

What happens to tree residuals in boreal forest fires and what causes the changes?



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2011

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Sault Ste. Marie, Ontario
Canada P6A 2E5

Library and Archives Canada Cataloguing in Publication Data

Main entry under title:

What happens to tree residuals in boreal forest fires and what causes the changes? [electronic resource]

(Forest research report ; no. 174)

Includes bibliographical references.

Electronic monograph in PDF format.

Issued also in printed form.

ISBN 978-1-4435-7269-9

1. Forest fires—Environmental aspects—Ontario. 2. Forest surveys—Ontario.

I. Perera, A. (Ajith) II. Ontario Forest Research Institute. III. Series: Forest research report (Online) ; no. 174.

SD387 F52 W43 2011

634.9'61809713

C2011-964039-2

© 2011, Queen's Printer for Ontario

Printed in Ontario, Canada

Single copies of this publication are available from:

Ontario Forest Research Institute

Ministry of Natural Resources

1235 Queen Street East

Sault Ste. Marie, ON

Canada P6A 2E5

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Abstract

How post-fire residuals change with time is of interest to ecologists as well as those developing and implementing policy related to emulating natural disturbance and salvage logging, but is rarely reported in the literature. This report details a study where temporal changes in tree and snag residuals were monitored annually following four boreal fires in Ontario using 50 field sample plots. Rapid changes in residual structure occurred within two years of fire; most (66%) residual trees died to become snags, and some trees (16%) and snags (10%) fell to become downed wood. The rate of change in each residual category varied widely both within- and among fires, and was not directly associated with the tree species or size of residuals. However, at plot-level, higher fire intensity appeared to cause higher tree-to-snag transition rates, and total stem density was negatively correlated with tree and snag fall rates. Based on simulations of continued changes, it is predicted that tree-to-snag transitions will cease within five years, and snag fall rates will increase initially, but then decrease with time. These results indicate that time of sampling matters in post-fire residual studies, and emphasize the need for different techniques of studying post-fire residuals, beyond field surveys, to better understand causal mechanisms of their temporal change.

Résumé

L'évolution des restes d'arbres au fil du temps après un feu intéresse les écologistes et ceux qui développent et appliquent les politiques relatives à l'émulation des perturbations naturelles et à la coupe de récupération, mais cette information est rarement mentionnée dans la littérature. Le présent rapport décrit une étude où les changements temporels des restes d'arbre et de chicot ont été surveillés tous les ans après quatre feux de forêts boréales en Ontario à l'aide de 50 placettes d'échantillonnage. Des changements rapides dans la structure des restes ont eu lieu dans les deux ans suivants l'incendie; la plupart (66 %) des arbres résiduels qui restaient sont devenus des chicots en mourant, et certains arbres (16 %) et chicots (10 %) ont chuté pour devenir du bois mort au sol. Le taux de variation de chaque catégorie de restes varie grandement au sein d'un incendie et entre les incendies, et n'était pas directement associé à l'espèce de l'arbre ou à la taille des restes. Cependant, au niveau des parcelles, les incendies plus intenses semblent causer des taux de transition arbre-chicot plus élevés, et la densité totale de la tige avait une corrélation négative au taux de chute des arbres et des chicots. Selon les simulations de changements continus, on prévoit que les transitions arbre-chicot s'arrêteront dans cinq ans, et que le taux de chute des chicots va connaître une croissance initiale suivie d'une décroissance progressive. Ces résultats indiquent que le moment de l'échantillonnage importe dans les études de restes après incendie, et mettent l'accent sur le besoin d'avoir différentes méthodes pour étudier les restes après incendie, en dehors des études sur le terrain, pour mieux comprendre la causalité de leur changement temporel.

Acknowledgements

We thank Tyler Smith and Ian Aho (OMNR) for field assistance, Rob Luik (OMNR) for providing fire suppression and other information about study fires, and Lisa Solomon and John Thomson (Ontario Parks) for permitting us to sample fires in Quetico and Wabikimi Provincial Parks and Windigo Bay Nature Reserve.

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Introduction

Understanding patterns and processes in post-fire residuals—trees and snags that remain after a forest fire—is a popular topic for research. This is evident from the several-fold increase in related publications during the last decade (Perera et al. 2007). Most research has focused on the ecological role of residuals in post-fire forest ecosystems. Habitat provision by post-fire residuals is a common topic, for example, for birds (e.g., Schwab et al. 2006, Koivula and Schmiegelow 2007), soil micro fauna (e.g., Phillips et al. 2006, Koivula and Spence 2006) and soil micro flora (e.g., Treseder et al. 2004, Bradbury 2006). Residuals are also considered important in various ecological processes during the post-fire recovery period, for example, establishment of vegetation (e.g., Haeussler and Bergeron 2004, MacDonald 2007); nutrient cycling (e.g., Ohmann and Grigal 1979, Brais et al. 2000); and carbon flux (e.g., Nalder and Wein 1999, Bond-Lamberty et al. 2003). Abundance of post-fire residuals has also been studied often, especially in relation to understanding their spatial patterns of occurrence (e.g., Hely et al. 2003, Haeussler and Bergeron 2004, Harper et al. 2004, Perera et al. 2009).

Most post-fire residual studies are one-time surveys, where the time of sampling varies from immediately after fire (e.g., Apfelbaum and Haney 1981, Hansen 1983, Hely et al. 2003) to three to five years after fire (e.g., Ohmann and Grigal 1979, Haeussler and Bergeron 2004). Occasionally, chronosequences are also constructed from forest patterns, to elucidate temporal changes that occur over many decades since fire by extrapolation (e.g., Hobson and Schieck 1999, Lee and Crites 1999, Lavoie 2004). However, all these report on the state of residuals at the time of sampling with little reference to how they arrived at those states or how they would change further. In other words, what is known about residuals does not address their temporal changes. Repeated sampling and monitoring of post-fire residuals is rarely reported in the literature: we encountered only two studies where the residual contents of burned areas were sampled over time (Viereck and Dyrness 1979, Stambaugh 2003). Consequently, a gap exists in the understanding of residuals with respect to their changes as a continuous process, and produces a level of uncertainty in the knowledge of ecological patterns and processes in the recovering post-fire ecosystem.

Tree residuals refer to live trees and snags remaining immediately after fire.

Furthermore, knowledge of post-fire residuals informs forest management policies and practices that attempt to emulate natural disturbances (BCMF 1995, OMNR 2001, ASRD 2006). The assumption here is that leaving residual trees and snags during timber harvest practices, based on patterns that occur in forest fires or other natural disturbances, will sustain the same ecological heterogeneity and processes that would occur after natural forest disturbances (Perera and Buse 2004). Templates for leaving residual trees and snags after timber harvest are based on abundance and spatial patterns of post-fire residual structure, typically gathered from studies that do not explicitly consider or acknowledge temporal changes. Another forest management practice that can be better informed by improved knowledge of post-fire residuals is salvage logging. This practice of harvesting dead trees from disturbed areas (Helms 1998) is gaining prominence, and drawing attention of ecologists due to its effects on post-fire ecological processes (Hutto 2006, Lindenmeyer et al. 2008). Therefore, attempts to fill the knowledge gap in post-fire dynamics of residuals will better inform the design of both natural disturbance emulation and salvage logging strategies and practices, in addition to reducing the uncertainty related to the ecological processes associated with residuals in boreal forest fires.

Goal

In this context, our broad goal here is to examine the changes in residual trees and snags during the immediate post-fire period in the boreal forest, where natural fire disturbances are common. The specific research questions we ask are:

- 1 What is the fate of residual trees and snags during the first few years post-fire?
- 2 How do changes in post-fire residual structure vary among fires and with time?
- 3 What causal factors of the variability in temporal changes of residual structure can be detected?

We expect the answers to these questions to inform researchers who study post-fire residuals, and forest managers who design plans for emulating natural forest disturbances during harvest or for salvage logging.



Methods

Study fires

Four study fires were selected from among the 1045 that occurred in northern Ontario during 2005. These were located in northwestern Ontario and were caused by lightning. Here we present only a brief description of the study fires as two other reports (Routledge 2007 and Perera et al. 2008) provide complete details of the selection criteria and other information. Three study fires (OMNR fire numbers THU-030, THU-031, THU-067) were located west of Lake Nipigon and one (OMNR fire number FOR-014) in Quetico Provincial Park (Figure 1).

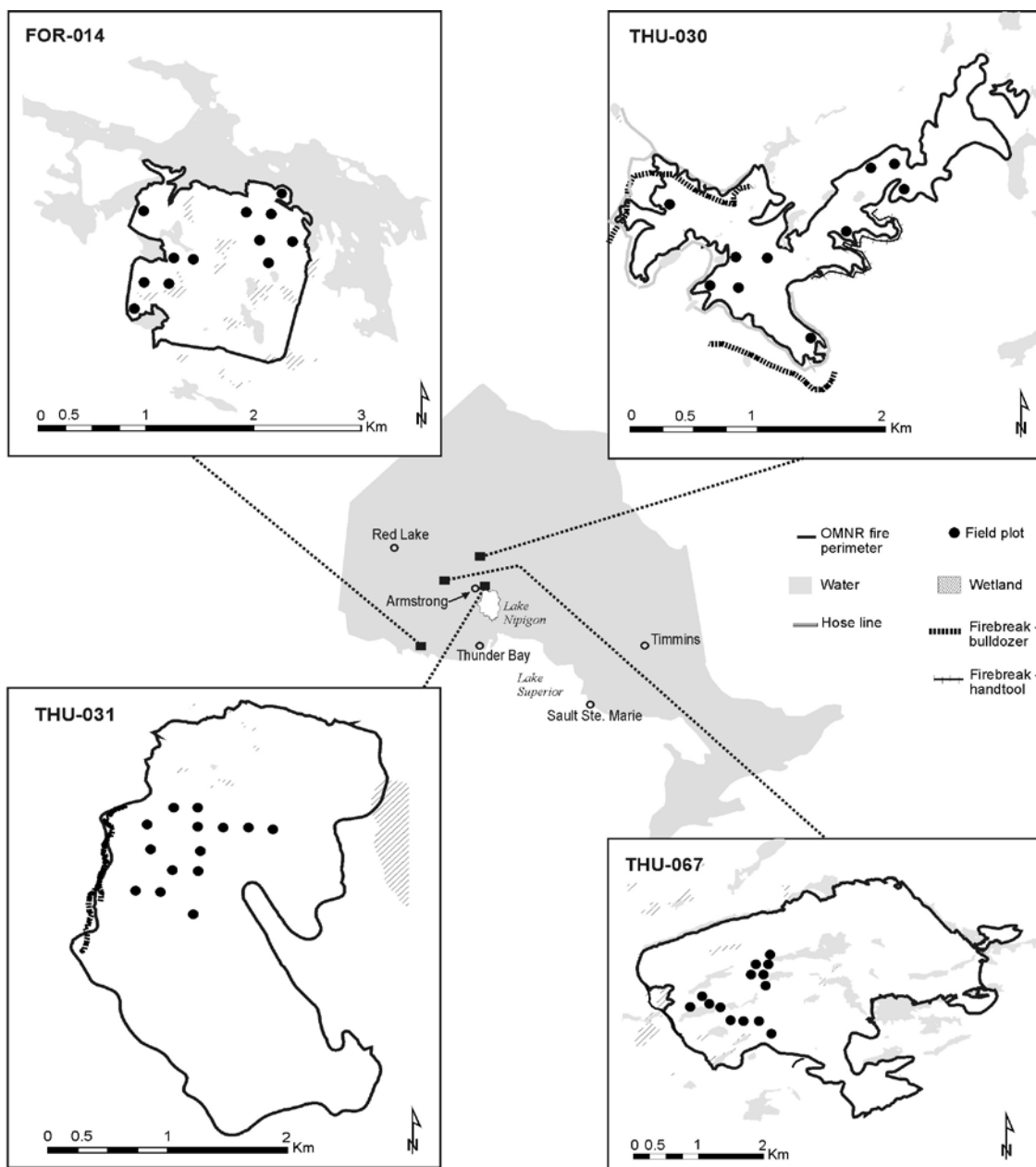


Figure 1. Location of study fires in northwestern Ontario and layout of sample plots within each fire.

The fires were ignited and naturally extinguished in summer, during periods of fire weather index (FWI) that indicate a high fire intensity rating (Perera et al. 2008). Fire sizes ranged from 429 ha to 2326 ha. In the fires west of Lake Nipigon, pre-fire forest cover was black spruce-dominated (based on MNR forest resource inventory; OMNR 2000). In the Quetico park fire, pre-burn vegetation was primarily conifer mixedwoods (based on the 2000 Quetico Forest Inventory). Pre-burn harvest activities had not occurred in the locations of fires and the ages of trees in the pre-fire stands ranged from 40 to more than 140 years (Table 1).

Study plots

Two study fires (THU-030 and THU-031) were subject to some fire suppression. Therefore we used OMNR fire records to identify those areas within study fires where fire suppression activities occurred, and exclude those from sampling. Each study fire was overlain with a series of east-west transects 200 to 400 m apart, covering the remaining area. Along each transect, circular plots, 25 m in diameter (0.05 ha), were placed 300 to 600 m apart. These plots were initially sampled using high resolution photography (HRP) in September 2005 (1 to 2 months post-fire) when the deciduous trees still had leaves (Perera et al. 2008). The images were photo-interpreted yielding counts of live and dead trees in each plot (see Routledge 2007 for details). Among the possible sample plots, 50 were selected based on the presence of at least one live tree in 2005¹ (as identified during HRP interpretation) and accessibility, resulting in the following number of sample plots in each of the study fires: 10 plots from THU-030, 14 from THU-031, 14 from THU-067, and 12 from FOR-014. Figure 1 shows the locations of the field sample plots within each of the study fires and Figure 2 illustrates sample plots within each fire.

Table 1. Location, fire characteristics, and pre-fire forest cover of the four study fires. All fires had high fire weather intensity rating based on Fire Weather Index (FWI), which combines prevailing weather and fuel conditions and indicates fire weather intensity at the start of fire based on the Canadian Forest Fire Weather Index System (Van Wagner and Pickett 1985).

MNR fire code for study fire	Location (centroid)		Fire characteristics			Pre-fire forest cover	
	Lat	Long	Ignition date	FWI	Size (ha)	Composition*	Age (yr)
THU-030	48.293	-91.659	July 24	11.4	429	Sb, Pj, Bw	40-60
THU-031	48.177	-91.371		11.4	1428	Sb, Pj, Po	60-80
THU-067	50.545	-87.981	August 4	12.4	2326	Sb, Pj	>140
FOR-014	47.767	-81.794	July 22	13.8	430	Cmix, Hmix, Pwr	n/a

* Sb – black spruce, Pj – jack pine, Bw – white birch, Po – poplar, Cmix – conifer mixedwood, Hmix – hardwood mixedwood, Pwr –white and red pine

¹To allow monitoring of changes in live residual trees over time

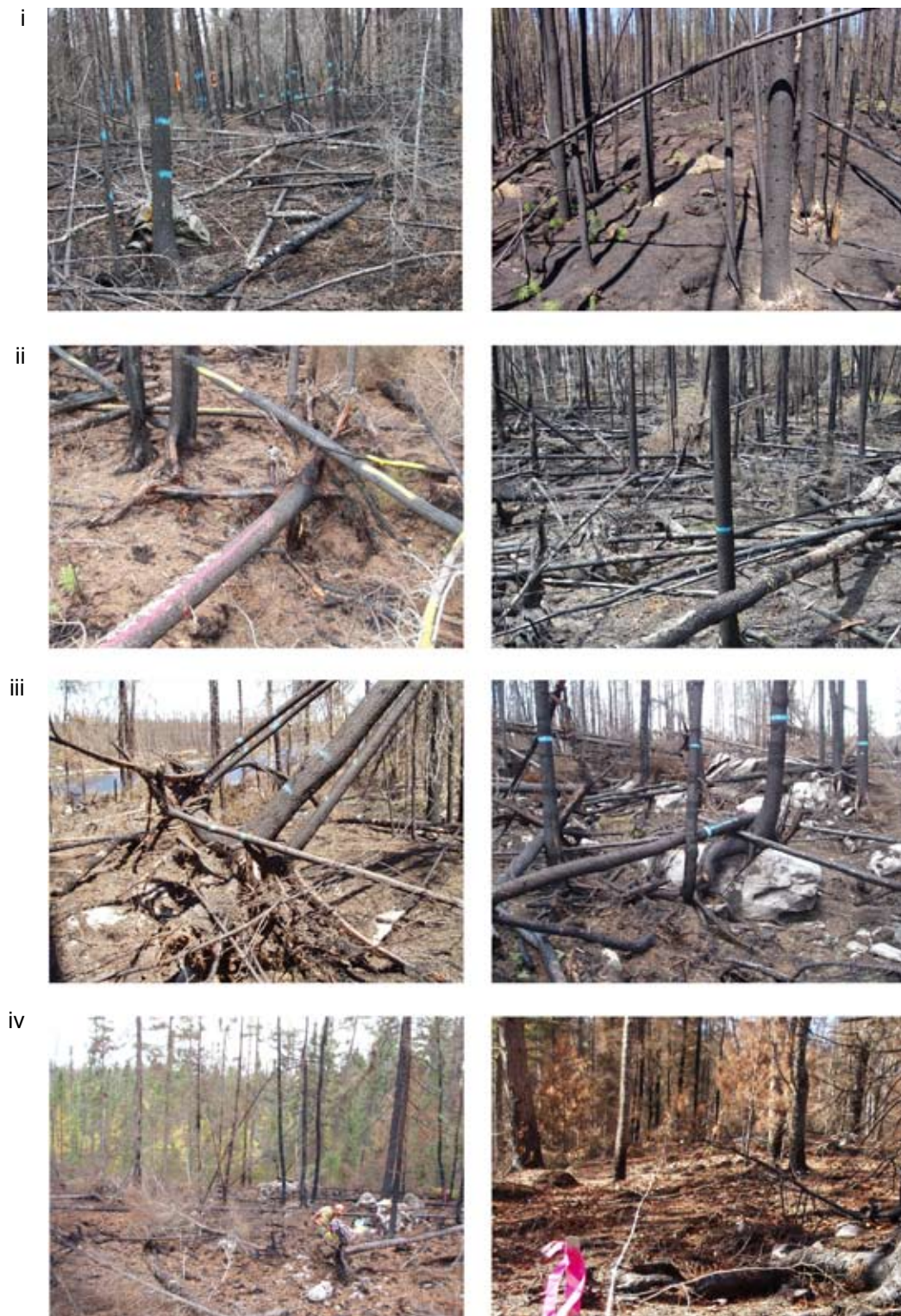


Figure 2. Examples of sample plots from the four study fires in the first year post-fire, showing the variability in fire intensity and residual structure. i. THU-030, ii. THU-031, iii. THU-067, iv. FOR-014

Estimating fire intensity

During our analyses of spatial variability in residuals, fire intensity had to be estimated as an independent variable, within and among fires (Perera et al. 2008, Dalziel and Perera 2009, Perera et al. 2009). However, no reliable method of quantitatively or categorically estimating fire intensity within fires exists that is independent of fire severity. Therefore, we used a technique devised by Smith et al. (2008) to describe the relative fire intensity at plot-level within fires. Briefly, plot-level fire intensity was estimated as five broad classes, each associated with a characteristic flame effect on the fine branch structure of snags (described as crown fraction burned in the Canadian Fire Behaviour Prediction System; Forestry Canada 1992). At very low intensity (Rank 1), fires smoulder leaving the fine branch structure intact; at slightly higher intensity (Rank 2), fires creep charring the trunk but leaving branch structure intact; as the intensity increases even more (Rank 3), fine branch structure is partially destroyed, and at higher intensities eventually most (Rank 4) or all (Rank 5) of the fine branch structure is destroyed (Table 2). Visual evidence of damage to the fine branch structure of snags in the HRP was used to infer local fire intensity in the sample plots. Fire intensity in the 50 plots selected for this study was predominantly rank 2 or 3; for analysis we converted intensity to a categorical variable with two levels: low for plots with fire intensity rank <3 (<500 kW m⁻¹) and high for plots with fire intensity rank ≥3 (≥500 kW m⁻¹).

Table 2. Empirical relationship between fire intensity rank and the percentage fine branch structure destroyed, based on the Canadian Forest Fire Prediction System (Forestry Canada, Fire Danger Group 1992). For details of the ranking methods, see Smith et al. (2008).

Fire intensity rank	Fire intensity (kW m ⁻¹)	Fire type	Percentage snag fine branch structure destroyed
1	<10	Smoldering	0
2	10-500	Creeping surface	0
3	500-2000	Surface	<10
4	2000-4000	Intermittent crown	10-90
5	>4000	Continuous crown	>90

Sampling residual dynamics

For the purpose of this study, we defined residuals as standing structure ≥2 m in height and with ≤45° lean from vertical (Routledge 2007). Residual trees were stems with evidence of green foliage, and snags were stems with no evidence of green foliage. We were not able to separate snags of pre-fire origin from those created by fire; for the scope of this analysis, immediate post-fire snag abundances and their origin are not relevant.

The sample (50) plots were visited in the fall of 2005 (within 3 months of fire) and summers of 2006 and 2007 to monitor the fate of the residual stems, providing us three sample points in time. In 2005, each tree and snag in a plot was identified with a unique number so that the mortality and fall rate of residual trees and the fall rate of residual snags could be enumerated in subsequent years. For all stems, status (live, dead, fallen), species, and diameter at breast height (DBH) were recorded in year 1 (year of fire) and their status noted in years 2 and 3 (1 and 2 years post-fire). These data were used to compare the status of all stems in a plot from year to year.

Data analysis

We calculated the plot-level annual transition (tree-to-snag and tree- and snag-to-downed wood) rates, which were used first to explore correlations within transition rates among fires and over time, and second to test hypotheses about the sources of plot-level variability in these rates. Based on the literature on interactions of forests and fire, we hypothesized that higher levels of local fire intensity will increase the plot-level transition rates, both tree-to-snag rates and tree and snag fall rates. Other unmeasured plot-level factors also may influence tree-to-snag rates, leading to variability among plots exposed to similar fire intensities. Because many of these factors are a function of the spatial location of the plot (e.g., local soil moisture and nutrient content), we predicted that they might result in a correlation between initial (immediate post-fire) tree-to-snag rates and the longer-term rates, since, to some extent, annual rates would be responding to the same unobserved stimuli. The statistical model for tree-to-snag transition rates thus included both fire intensity and initial tree-to-snag rates.

For tree and snag fall rates, we hypothesized that wind shelter was the dominant controlling factor, leading to the prediction that increased fall rates would be associated with lower stem density, where fewer standing trees and snags are available to act as windbreaks. The statistical model for tree and snag fall rates thus included both fire intensity and stem density.

Hypothesis testing for this plot-level data was accomplished via logistic regression using general linear models (GLMs; McCullagh and Nelder 1989) and the software package R (R Development Core Team 2008). We fit GLMs to the data for each year separately and for both years combined (hereafter referred to as the 'cumulative' model). Because the data was in the form of probabilities or rates, we used the logit transform to link the data to the linear model. This transformation is given by

$$\text{logit}(p) = \log\left(\frac{p}{1-p}\right) \quad [1]$$

where p is the observed rate.

To assess the ongoing changes implied by the results of the GLMs, we fed the coefficients into a simple model of temporal stand dynamics. We let L_t and S_t represent the numbers of trees and snags, respectively, at time t . The expected proportion of trees remaining in a given year is the product of the probabilities of not transitioning to a snag and not falling times the number of trees standing. Similarly, the expected number of snags remaining in a given year is specified by the probability of not falling times the number of snags standing plus the number of trees transitioning to snags in the plot that year. Thus,

$$\begin{aligned} L_{t+1} &= (1-\alpha)(1-\beta_t)L_t \\ S_{t+1} &= (1-\gamma_t)S_t + \alpha L_t \end{aligned} \quad [2]$$

where α , β , and γ represent the tree-to-snag transition rate, tree fall rate, and snag fall rate, respectively. Initial numbers of trees and snags were calculated from specified initial stand density, N_0 , as

$$\begin{aligned} L_0 &= (1-\delta)N_0 \\ S_0 &= \delta N_0 \end{aligned} \quad [3]$$

where δ is the initial tree-to-snag rate immediately after the fire. The coefficients from the GLMs indicate how the parameters in [2] and [3]—the transition rates—may vary with fire intensity, and over time, as stand density changes. Thus,

$$\text{logit}(\alpha) = \alpha_0 + \alpha_1 FI + \alpha_2 \frac{L_0}{L_0 + S_0} + \alpha_3 \frac{FI \cdot L_0}{L_0 + S_0}$$

$$\text{logit}(\beta_t) = \beta_0 + \beta_1 (L_t + S_t)$$

$$\text{logit}(\gamma_t) = \gamma_0 + \gamma_1 (L_t + S_t)$$

$$\text{logit}(\delta) = \delta_0 + \delta_1 FI \quad [4]$$

where FI is a binary variable (0 or 1) representing fire intensity category (low or high). Using the coefficients from the GLMs fit to cumulative data (2005-2007), we ran this model over 10 simulated years post-fire (in 2-year steps) for different fire intensities and initial stand densities.

Results

First we report the plot-level average changes in residuals through time, for each type of residual transition (tree to snag, tree fall, and snag fall) during the 2 years post-fire, without considering potential statistical significances between these values. Then we describe the variability around these averages, and test potential sources of variability as formal hypotheses. Finally, we present predicted rates of change in residuals beyond the sample period based on simulations.

Average rates of change in abundance of post-fire residuals

Per-plot (0.05 ha) abundance of residual trees ranged from 3 to 134 (mean= 27.9 ± 3.9) soon after fire. Corresponding snag abundance ranged from 0 to 211 (mean= 49.2 ± 6.0) per plot across the 50 sample plots. Per-plot abundance of both residual trees and snags were highly dynamic over the two years following fire: trees became snags, trees fell and became downed wood, and snags fell and became downed wood (Figure 3a,b).



Figure 3a. Study plots contained live trees immediately after fire (i) (shown here in a high resolution photo), but most died and/or fell during the subsequent years (ii,iii).



Figure 3b. Study plots contained many snags immediately after fire (i, ii), but some fell over the subsequent years (iii and iv).

The per-plot average rate of residual trees becoming snags was 11.2 in the first year after fire and 6.5 in the second (Table 3). This corresponds to an addition of approximately 224 snags per hectare over the first year, and 130 the second year, assuming that a 0.05 ha sample plot is an unbiased estimator of the surrounding hectare of forest. Transitions of trees to downed wood were relatively low: the per-plot average number of trees that fell was approximately 3.9 in the first year after fire and less than 0.5 in the second. This translates to 114 residual trees remaining in a hectare (5.7 per plot) after 2 years, down from 558 trees per hectare (27.9 per plot) present immediately after fire.

The plot-level average change in snags over time was lower than that in trees; 2.2 snags per plot fell in the first year to become downed wood, and 3 fell in the second year. Together, these fall rates correspond to an estimated addition of 104 downed wood stems during the two years post-fire, leaving 1234 snags per hectare on the average.

Table 3. Per-plot (0.05 ha) average of residual transitions: trees to snags, trees to downed wood (DWD), and snags to downed wood over 2 years post-fire.

Fire # (number of plots)	Immediate post-fire abundance (2005)		First year post-fire (2005-2006)			Second year post-fire (2006-2007)			Abundance 2 years post-fire (2007)	
	Trees	Snags	Trees to snags	Trees to DWD	Snags to DWD	Trees to snags	Trees to DWD	Snags to DWD	Trees	Snags*
FOR-014 (n=12)	20.3	41.5	6.9	5.8	3.8	1.2	0.3	2.6	6.1	43.2
THU-030 (n=10)	28.2	89.7	6.9	0.6	0.4	13.1	0.1	3.8	7.5	105.5
THU-031 (n=14)	28.8	49.4	22.4	0.7	0.9	3.8	0.4	2.2	1.5	72.5
THU-067 (n=14)	33.1	26.9	6.9	7.9	3.4	9.1	1.2	3.5	8.1	36.0
Overall (n=50)	27.9	49.2	11.2	3.9	2.2	6.5	0.5	3.0	5.7	61.7

* Includes snags created over 2 years post-fire.

Variability in the changes of post-fire residuals

As detailed in Table 3, changes in abundance of trees and snags from one residual category to another (i.e., transitions) varied widely within and among fires. Here we examine the variability in the *rates* of these transitions, where rates are defined as the proportion of change in the abundance of one residual category towards another specified category in a sample plot. For example, a transition rate of 0 indicates no change in abundance in a specific category of residuals and a value of 1 indicates that all residuals in a specific category changed to another category.

The annual tree-to-snag transition rates were highly variable across sample plots, distributed almost evenly between 0 and 1, but the cumulative transition rates were left-skewed, i.e., more plots with high transition rates (Figure 4). Overall, after the second year post-fire, all sample plots had tree-to-snag transitions and the majority of plots had a transition rate >0.5. As well, after two years over one third of sample plots had a tree-to-snag transition rate of 1.

In contrast, annual fall rates of both trees and snags (transition to downed wood), per plot, showed a highly right-skewed unimodal distribution. Many sample plots had no tree or snag fall during the first and second years. The cumulative rate distribution was also right-skewed, with the majority of plots having no tree- and snag-to-downed wood transitions. Even after two years, higher rates of transition to downed wood were increasingly rare.

The among-fire variability of rates in tree-to-snag and tree-to-downed wood transitions was high, but did not show any significant patterns per year or through time (Figure 5). However, the rates of snag-to-downed wood transitions increased with time across all fires, and appeared to differ among fires over time.

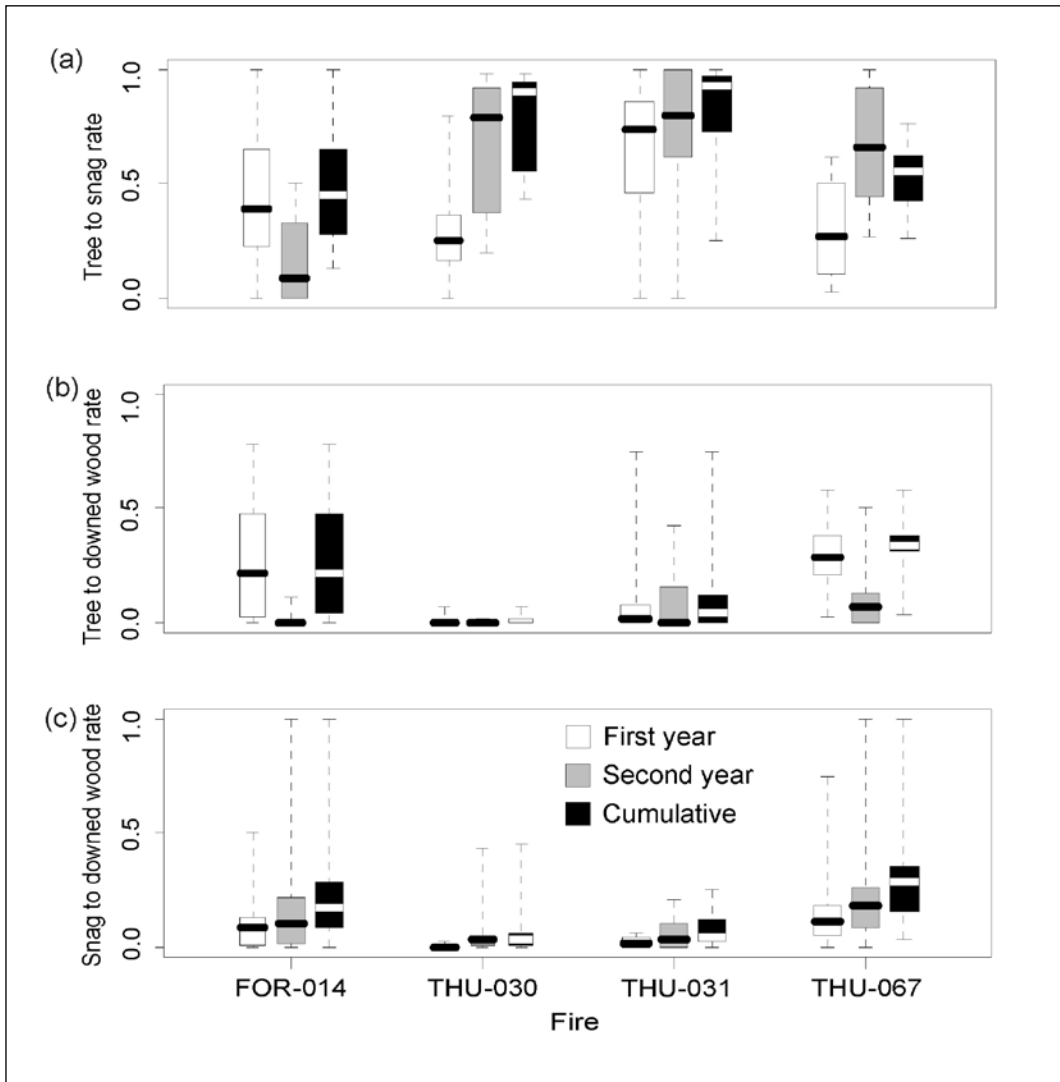


Figure 5. Box plots comparing the distributions of (a) tree-to-snag, (b) tree-to-downed wood, and (c) snag-to-downed wood transition rates over time and across sample fires. The horizontal axis provides the OMNR fire number with the first year, second year, and cumulative rate distributions colour-coded above each one. Boxes show the interquartile range, lines the median, and whiskers the min-max rate values.

To examine transition rates of residuals by individual species, we considered only the dominant species; white birch, jack pine, and black spruce. Balsam fir, red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), and poplar (*Populus* spp.) formed very minor components of the total stems, accounting for less than 10% of the data set, and were removed prior to this analysis. Figure 6 illustrates the species composition of the residuals that changed as well as those that did not. Differences among species were not distinct, except for white birch, for which the tree-to-snag and tree-to-downed wood transition rates appeared low.

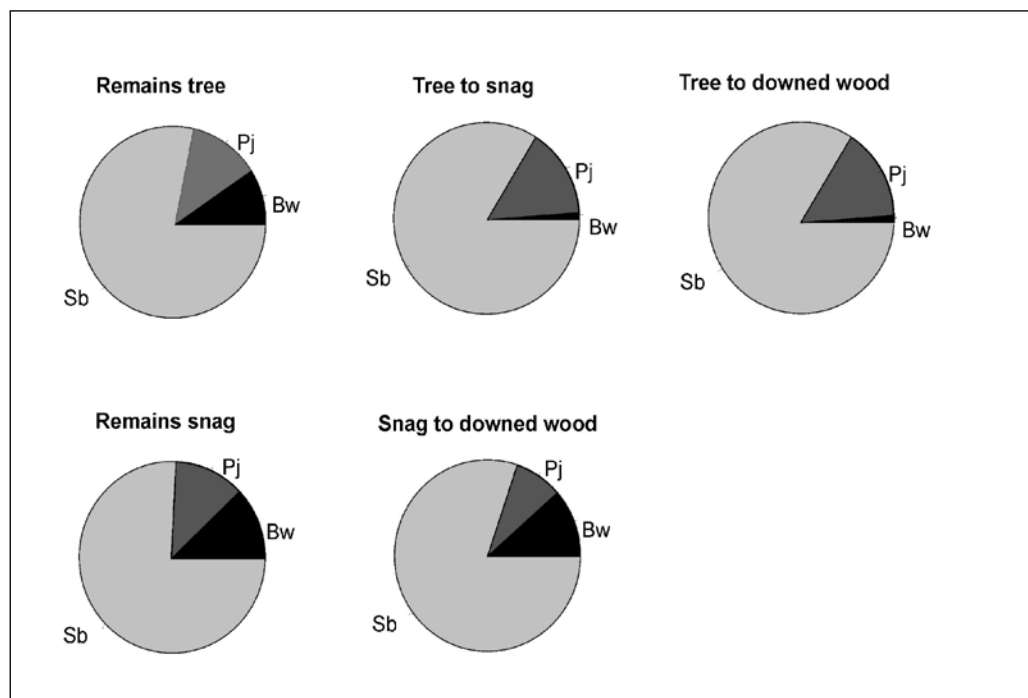


Figure 6. Relative abundance of dominant tree species for each type of residual transition. Each pie chart represents data pooled over 4 fires, 50 plots, and 2 years; Sb – black spruce, Pj – jack pine, Bw – white birch.

Similarly, Figures 7 and 8 illustrate the size (DBH) distribution of trees that transitioned to snags and downed wood, and snags that transitioned to downed wood, with the respective distributions of trees and snags that did not transition, on a species by species basis, pooled across plots and fires over 2 years. No discernible trends were evident in temporal changes of residuals with respect to their size.

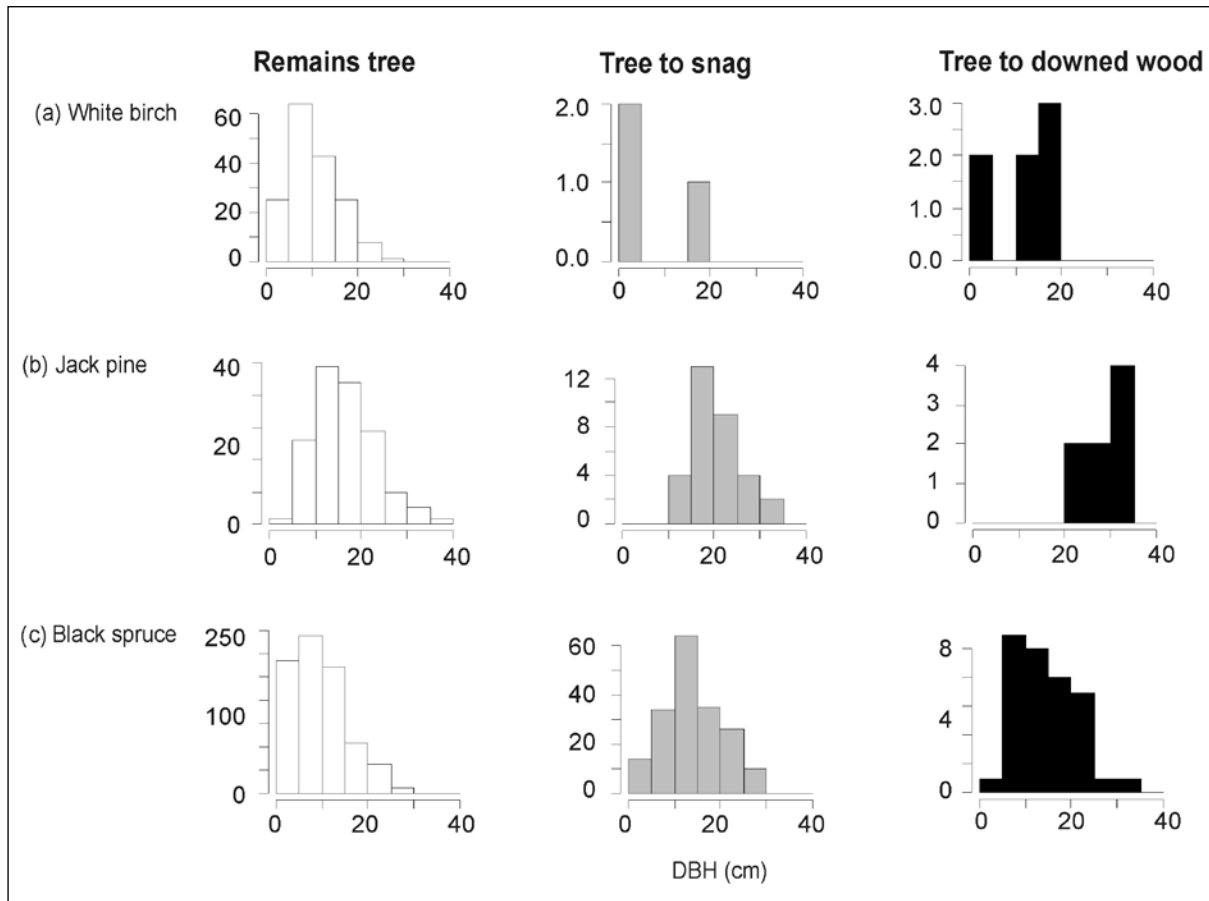


Figure 7. Size (DBH=diameter at breast height in cm) distributions of trees by dominant species (a) white birch, (b) jack pine, and (c) black spruce for different types of residual transitions (respective columns). Vertical axis shows the number of trees pooled over 4 fires, 50 plots, and 2 years.

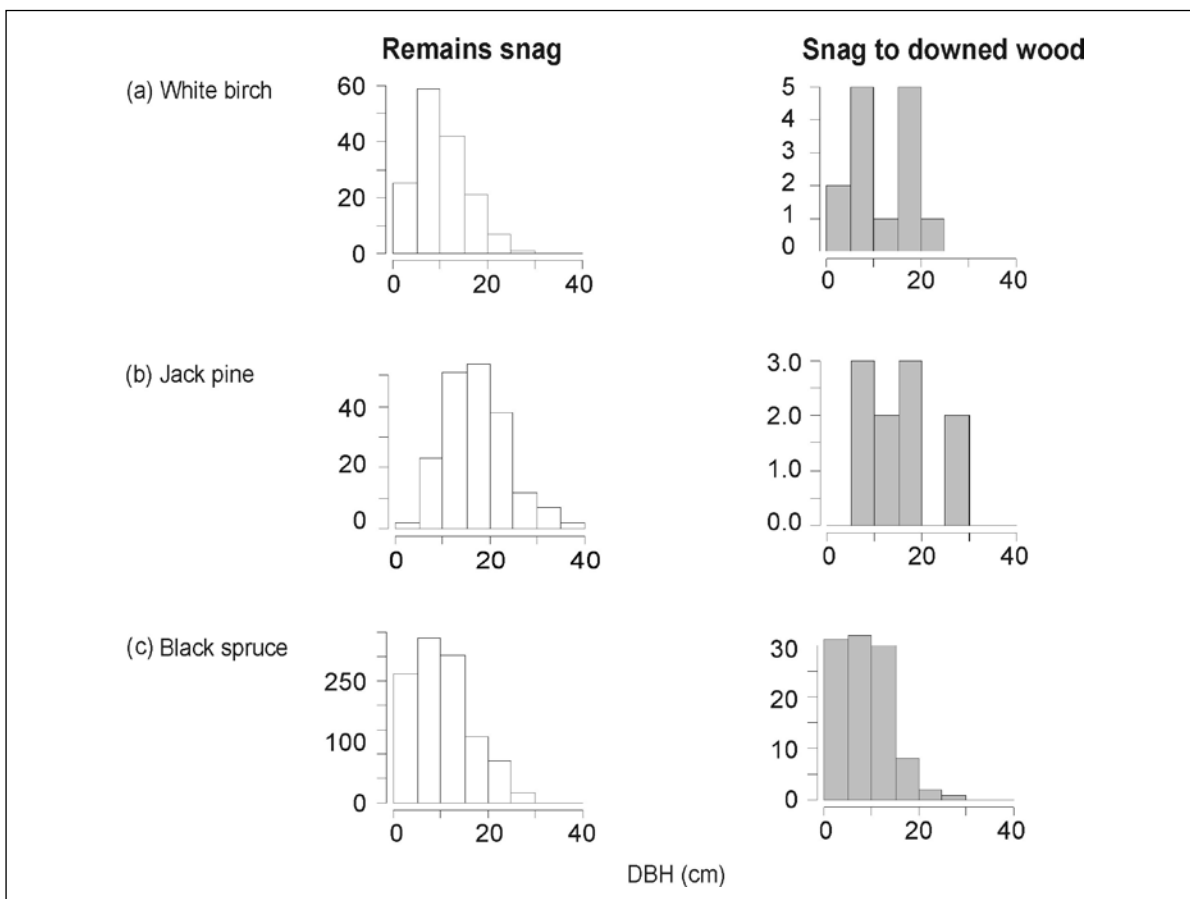


Figure 8. Size (DBH=diameter at breast height in cm) distributions of snags by dominant species (a) white birch, (b) jack pine, and (c) black spruce for different types of residual transitions (respective columns). Vertical axis shows the number of trees pooled over 4 fires, 50 plots, and 2 years.

Sources of variability in the changes of post-fire residuals

Among-fire differences accounted for 21% of the variability in tree-to-snag transition rates and 29% of the tree- and snag-to-downed wood transition rates. Corresponding rates for among-plot differences were 33% and 24%. Specific sources of variability in transition rates differed among the residual categories and time since fire. Plot-level fire intensity, as estimated by Smith et al. (2008), was a significant factor for tree-to-snag transition rates in the first year post-fire. However, it was no longer significant in the second year, and was only weakly significant in the GLM for the cumulative rate (Table 4).

Table 4. Slopes and probability of Type I error from the general linear models (GLM) of plot-level rates (n=50) of residual changes as a function of fire intensity, initial tree-to-snag rate (immediate post-fire), and stem density, for each of the 2 years post-fire and cumulative over 2 years.

Transition type	Effect	Symbol	First year post-fire (2005-2006)		Second year post-fire (2006-2007)		Cumulative (2005-2007)	
			Estimate	p	Estimate	p	Estimate	p
Tree to snag	Intercept	α_0	-3.76	< 0.001	-1.54	< 0.001	-1.91	< 0.001
	Fire intensity (F)	α_1	2.29	< 0.001	-0.64	0.174	0.63	0.107
	Initial tree to snag rate (T)	α_2	6.18	< 0.001	2.75	< 0.001	5.11	< 0.001
	F x T	α_3	-4.37	< 0.001	0.43	0.620	-1.75	0.022
Tree to downed wood	Intercept	β_0	-0.47	0.054	-2.62	< 0.001	-0.32	0.171
	Fire intensity (F)	β_1	1.96	< 0.001	0.99	0.195	1.85	< 0.001
	Stem density (D)	β_2	-0.01	< 0.001	-0.01	0.026	-0.01	< 0.001
	F x D	β_3	-0.03	< 0.001	-0.00	0.631	-0.02	< 0.001
Snag to downed wood	Intercept	γ_0	-2.00	< 0.001	-0.98	0.006	0.11	0.624
	Fire intensity (F)	γ_1	1.50	0.032	-0.25	0.568	0.45	0.157
	Stem density (D)	γ_2	-0.01	0.014	-0.02	< 0.001	-0.01	< 0.001
	F x D	γ_3	-0.01	0.1823	0.01	0.3512	-0.01	0.0038

In contrast, initial tree-to-snag rate (observed immediately post-fire) was strongly significant the first year after fire, the second year after fire, and cumulative over both years. The interaction between fire intensity and initial tree-to-snag rate was significant in the first year and over both years combined. This translates to a clear positive relationship between tree-to-snag transition rate during the first year post-fire and delayed tree-to-snag rate in the subsequent years. Furthermore, the shape of this relationship depends on the year after fire and plot-level fire intensity, as evident from Figure 9a.

Plot-level fire intensity was also significant for tree-to-downed wood transition rates in the first year post-fire. Although not significant in the second year, fire intensity was significant in the GLM for cumulative rate over 2 years (Table 4). In contrast, stem density (per-plot total of trees and snags) was strongly significant in all three GLMs. The interaction between fire intensity and stem density was significant in the first year and over both years combined. Tree-to-downed wood rates were thus related predominantly to stem density, with the shape of this negative relationship varying slightly with fire intensity and from year to year (Figure 9b). In the GLM of snag-to-downed wood transition rates, both fire intensity and stem density were significant in the first year after fire but their interaction was not. In the second year after fire, only stem density was a significant predictor of snag fall rates and the cumulative interaction between stem density and fire intensity was important. Thus, as for trees, stem density was consistently the strongest predictor of snag-to-downed wood transition rates, with fire intensity playing a lesser role depending on the timeframe (Figure 9c).

Overall, plot-level fire intensity significantly influenced residual transition rates in the first year but not in the second year, either directly or through interactions. In the second year, internal plot factors, i.e., initial mortality rate of trees and stem density, were more strongly related to changes in residuals than plot-level fire intensity. Since these rates determine future stand density, intrinsic nonlinear dynamics may have a significant role in temporal changes in post-fire residuals at the plot level.

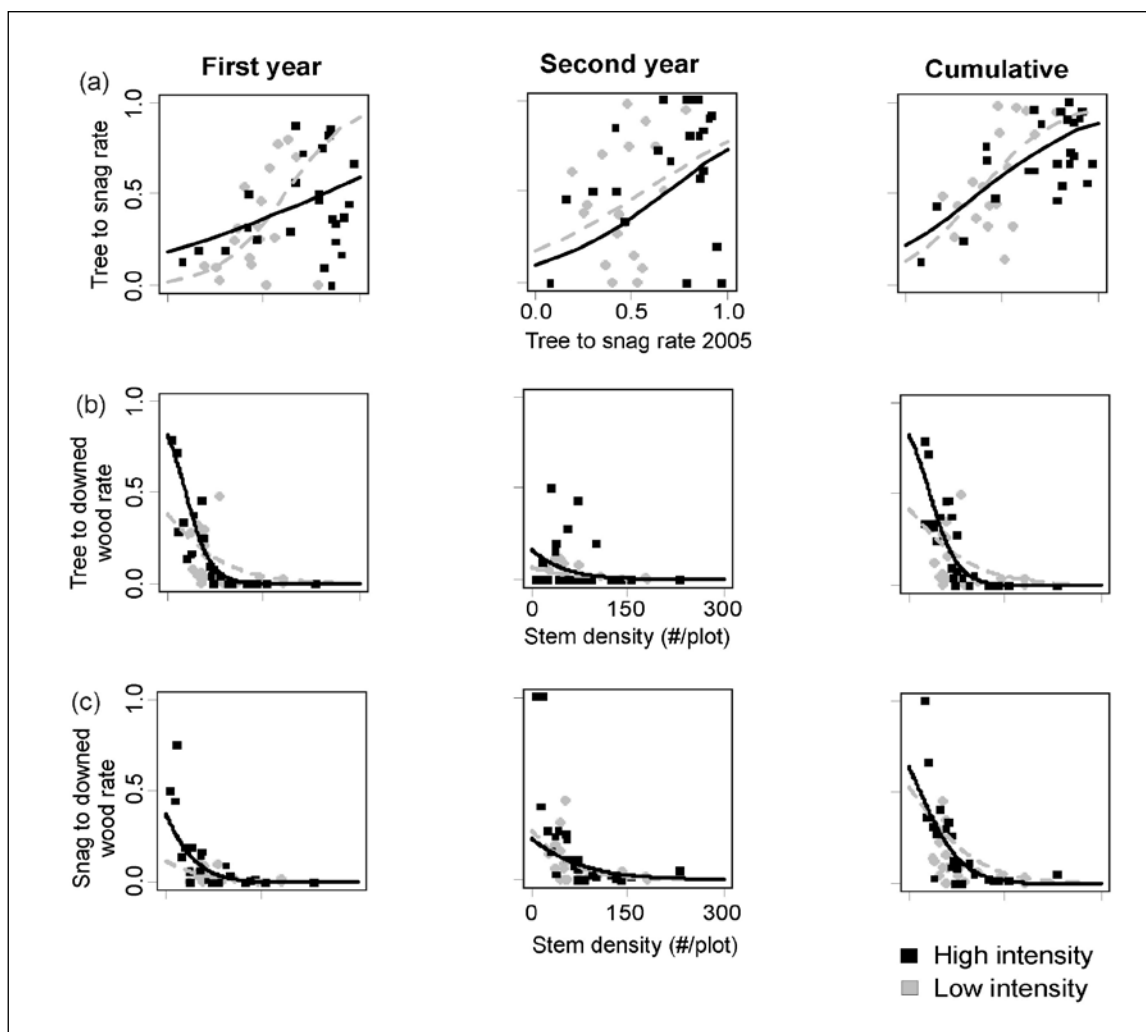


Figure 9. (a) Tree-to-snag transition rates in the first and second year post-fire and over both years combined as a function of initial (2005) tree-to-snag transition rates and fire intensity. The rate for each plot is represented as a point, colour-coded by its fire intensity, and the lines represent the fit of a logistic regression model that includes fire intensity, initial tree-to-snag rates, and their interaction. The dashed line represents the predicted relationship for low fire intensity and the solid line represents the predicted fit for high fire intensity. Results of similar analyses of (b) tree-to-downed wood and (c) snag-to-downed wood rates are shown as a function of fire intensity and per plot stem density.

Predictions of post-second-year changes

To predict residual changes following the first 2 years post-fire, we parameterized a simple plot-level prediction model with the coefficients from the cumulative GLMs presented in Table 4. As illustrated in Figure 10, the model predicted exponential rates of decline in tree abundance until 5 years post-fire, resulting from rapid transitions of trees to snags and trees to downed wood.

Correspondingly, the number of snags in a plot increased during the first few years of simulation when tree-to-snag transitions dominated the dynamics. In subsequent years, tree-to-snag transitions continued but at a lower rate. Therefore, the changes in snag abundance in later years were dominated by snag-to-downed wood transitions, causing net decreases in snag abundance. Different fire intensities resulted in different dynamics in snag abundance. Specifically, at high initial stem densities (solid lines in Figure 10), snag abundance in plots subjected to high fire intensity (darker lines in Figure 10) declined more quickly than those in plots subjected to low fire intensity (grey lines in Figure 10). As well, transition of both trees and snags to downed wood decreased considerably as stem density increased beyond approximately 100 stems per plot.

Overall, post-fire residual dynamics were initially dominated by tree-to-snag transitions and subsequently by snag-to-downed wood transitions. Fire intensity (positive) and stem density (negative) appeared to influence these transitions rates. Together, the two transition processes resulted in a continuous increase in downed wood, the rate of which appeared to increase approximately linearly over the longer term.

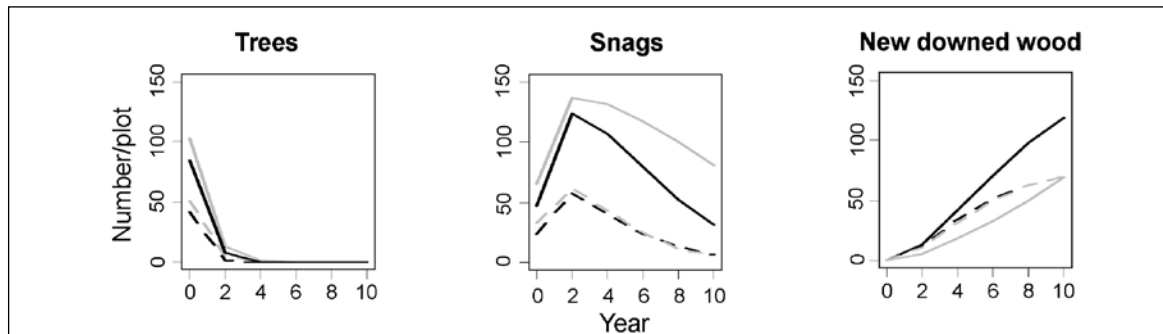


Figure 10. Predicted trajectories of residual trees and snags and new downed wood over time since fire. Four realizations of the model were run with different fire intensity and initial stem density. Solid lines indicate high initial stem density and dashed lines low density. Darker lines indicate high fire intensity and grey lines the low fire intensity. The model was parameterized from the plot-level data using coefficients (as detailed in Table 4) from the logistic regression models over both study years combined.

Discussion

Post-fire changes in residuals and sources of variability

Immediately post-fire, we encountered large number of residual trees (1316) in the 50 plots sampled. However, that number declined rapidly over the next two years – by 66% – mostly due to mortality (i.e., trees becoming snags). This was over three times the rate of tree-to-downed wood transition during the same period. The combined effect of these transitions left approximately 13% of the original compliment of residual trees 2 years post-fire (Figure 11). Snag transitions were less drastic – only few became downed wood over 2 years, leaving almost 90% of the original post-fire snags intact.

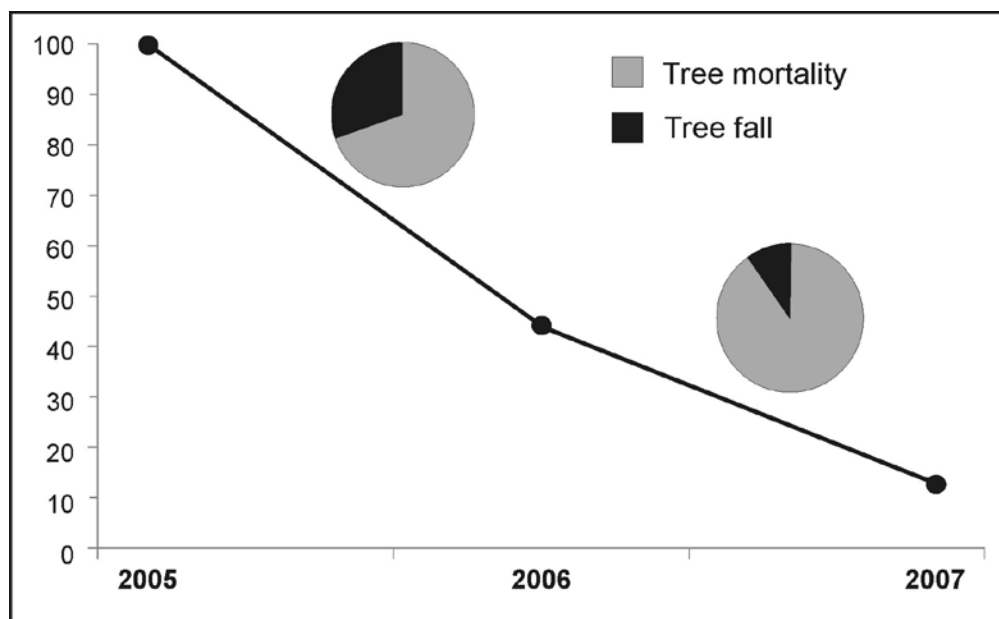


Figure 11. Decline in residual trees (as a percentage of the immediate post-fire abundance; $n=1316$) over two years for all residuals pooled across 50 plots in the four fires. The pie charts specify the reason for the decrease each year.

As a result, very few residual trees remained 2 years post-fire, while most snags remained standing. Figure 12 summarizes plot-level changes in residuals immediately post-fire; trees had more dynamic fates than snags.

Little information from boreal forests was found in the literature for direct comparison with our findings on temporal changes in post-fire residuals. Those who addressed tree mortality did so immediately after fire (e.g., Beverly and Martell 2003, Hely et al. 2003), and those who addressed snag and tree fall did so over the long term via chronosequence studies (e.g., Moroni 2006). Reports of monitoring early dynamics such as ours are rare. Stambaugh (2003) offers some data from boreal Alberta, where snag recruitment (via tree mortality) was 20% in the first year after fire and 6% in the second year, which is much less than our findings.

Published literature that provides insights on reasons for temporal changes in tree-to-snag transitions is also rare. Hely et al. (2003) reported species differences in tree mortality within one boreal fire. However, in our study the plot-level rates for tree-to-snag transitions were highly variable both among fires and among plots within fires, and we could not discern any among-species differences of effect of tree size. Except for a few studies that focused on certain species (e.g., Beverly and Martell 2003), tree mortality studies from boreal forests that examine species-diameter interactions are rare. Tree-to-snag transition rates had a weaker relationship with fire intensity than we expected, particularly in the second year post-fire. This may be because spatial patterns in probability of residual occurrence are more variable at lower fire intensity (Perera et al. 2009). At lower levels, fire intensity *per se* appears to exert direct control for only a short time (i.e., affecting initial tree-to-snag rate). The longer-lasting response of tree-to-snag transition rates are probably the sum of site-species-fire interaction effects that may operate at multiple scales in boreal fires (Dalziel and Perera 2009).

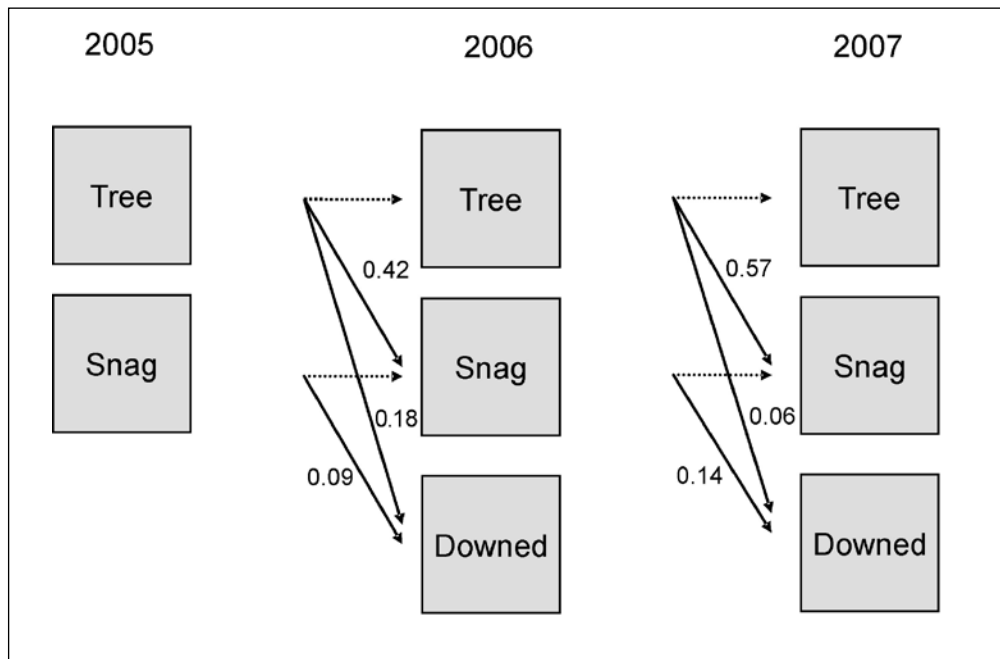


Figure 12. Plot-level average ($n=50$) transition rates of residual trees and snags during 2 years post-fire.

One hypothesis for the negative correlation between fall rates and stem density is that at high densities trees shelter each other from the wind resulting in lower fall rates. The predictive model we used suggested that stands were particularly susceptible to increased fall rates at densities of less than approximately 100 stems per 0.05 ha. A simple model of post-fire dynamics using the coefficients from the GLMs showed how different initial fire intensities produce different dynamics for trees and snags (i.e., at high fire intensities, snag density initially increases before decreasing due to fall rates). Despite being essentially a combination of exponential curves, stem density and snag density declined almost linearly over 5 years.

Implications for further research

The many post-fire ecological processes such as habitat supply, nutrient cycling, and carbon flux, implied based on estimates of residual structure must account for the rapid changes that occur within the first few years of fire. Rapid decline in the live tree abundance and the subsequent increase in snags may result in overestimates of the rates of ecological processes that rely on tree residuals and underestimates of those based on snags.

High levels of variability, both within and among fires, make it difficult to model post-fire residual changes simply based on plot-level estimates. Within-fire variability of fire intensity, site conditions, species characteristics, and their interactions make the GLMs of individual residuals difficult to interpret (Perera et al. 2009). Moreover, broader scale processes that operate at among-fire level, such as fire weather, also influence the changes of individual residuals by imposing constraints, resulting in thresholds and/or non-linear responses (Dalziel and Perera 2009). Thus, the specific causal factors of temporal variation in residual dynamics may be difficult to understand in isolation from its broader scale drivers.

We assert that most literature published to date on post-fire residual dynamics overgeneralize patterns and causes: to identify specific effects of causal factors, such as species, on changes of each residual component would require that each species were replicated many times at each fire intensity, stem density, and site condition, as well as fire weather conditions, etc. As well, a hierarchical analytical/modelling approach is required to explain the variability in post-fire residuals at different scales. The data set required for such analyses necessitates replicates of every species exposed to every 'treatment' (where a treatment is an integrated set of ecological conditions that vary over space, time, and sampling scale), which would require a much larger data set than the one we assembled here. In fact, we suggest that continuing the field survey-type studies conducted hitherto may not be useful in addressing the spatial and temporal variability in post-fire residuals and isolating causal factors that interact, and influence residual occurrence and longevity at multiple scales. We propose that researchers instead embrace alternate approaches, such as remotely sensed data collection, to study post-fire residuals.

Management implications

Our findings of residual dynamics during the early post-fire years are relevant to forest management strategies that attempt to emulate boreal forest fires. A strategy employed in typical emulation approaches is to develop residual tree and snag targets that minimize differences in structure between harvested and burned sites so that the time required for functional convergence can be minimized. Development of such targets must account for rapid rates of post-fire transitions of residuals. For example, live tree abundance observed immediately after fires may overestimate the number of post-harvest residual live trees required to emulate a fire in the longer term. Similarly, when comparing multiple sources of information to develop these targets, variations in definitions, timing of measurement and replication must be considered. Moreover, rates of temporal changes in residuals are not homogenous within a fire; this spatial heterogeneity needs to be considered in designing emulation management strategies.

Our findings indicate that a higher incidence of immediate post-fire wind throw of trees and snags is seen in fires where stem density is lower. Consequently, if the overall goal is long-term retention of standing residuals, to reduce the incidence of post-harvest wind throw some clumping of post-harvest trees and snags may be preferable to evenly and sparsely distributing residuals as suggested by some emulation guidelines (e.g., OMNR 2001). This finding also applies to salvage logging in areas where stems densities are low and the intent is to retain some vertical residual structure after harvest.

Conclusions

Many residual trees and snags are observed immediately after the occurrence of boreal fires, but these undergo rapid transitions during the first couple of years after fire: trees die to become snags, and both trees and snags fall to become downed wood. Changes in residual trees are more dynamic than those of snags during this period.

While specific causal factors of post-fire residual changes could not be discerned due to high among- and within-fire variability, there are some indications of common trends. For example, tree-to-snag transition rates appear to be positively autocorrelated in time and both tree- and snag-to-downed wood transition rates were strongly related to stand density, signaling a positive feedback loop. Specific rates of these transitions varied among- and within fires, and many simple mechanistic processes such as fire intensity and stem density accounted for much of the temporal dynamics of forest fire residuals.

Isolating exact causal mechanisms of this variability may require non-linear and hierarchical analytical approaches, requiring parameterizations with larger, more complex data sets that are beyond the realm of typical field surveys. This high degree of dynamism in residuals during the early years needs to be considered in studies of post-fire processes such as habitat supply, nutrient cycling, and carbon flux, as well as in forest management strategies for emulating natural fire disturbances and for salvage logging.



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(0.2k P.R., 11 09 30)
ISSN 0381-3924 (print)
ISBN 978-1-4435-7268-2 (print)
ISBN 978-1-4435-7269-9 (PDF)