail impacts were the most important predictor of postharvest mortality in this study. Skid trails have no natural analog, and therefore mortality rates following structural retention harvests may be elevated well above those found after natural disturbance. Thus, while partial harvesting has been motivated by attempts to emulate natural disturbances, our results suggest that stand dynamic patterns and concomitant ecological processes may differ markedly in harvested compared to naturally disturbed stands.

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