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Deadwood abundance in post-harvest and post-fire residual patches: An evaluation of patch temporal dynamics in black spruce boreal forest

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ABSTRACT

In managed boreal forests, variable retention harvest is considered by forest managers as a means of mitigating harvest impacts on biodiversity. Variable retention harvest consists of maintaining within a cutblock structural attributes of the original forest stand in intact forest patches that could provide quality habitat (i.e., with large trees and deadwood) for many forest species during forest regeneration. However, retention patch modalities (size, shape, age of the forest) allowing both persistence and sustainable recruitment of deadwood over time remains unknown. The objective of this study is to evaluate the abundance of recent deadwood in post-harvest and post-fire residual patches and to compare their temporal dynamics in black spruce dominated stands located in northwestern Quebec. Abundance of the recent deadwood, estimated as the sum of recent standing deadwood volume and recently fallen deadwood volume was analyzed in 41 post-fire residual patches, and in 45 post-harvest retention patches of varying ages (i.e. exposure time to the disturbed matrix) and in 37 continuous black spruce forest stands (controls). This study shows that post-fire residual patches appear in general more durable than post-harvest retention patches after disturbance. In a management context, our results indicate that: (1) large island patches and large linear separators oriented to escape windthrow usually have deadwood recruitment dynamics similar to that of post-fire patches; (2) retention patches with an initial stand volume greater than 60 m^3/ha will generate more deadwood volume over time. This suggests that the selection of large retention patches in the shape of an island or a separator, with high volume (between 60 and 300 m^3/ha) should help increase the persistence of post-harvest retention patches in black spruce forest, and simultaneously ensure quality habitat for several forest species while the adjacent managed forest regenerates.

1. Introduction

In recent decades the progressive loss of old-growth forests has been of particular interest because of the potential impacts on biodiversity (Bergeron et al., 2002; Perron et al., 2008). In boreal ecosystems, the predominance of clearcutting and the absence of consideration of the cumulative landscape scale effects in planning, results in the rejuvenation and simplification of forest structure across the landscape (Harper et al., 2004; Bergeron et al., 2007; Kuuluvainen et al., 2015). In a forest landscape subject to relatively short harvest rotations, the old-growth forest matrix is gradually replaced by smaller residual forests, dispersed in a matrix dominated by post-harvest regenerating stands (Gauthier et al., 1996; Bergeron et al., 2002). In managed landscapes, these residual forests are likely to be the only structural legacies of the original forest. As several species are partially or entirely dependent on old-growth forests (Drapeau et al., 2000), their decline is likely to influence both fauna and flora (Franklin et al., 1997). To limit the impact of forest harvest on biodiversity, variable retention harvesting is a frequently proposed technique (Gustafsson et al., 2012; Lindenmayer et al., 2012). Variable retention harvesting consists of maintaining structural attributes (live and dead trees, woody debris), of the original forest stand in intact forest patches dispersed across the cutblock (Gauthier et al., 2001, 2008; Beese et al., 2003). In freshly disturbed areas, variable retention can be considered ecosystem based management if its modalities are inspired by patterns generated by natural disturbances (Payette, 1992; Franklin, 1993; Gauthier et al., 1996; Harvey et al., 2002).

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In boreal forests, fire shapes the structure of forest mosaics (Kafka et al., 2001). However, fire does not generally burn all trees within its boundaries, and intact patches, here called "post-fire residual patches" of varying size and age remain (Gasaway and DuBois, 1985; DeLong and Kessler, 2000; Bergeron and Fenton, 2012). Several studies suggest that post-fire residual patches could represent significant and unique refuge habitats for many plant (Ferron and St-Laurent, 2005; Perhans et al., 2009; Hylander and Johnson, 2010), or animal species (Gandhi et al., 2001; Pearce et al., 2005; Schmiegelow et al., 2006). Over time, these post-fire residual patches could also constitute seed banks providing propagules for recolonization of the burned surrounding areas (DeLong and Kessler, 2000; Madoui et al., 2011). In contrast, the selection of retention patches during variable retention harvesting is generally based on operational criteria, such as proximity to water bodies, tree age and species, and accessibility. Therefore, these post-harvest retention patches could present different habitat conditions and different forest dynamics than those that characterize post-fire residual patches (Harper et al., 2004; Work et al., 2004).

The tree mortality dynamics, i.e. the recruitment of snags or fallen deadwood and their eventual decomposition, has been little studied in post-harvest residual patches. In addition, most of the research conducted to date has taken place in the boreal mixed forest (Bose et al., 2013). Forest retention patches, as currently established, are often small in size (clumps) or linear (cuts separators) and subject to significant windthrow events (Ruel et al., 2001; Dragotescu and Kneeshaw, 2012; Lavoie et al., 2012), especially during the first years after establishment (Scott and Mitchell, 2005; Hautala and Vanha-Majamaa, 2006; Lavoie et al., 2012; Urgenson et al., 2013). Although mortality observed in the first years after harvest can be a significant source of deadwood (Mitchell and Beese, 2002; Beese et al., 2003; Thorpe and Thomas, 2007), this contribution could be short-lived if the rate of mortality of large trees exceeds their rate of recruitment in the canopy (Thorpe and Thomas, 2007). In other words, these post-harvest retention patches could open up over time, thereby eroding their ecological value. In managed areas, these retention patches need to remain for at least 100 years, a period necessary for the surrounding black spruce regenerated forests to become a mature forest (Burns and Honkala, 1990). Therefore it is important to document the durability of these post-harvest retention patches. In boreal forests, tree mortality dynamics observed in retention patches have been found to be influenced by many local factors (Dragotescu and Kneeshaw, 2012; Lavoie et al., 2012), including characteristics of the trees (height and average diameter), of the stands (size, shape, age) (DeWalle, 1983; Cyr et al., 2009), of the soil (type and depth), of the surrounding context (time since last disturbance) as well as of forest harvesting techniques (Ruel, 1995; Jönsson et al., 2007; Lavoie et al., 2012).

The main objective of this study is to evaluate the abundance of recent deadwood in post-harvest and post-fire residual patches and to compare their durability over time, considering continuous black spruce forest as a control. The first specific objective is to compare recent deadwood volumes between post-harvest retention patches and post-fire residual patches of varying ages (i.e. exposure time to the disturbed matrix). In this case, we anticipate that due to their greater vulnerability to wind, there will be greater volumes of recent deadwood in the post-harvest retention patches than in the post-fire patches and this especially during the first years of exposure to the disturbed matrix. The second specific objective is to evaluate the effect of stand volume of the pre-disturbance forest on the volume of recent deadwood in post-harvest and post-fire patches of different ages. We estimate that regardless of their age and their original disturbance i.e. harvest or fire, pre-disturbance volume of the patches will be positively correlated with recent deadwood volume. The third specific objective is to determine which explanatory factors explain recent deadwood volume in residual patches. The potential explanatory factors are: time since the last fire, which corresponds to the age of the original forest from which the patch was formed; patch area and shape; tree anchoring substrate, estimated by the thickness of the organic layer; and mean diameter and height of living trees. Finally, these results are integrated to generate a predictive model that will allow us to make recommendations in terms of size, shape and type of forest stand that should be targeted for post-harvest retention in order to increase persistence of patches and ensure the expected ecosystemic services are provided.

2. Material and methods

2.1. Study area

This study was conducted in eastern Canada's boreal forest, between 74–80°W and 49–51°N; in the black spruce-feathermoss bioclimatic subdomain (Fig. 1). The topography of this area forms an undulating plain. The mineral soil type is composed primarily of glaciolacustrine clay in the west, and clay till in the east (Robitaille and Saucier, 1998). The mean annual temperature varies between −2.5 and 0.0 °C, and the mean annual precipitation varies between 700 and 900 mm and the climate is subpolar, continental sub-humid (J.-F. Bergeron et al., 1999; Blouin and Berger, 2005). Forest stands are dense (canopy cover 40–80%) and dominated by black spruce (*Picea mariana* Mill., BSP) with jack pine (*Pinus banksiana* Lamb), balsam fir (*Abies balsamea* [L.] Mill), birch (*Betula papyrifera* Marsh) and trembling aspen (*Populus tremuloides* Michx.).

Fire is the main natural disturbance that shapes the forest landscape in the study area (Payette, 1992), with historically a relatively short fire cycle, on the order of 100–200 years (Bergeron et al., 2001). Currently this fire cycle is lengthening and is now over 400 years. As the fire cycle has lengthened, the effects of forest harvest have become the main source of disturbance on the landscape (Bergeron et al., 2004; Cyr et al., 2009). Since the late 1980s, the harvesting method commonly used has been harvest with protection of regeneration and soils (CPRS in French), which consists of harvesting all merchantable stems (DBH > 9 cm) in cutblocks with a maximum size of 250 hectares. Retention patches were placed linearly between these cutblocks (separators) with a width of 60–100 m and in the form of large patches (3–10 ha) within the cutblocks for moose (*Alces alces*) (Gouvernement du Québec, 1988). In the ten last years, two new retention types have been used: small clumps and large intact forest patches, which are supposed to maintain structural attributes similar to those created by fires (Y. Bergeron et al., 1999; Harvey et al., 2002).

2.2. Location of the study sites

We used three types of study sites: post-fire residual patches, post-harvest retention patches and undisturbed continuous forest stands (Table 1). Six fires i.e. three young fires (0–19 years old) and three old fires (20–40 years) were selected using the fire maps of the Ministère des Ressources Naturelles et de la Faune du Québec (MRNF). Thereafter, we selected between five to eight residual patches by fire for a total of 41 post-fire residual patches (Fig. 1). The selection of cutblocks was undertaken using eco-forestry maps and recent harvest GIS layers of three forestry companies and harvest licenses (TEMBEC UAF 085-51, and EACOM UAF 086-64 and PF Résolu PRAN 087-62). Thirteen cutblocks were studied: seven young cutblocks (0–19 years) with retention in clumps and large islands, and six old cutblocks (20–40 years) with linear

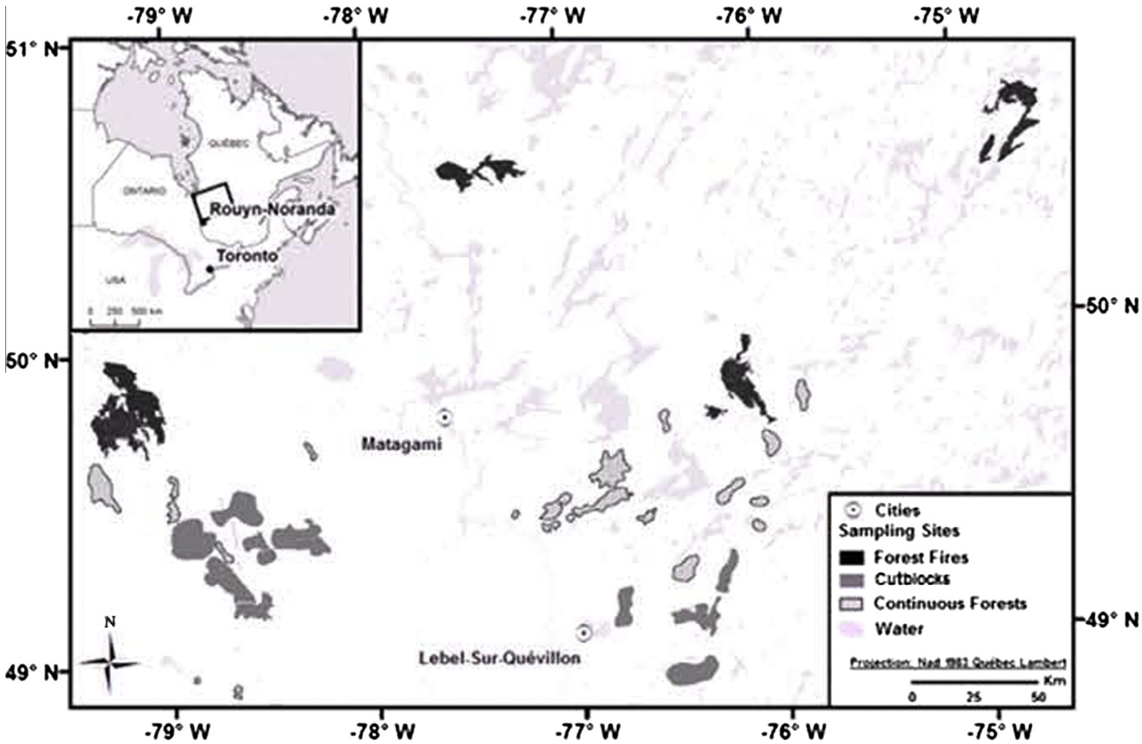

Fig. 1. Location of the study sites in the black spruce boreal forest. Post-fire residual patches located in forest fires (black); post-harvest residual patches located in cutblocks (dark gray) and the continuous forest stands are represented in pale gray surrounded in black.

separators and large islands. Three to five retention patches were selected per cutblock for a total of 47 post-harvest retention patches (Fig. 1). The residual patches were: (1) randomly selected from accessible patches (<1 km from a road) using ArcGis® mapping software based on the fire and eco-forestry maps, and recent harvest GIS layers and harvest licenses; then (2) validated in the field according to the criteria of representativeness, accessibility, presence of late successional species (*P. mariana* Mill., BSP) and absence of salvage logging in the case of fires. 37 old-growth forest stands (control), aged between 74 and 1320 years were selected (Chaieb et al., 2015) from the same landscape.

Six residual patch types were considered in the analyses based on their origin (fire or cut), their age (exposure time (EXT) to the matrix) and the retention types: (1) young clump retention patches, (2) young island retention patches, (3) old island retention patches, (4) old separator retention patches, (5) old fire residual patches, and (6) young fire residual patches (Table 1).

2.3. Data collection

Field data was collected in post-fire residual patches during the summers of 2012 and 2013 and in post-harvest retention patches during the summer of 2014. At the core of each retention or residual patch, one representative circular plot with a radius of 11.28 m (400 m^2) was established. In the young clump retentions with an area less than 400 m^2, a circular 200 m^2 plot was used to avoid edge effects.

In each circular plot, diameter at breast height (DBH) of all commercial stems of all tree species (DBH $\geqslant$ 9 cm) were measured, their species were noted, and their average height was measured with a clinometer. The DBH and the decomposition class of all snags was also measured (Fig. 2). The volume of living trees and snags (per hectare) was calculated following (Fortin et al., 2007). The line intersect method was used to sample fallen deadwood (logs) $\geqslant$5 cm in diameter by decay classes (Fig. 2) and their volume per hectare was calculated as in (Van Wagner, 1968).

Other factors that could affect the volume of recent deadwood in residual patches were measured in each plot (Table 1). The thickness of the organic layer (TOL) of each patch representing the tree anchoring substrate was determined in a soil pit dug in the center of each sample plot. Time since last fire (TSF), i.e. the age of the original forest from which the patch was formed, was estimated by coring and counting growth rings in ten individuals of the tallest cohort (Wagner, 1978). The average shape index (MSI) was calculated from the perimeter and the area of each residual patch according to (McGarigal and Marks, 1995). The perimeter and the area of each residual patch were measured by (1) tracing the exterior of the patches on foot with a handheld GPS, then (2) generating polygons from the lines generated by the GPS and (3) calculating the perimeter and area of the polygons using ARCGIs mapping software.

3. Data analyses

3.1. Estimation of deadwood abundance in residual patches

Deadwood abundance in post-fire residual patches, and post-harvest retention patches and in the continuous forest stands was characterized by recent deadwood volume (m^3 ha^{-1}), the proportion of recent deadwood (ratio of the recent deadwood volume on the initial stand volume) and old deadwood volume.

Angers et al. (2012) found that the first stages of black spruce decomposition persist typically between 5 and 15 years, i.e., the persistence of a recent deadwood of the black spruce can range from 5 to 15 years. In this study, recent deadwood volume of post-fire patches, post-harvest retention patches and continuous forest stands was estimated as the sum of recent standing deadwood volume (classes 3 and 4; Fig 2), and the recent fallen deadwood volume (classes 1 and 2; Fig 2) based on Thomas et al.'s

Table 1
Characteristics of the sampled residual patches and the continuous forest stands. All factors considered are given as mean (range): EXT, exposure time since the last disturbance (year); TSF, time since the last fire (year); MSI, mean shape index; ARP, area of residual patch (ha); TOL, thickness of the organic layer (cm); MHT, mean height of living trees (m); DBH, mean diameter at breast height (cm); ISV, initial stand volume ($m^3\ ha^{-1}$); LSV, living stand volume ($m^3\ ha^{-1}$); %RDV, proportion of the recent deadwood volume (%). The residual patch types ST are: OF, old fire; YF, young fire; OCs, old cut separator; OCi, old cut island; YCc, young cut clump; YCi, young cut island. C, continuous forest. CPRS: harvesting with the protection of regeneration and soils.

Disturbance type	Site name	EXT (an)	ST (n)	TSF (an)	MSI	ARP (ha)	TOL (cm)	MHT (m)	DBH (cm)	ISV ($m^3\ ha^{-1}$)	*ln* (ISV)	LSV ($m^3\ ha^{-1}$)	%RDV
Fire	Casa	36	OF (23)	138.1	1.3	2.78	61.39	14.36	14.86	211.6	5.24	34.2	0.11
	Chapais	37		(80–216)	(0.9–1.6)	(0.06–12.11)	(19–169)	(10–17.8)	(11–18.9)	(32.66–370.8)	(3.49–5.92)	(1.6–107.8)	(0.01–0.31)
	Lebel	30											
		27											
	Matagami	15	YF (18)	152.2	1.37	2.55	54.39	13.23	13.49	131.62	4.54	50.07	0.17
	Selbaie	16		(70–240)	(1.1–2)	(0.2–11.13)	(23–130)	(7.6–19.3)	(10.6–18.7)	(19.6–310.2)	(2.98–5.74)	(0–164.32)	(0–0.38)
	Lebel	17											
		16											
Harvest	Separator 1	24	OCs (9)	124.6	1.61	5.59	41.22	15.48	15.26	240.8	5.44	79.66	0.14
	Separator 2	21		(84–199)	(1.3–1.9)	(0.31–13.44)	(21–73)	(13.1–18.4)	(13.3–17.5)	(146.3–338.7)	(4.99–5.83)	(10.4–198.6)	(0.02–0.3)
	Separator 3	23											
	Island 1	21	OCi (9)	134.3	1.17	5.29	56.22	14.83	15.47	188.2	5.15	90.89	0.31
	Island 2	21		(97–222)	(1.1–1.3)	(3.57–7.32)	(36–75)	(9.6–18.4)	(12.7–17.8)	(106.9–382.8)	(4.67–5.95)	(10.7–245.8)	(0.05–0.9)
	Island 3	24											
	CPRS-Clump 1	5	YCc (20)	91.2	1.1	0.04	37.85	11.91	13.75	247.9	4.6	38.57	0.22
	CPRS-Clump 2	3		(71–134)	(1–1.4)	(0.2–0.7)	(18–65)	(8.7–18.2)	(10.4–23.4)	(122.1–439.8)	(3.1–6.08)	(0.7–173.1)	(0.01–0.52)
	CPRS-Clump 3	7											
	CPRS-Clump 4	4											
	CPRS-Island 1	1	YCi (9)	104.7	1.08	1.21	40	15.83	15.17	246.6	5.35	50.45	0.14
	CPRS-Island 2	2		(81–147)	(0.9–1.1)	(0.5–1.74)	(26–50)	(10.3–20.6)	(11.6–18.9)	(48.3–474.2)	(3.87–6.16)	(3.7–119.1)	(0.06–0.4)
	CPRS-Island 3	1											
Continuous forest	Control	–	C (37)	151.2	1	31.98	22.16	15.25	14.57	177.26	5.13	50.16	0.23
				(74–1320)		(10.14–360.62)	(10–60)	(11.3–18.8)	(11.1–19.8)	(89.4–292.3)	(4.49–5.68)	(1.5–190.2)	(0.02–0.64)

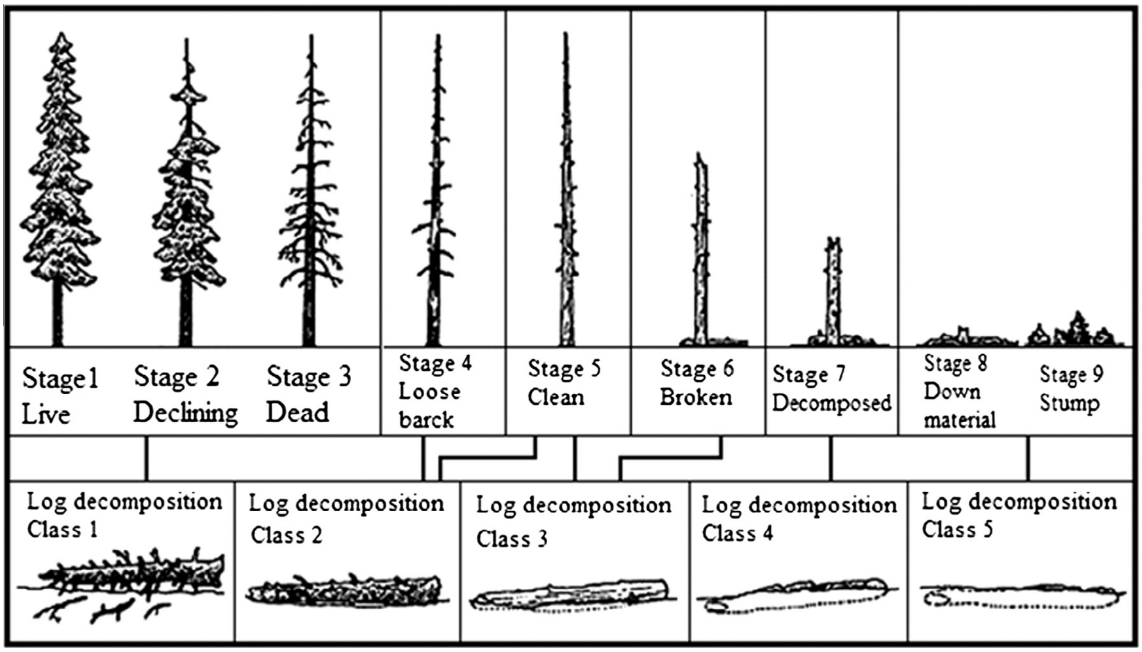

Fig. 2. Visual representation of Thomas et al.'s (1979) decay classification system for snags and logs.

(1979) decay classification system for snags and logs. Class 1 corresponds to fallen dead trees with bark still intact and having all the branches without moss or lichen, and Class 2 fallen trees with intact bark and having only a few branches (Thomas et al., 1979). Assuming an average mortality rate of 1–2% per year in the black spruce forest (Lussier et al., 2002; Bouchard et al., 2005; Aakala et al., 2006) and a potential residence time of 5–15 years for recent deadwood, we expect that a proportion of recent deadwood exceeding 5–30% of canopy volume could be indicative of loss of durability. We retain the maximum limit of 30% as a threshold over which sustainability in deadwood production is compromised or unlikely. Under this level of 30%, patch durability is not completely guaranteed but is less at risk.

The initial stand volume (ISV) at the time of the formation of each residual patch is estimated as the sum of current living volume and recent deadwood volume. The proportion of recent deadwood is estimated as the ratio of the recent deadwood volume on the initial stand volume. The old deadwood volume is the sum of standing deadwood volumes (snags) in classes 5, 6 and 7 (Fig. 2) (Thomas et al., 1979) and fallen deadwood (logs) in the last three classes of decaying woody debris on the ground (Fig. 2).

3.2. Comparison of post-fire residuals patches versus post-harvest retention patches

Differences in recent and old deadwood volume among patches of different ages and origins (i.e. the six types of residual patches) and continuous forest stands (control) were tested using single factor analysis of variance (ANOVA) by means of a mixed linear model (Pinheiro and Bates, 2000), using the software package nlme R (Pinheiro et al., 2007; RDevelopment-Core-Team, 2011). The differences in proportion of recent deadwood (ratio of the recent deadwood volume on the initial volume inherited from the original forest) between the six types of residual patches and continuous forest were tested in the same way but using logistic regression. In both cases, the location of a residual patch in a particular cutblock or fire event is considered as a random effect. The assumptions of homogeneity of variances and normality of residues were verified graphically in R.

3.3. Relationship between recent deadwood and initial stand volume

To take into account the effect of the initial stand volume on the recent deadwood volume, the recent deadwood volume in the six types of residual patches (classified according to their origin and age) and continuous forest was analyzed using an ANCOVA by means of a mixed linear model (Pinheiro and Bates, 2000), using the software package nlme R (Pinheiro et al., 2007; RDevelopment-Core-Team, 2011). The initial stand volume (cofactor) and the interaction between initial volume and residual patch type were included in the model, and the location was considered as a random effect. The assumptions of homogeneity of variances and normality of residues were verified graphically. As these assumptions were not respected

Table 2
Model selection results of the factors influencing recent deadwood volume in different residual patch types (YCc, YCi, YF, OCi, OCs, OF) and the continuous forest C, based on Akaike's information criterion (AIC). ST, residual patch type; TSF, time since the last fire (year); MSI, mean shape index; ARP, area of residual patch (ha); TOL, thickness of the organic layer (cm); MHT, mean height of living trees (m); DBH, mean diameter at breast height (cm); ISV, initial stand volume ($m^3\ ha^{-1}$). Elements in bold indicate the best models (ΔAICc < 1). *K*: number of parameters, AIC_c: Akaike's information criterion corrected for small sample sizes, ΔAIC_c: AIC_c relative to the most parsimonious model, w_i: AIC_c model weight.

Models tested	Log-likelihood	*K*	AICc	ΔAICc	w_i
1. MHT	−117.25	4	242.93	6.74	0.01
2. ISV	−118.94	4	246.30	10.11	0.00
3. ISV + TSF	−114.84	5	240.32	4.13	0.03
4. ISV + ST	−111.62	10	245.74	9.55	0.00
5. ISV + TSF + ST	**−105.58**	**11**	**236.19**	**0.00**	**0.25**
6. ISV + TSF + ST + ARP	**−104.49**	**12**	**236.62**	**0.43**	**0.20**
7. MHT + TSF + ST + ISV	**−104.62**	**12**	**236.87**	**0.68**	**0.18**
8. MHT + TSF + ST + ISV + MSI	**−103.38**	**13**	**237.05**	**0.86**	**0.16**
9. MHT + TSF + ST + ISV + DBH	−104.18	13	238.64	2.45	0.07
10. MHT + TSF + ST + ISV + DBH + MSI	−102.95	14	238.89	2.70	0.07
11. ISV + TSF + ST + MHT + MSI + ISV:ST	−97.02	19	241.66	5.47	0.02
12. ISV + TSF + ST + MHT + MSI + DBH + ARP + TOL + ISV:ST	−96.41	22	250.14	13.95	0.00

in the variable recent deadwood, it was transformed with the logarithmic transformation.

3.4. Factors influencing the abundance of recent deadwood in residual patches

In order to explain variations in recent deadwood volume observed between the residual patches (origin and age) using explanatory factors documented in the literature, eight variables ($k = 8$) were considered (Table 1). Model choice was performed using an approach based on Akaike's information criterion, corrected for small samples (Burnham and Anderson, 2002; Mazerolle, 2006). We started by checking the potential effect of each explanatory variable individually using mixed linear models (Table 1). Based on univariate models with the smallest AIC values, we subsequently built models with two variables. The best two variable models were then selected and nested in models with three variables. We repeated this procedure several times until the variables or the interactions did not improve the models, with an approach based on Akaike's information criterion (AIC) (Burnham and Anderson, 2004). It should be noted that the explanatory variables were considered independent and were only used in models when the Pearson correlation coefficient was less than 0.5. This procedure permitted us to screen twelve applicant models to identify potential factors that could affect the volumes of recent deadwood residual patches after fire and harvest (Table 2).

In the models considered, location was treated as a random effect. We verified the assumptions of normality of the residuals and homogeneity of the variances using the most complex model. We log-transformed the variable recent deadwood to normalize residuals and homogenize variances. Multiple regression models were used to estimate the statistical parameters using the maximum likelihood method (Aitchison and Silvey, 1957) with R (RDevelopment-Core-Team, 2011).

Model selection and multimodel inference were implemented in R using the AICcmodavg package (Mazerolle, 2011). Akaike weights were computed to evaluate the support of each model. When the top-ranked model had an Akaike weight <1, we used multimodel inference to compute the model-averaged estimates of the explanatory variables and 95% confidence intervals (Burnham and Anderson, 2002). Confidence intervals that excluded 0 indicated that the response variable varied with the explanatory variable of interest (Burnham and Anderson, 2002; Mazerolle, 2006).

Finally, the results of the preceding sections are integrated to generate a predictive model by projecting recent deadwood proportion on current living volume in order to make recommendations in terms of size, shape and type of forest stand that should be targeted for post-harvest retention in order to increase patch lifespan.

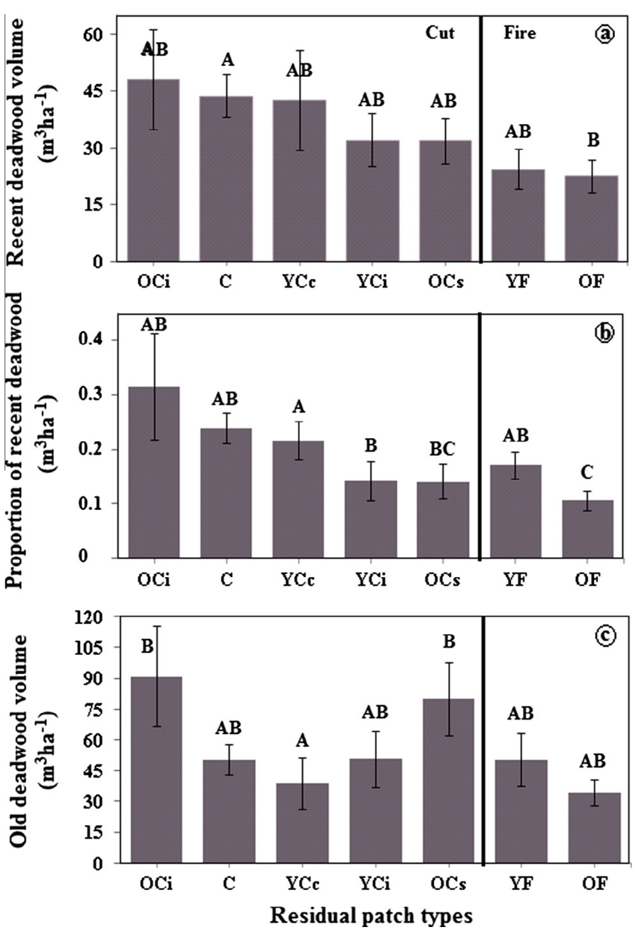

Fig. 3. Bar charts showing recent deadwood volume $m^3\ ha^{-1}$ (a), and its proportion (ratio of the recent deadwood volume on initial volume) in (b) and old deadwood volume ($m^3\ ha^{-1}$) (c) in six residual patches types and in continuous forest stands. Bar error represents the standard error. Young cut clump (YCc); young cut island (YCi) and young fire (YF): EXT: 0–19 years; old cut island (OCi), old cut separator (OCs), and old fire (OF): EXT $\geqslant$ 20 years and continuous forest (C): control. The proportion of recent deadwood volume is the ratio of the recent deadwood volume on the initial stand volume before disturbance. EXT, exposure time since the last disturbance. Letters illustrate the significantly different values among residual patches, following ANOVA and Tukey's HSD post hoc tests ($p < 0.05$).

4. Results

4.1. Abundance of deadwood after harvest and after fire

Recent deadwood volume was ordered by origin in the six types of residual patch and continuous forest (Fig. 3a) with greater volumes in harvested patches and continuous forest compared to fire patches. However, only the volumes in old fire patches and continuous forest were significantly different. Continuous forest was also characterized by less variability (Fig. 3a).

The proportion of recent deadwood (ratio of the recent deadwood volume on the initial volume) generally followed the same pattern, with a higher proportion of the recent deadwood in harvested patches, particularly old islands and young clumps (OCi; 31.4 ± 10%, YCc; 21.6 ± 3%), and continuous forest (C, 23.8 ± 3%), and a significantly lower average proportion in old fire patches (OF; 10.5 ± 2%; Fig. 3b). Young post-harvest clump patches (YCc) were also significantly different from young post-harvest island patches and old post-harvest separators. With the exception of OCi and YCi, residual patches were organized by their ages (exposure time) in terms of the proportion of recent deadwood. Young patches (YCc and YF) had a higher proportion of the recent deadwood with averages ranging from 14% to 22% while old patches (OCs and OF) had averages from 10% to 14.1% (Fig. 3b).

The volume of old deadwood was greater in old harvested island patches and old separators compared to young clump patches, and all other retention types and continuous forest stand had variable and comparable volumes of old deadwood (Fig. 3c).

4.2. Effect of initial stand volume on recent deadwood after harvest and after fire

The recent deadwood was highly positively influenced by the initial stand volume at the time of patch formation (t (113) = 3.19 ± 0.24; p-value = 0.002). Furthermore, the results of the ANCOVA of the recent deadwood volume based on both initial stand volume and patch type (origin and age class) illustrated that,

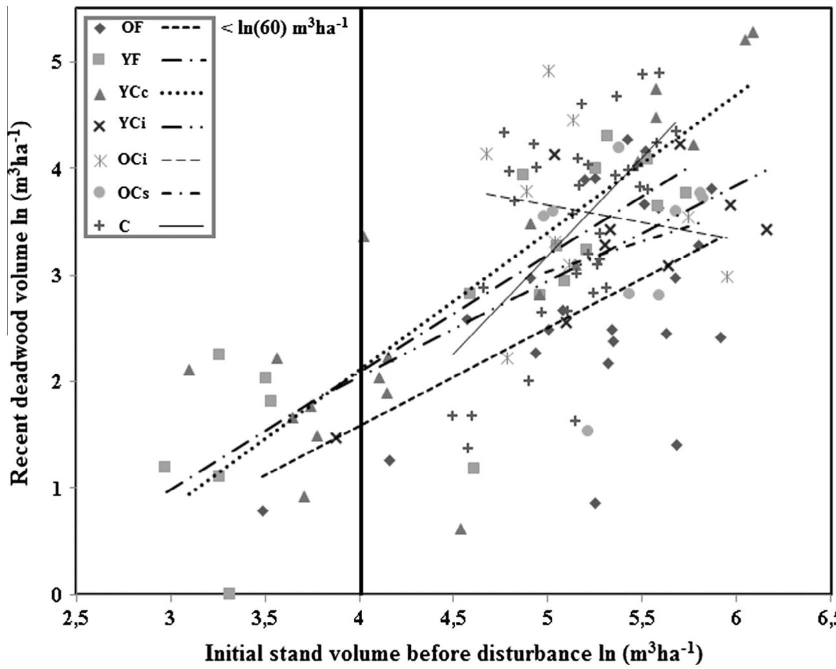

Fig. 4. Recent deadwood volume *ln* ($m^3\ ha^{-1}$) in relation to initial stand volume before disturbance *ln* ($m^3\ ha^{-1}$) on the six residual patches types and the continuous forest stands and their interaction: The seven residual patches types considered are: young cut clump (YCc); young cut island (YCi) and young fire (YF): EXT: 0–19 years; old cut island (OCi), old cut separator (OCs), and old fire (OF): EXT ⩾ 20 years and continuous forest (C): control. EXT, exposure time since last disturbance.

Table 3
Model-averaged estimates (β) of explanatory variables influencing recent deadwood volume in different residual patch types and continuous forest stands with their respective 95% unconditional confidence intervals. Elements in bold indicate that the effect of the explanatory variable on the response variable excludes 0. For acronyms see Table 1.

Parameter	Estimate (β)	Lower CI at 95%	Upper CI at 95%
Initial stand volume (ISV, $m^3\ ha^{-1}$) (+)	**0.79**	**0.24**	**1.34**
Mean diameter at breast height (DBH, cm) (+)	0.04	−0.04	0.11
Mean Shape Index (MSI)	−0.91	−2.03	0.2
Area of residual patch (ARP, ha)	−0.18	−0.42	0.16
Mean height of living trees (MHT, m)	0.07	−0.02	0.16
Time since the last fire (TSF) (+)	**0.05**	**0.02**	**0.09**
Residual patch type (ST)			
OF – Ycc	**−1.38**	**−1.99**	**−0.76**
OCi – Ycc	−0.43	−1.22	0.35
OCs – Ycc	**−0.86**	**−1.68**	**−0.04**
YF – YCc	**−0.82**	**−1.53**	**−0.11**
YCi – Ycc	**−0.82**	**−1.56**	**−0.08**
C – Ycc	−0.39	−1.29	0.5
OCi – OF	**0.94**	**0.33**	**1.56**
OCs – OF	0.51	−0.11	1.14
YCi – OF	0.56	−0.08	1.19
YF – OF	**0.55**	**0.03**	**1.08**
C – OF	**0.98**	**0.27**	**1.7**
OCi – YF	0.39	−0.28	1.06
OCs – YF	−0.04	−0.73	0.65
YCi – YF	0	−0.71	0.71
C – YF	0.43	−0.33	1.19
OCs – Oci	−0.43	−1.22	0.36
YCi – Oci	−0.39	−1.1	0.32
C – Oci	0.04	−0.57	0.66
YCi – Ocs	0.04	−0.8	0.88
C – Ocs	0.04	−0.65	0.73
C – Yci	0.43	−0.29	1.15

regardless of origin (fire or cut) and time of exposure to a disturbed matrix (age of the patch), recent deadwood volume remained low when the initial volume of the original forest was less than 60 $m^3\ ha^{-1}$ (Fig. 4). Thereafter, the recent deadwood volume increased linearly with increasing initial volume. Finally, except in case of old island retention patches (OCi), we generally observed a positive effect of initial volume on recent deadwood volume (Fig. 4). Once the effect of initial stand volume is taken into account, more recent deadwood was observed in the younger patches (YF, YCi, and YCc) than in the old patches (OCs and OF). Continuous forest (C) was found between the YCc and OCi, and was characterized by a lot of variability. Moreover, except for the youngest retentions (YCi), the relationship between recent deadwood volume and initial volume was significant in young patches with a determination coefficient R^2 of 0.85 (*p-value* = 0.001) in YCc and of 0.47 (*p-value* = 0.01) in YF but not in old patches (OF, OCi, OCs), which had with determination coefficient of R^2 below 0.06.

4.3. Factors influencing the abundance of recent deadwood in residual patches

Model selection to determine which factors explained variations in recent deadwood volume indicated that four of the twelve models (5, 6, 7 and 8) had delta AIC_c less than 2 and comparable AIC_c weights. Model 5, which included the additive effects of initial stand volume, time since the last fire and type of residual patch (ST), had the highest AICc weight (Table 2; $AIC_c = 236.19$, $w_{ic} = 0.25$), followed by model 6, which included the additional effect of area of residual patch ($AIC_c = 236.62$; $w_{ic} = 0.20$), than by model 7, which included the additive effect of mean height of living trees ($AIC_c = 236.87$; $w_{ic} = 0.18$), and finally by model 8, which included the additive effects of mean height of living trees and mean shape index of the patch ($AIC_c = 237.05$; $w_{ic} = 0.16$). As no single candidate model dominated ($w_{ic} \geqslant 0.9$; Table 2), we used multi-model inference to compute the model-averaged estimates of the explanatory variables and their 95% confidence intervals (Table 3). Multi-model inferences indicated that type of residual

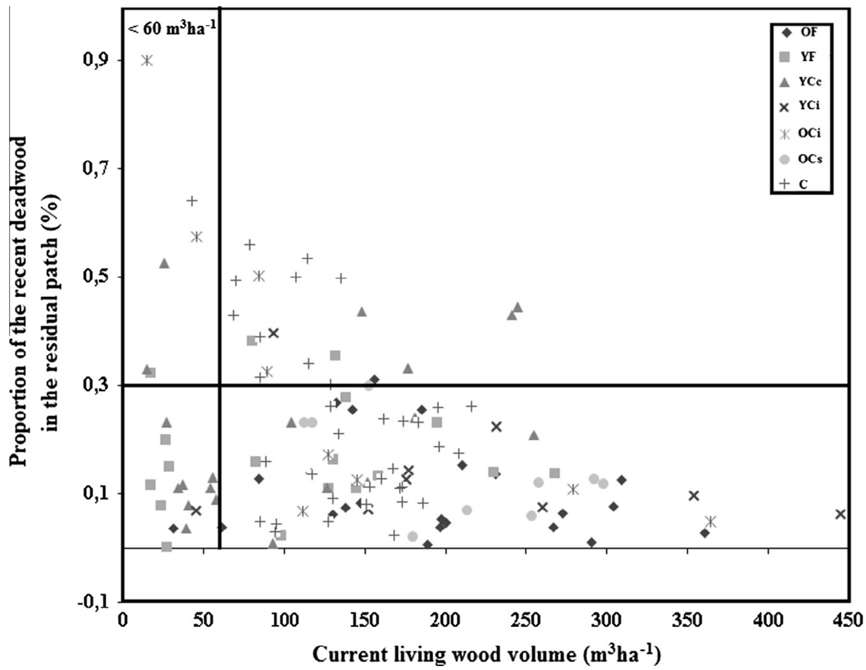

Fig. 5. Relation between the proportion of the recent deadwood volume $m^3\ ha^{-1}$ and the current living wood volume ($m^3\ ha^{-1}$) in six residual patches types and continuous forest stands. The proportion of the recent deadwood volume is the ratio of the recent deadwood volume on the initial stand volume before disturbance. Young cut clump (YCc); young cut island (YCi), and young fire (YF): EXT: 0–19 years; old cut island (OCi), old cut separator (OCs), and old fire (OF): EXT ⩾ 20 years and continuous forest (C): control.

patch (origin and age) influenced the recent abundance of deadwood after disturbance (fire or cut) with additional positive effects of initial stand volume and age of the original forest (Table 3). Generally, greater recent deadwood volume was associated with strong initial volumes ($\beta = 0.79$, $p < 0.05$, Table 3) and with the older stands ($\beta = 0.05$, $p < 0.05$; Table 3).

4.4. Recent deadwood recruitment versus temporal dynamics of residual patches

The relationship between the proportion of recent deadwood volume and current living volume in each patch was used to show two important properties of residual patches, their deadwood productivity versus their durability after fire or harvest (Fig. 5). The recent deadwood proportion in the canopy, i.e., the ratio of recent deadwood volume over initial stand volume was considered to reflect the durability of the patch (Fig. 5, *Y* axis) and the current living volume of wood was considered as the recent deadwood recruitment (Fig. 5, *X* axis). This graphic can be divided into four quadrants, formed by the 30% maximum sustainable limit of recent deadwood in canopy, and a current living volume threshold of $60\ m^3\ ha^{-1}$ suggested by the results of Section 2, which corresponds to the threshold for open black spruce stands (and for commercial volume), which are unlikely to generate significant deadwood volume. In the lower left quadrant, residual patches were stable because of their low living volume but they produced relatively little deadwood. The residual patches in the lower right quadrant appear stable as the recent deadwood proportion compared to the living volume is low, however these patches also produce significant quantities of recent deadwood. Residual patches in the upper left quadrant have a high proportion of recent deadwood compared to their living volume and they consequently are probably unsustainable. These residual patches are likely to open up and join the low living volumes patches. Finally, the residual patches occupying the upper right quadrant were likely in transition phase towards the upper left quadrant as evidenced by the large amount of deadwood on the ground (Fig. 3c).

This model illustrates that most of residual patches (post-fire and post-harvest) appear sustainable with a proportion of recent deadwood lower than the maximum 30% of the current living volume (Fig. 5). Moreover, some continuous forest stands (7 of 37) showed signs of collapse with recent deadwood proportions exceeding the 30% threshold. However, 30 of 37 continuous forests were characterized by proportion of recent deadwood lower than 30% of the living volume. Some old island retention patches OCi (3 of 9) showed also advanced signs of collapse with recent deadwood proportions beyond 30% (Fig. 5). Six of the nine old islands, however, had survived and had a similar dynamic to that of the old post-fire residual patches. Furthermore, half of young clump retention patches YCc (10 of 20) produced relatively little deadwood and characterized by low living volume, and the rest of YCc showed generally signs of collapse with recent deadwood proportion exceeding 30%.

5. Discussion

Our results support our first hypothesis that in black spruce boreal forests, post-fire residual patches have less recent deadwood than post-harvest retentions. However, this study emphasizes that regardless of the origin of the residual patch (fire or cut), the abundance of the recent deadwood in residual patches was strongly linked to the initial characteristics of the patch, i.e., that of the forest they originated from. First, we discuss the factors of the original forest that explained the variations in post-fire and post-harvest deadwood abundance observed in the studied residual patches. Secondly, we attempt to discuss the possibility of using the relative abundance of deadwood to evaluate the durability of post-disturbance patches in the black spruce boreal forest in western of Quebec.

5.1. Factors responsible for variations of abundance of post-disturbance deadwood

This study, as with others in the boreal forest, indicates that the initial conditions of forest stands influence the evolution of residual patches (Cyr et al., 2009; Smith et al., 2009; Ouarmim et al., 2014; Bolton et al., 2015). We found that regardless of their origin and age, residual patches with a high initial stand volume generated more deadwood over time. This result supports our second hypothesis that in the black spruce boreal forests of north-western Quebec, forests with greater living volume results in residual patches with a greater volume of deadwood than stands that were initially open (Ruel, 1995; Harper et al., 2005). Moreover, when the original volume is less than 60 m^3 ha^{-1} (open stands) the abundance of recent deadwood in the residual patches remains low regardless of exposure time. Nevertheless, this result is not surprising knowing that black spruce growing in open areas are generally pre-adapted to an open environment and are thus more resistant to post-disturbance mortality (Gardiner et al., 1997; Rich et al., 2007). However, a closed stand generates more recent deadwood after its unexpected exposure to the new open environment (Ruel, 1995). Having never previously been exposed to the wind, dense stands are more vulnerable to windthrow, especially in a forestry context where tree retention patches are generally characterized by abrupt edges surrounded by a completely open environment (Ruel, 1995; Lecomte et al., 2006). In addition, this can be due to the structural type of residual patches or continuous forest. Small trees in irregular stands that grown in more open conditions can reduce the wind weight applied on dominant trees by dissipating part of the wind energy (Gardiner et al., 2005).

Our analyzes also confirm the hypothesis anticipating the positive effect of age of the original forest (TSF) on the abundance of recent deadwood (Bouchard et al., 2009; Cyr et al., 2009). This is in contrast with other studies that revealed the opposite relationship, i.e., a greater susceptibility of younger regular stands to windthrow compared with older irregular forest stands, which are generally characterized by a more open structure (Ruel, 1995; Rich et al., 2007; Lavoie et al., 2012). Deadwood recruitment dynamics are generally believed to follow the form of a U (Harmon et al., 1986) with greater recruitment of deadwood immediately after fire, which then decreases over time until it increases again in old forests. In our case, the low and positive effect of TSF on the abundance of deadwood in the studied residual patches may simply be due to the gradual opening of the original forest over time due to secondary disturbances (Kneeshaw, 2001; McCarthy, 2001; Kneeshaw et al., 2011).

Mean diameter at breast height and mean height of living trees were not significant factors explaining the abundance of recent deadwood in the residual patches even though these two variables are often identified as important factors for explaining mortality at the tree scale (Jönsson et al., 2007; Rich et al., 2007). This inconsistency of our results with previous studies is probably due to the low range of variation in the mean diameter and height of living trees measured in this study (Table 1).

At the residual patch scale, although models that integrate the variables residual patch area and mean shape index (Table 2) were selected by the model comparison procedure, these two factors were not significant when the confidence intervals were examined (Table 3). The absence of effect of area and shape may result from an interaction with the exposure time. For instance, linear separators that accumulate less recent deadwood are old (EXP > 20 years) and clump retentions that accumulate high proportion of deadwood are young. Moreover, among the smaller post-harvest retention patches included, those in the clump retention patches YCc (EXT between 3 and 7 years) were older than the island retention patches YCi (EXT $\leqslant$ 2 years). Therefore, the young island patches could not accumulate as much deadwood as the clump retention patches because they have had almost no exposure time since the last disturbance.

5.2. Recruitment dynamics of deadwood and patch temporal dynamics

This study shows that post-fire residual patches appear in general more durable than post-harvest retention patches after disturbance. This could be related to the type of buffer zone surrounding the residual patches left after the passage of fire. Post-fire residual patches are usually surrounded by a buffer zone in which the fire severity is slowed, because of the site characteristics including fuel quality, topography and soil moisture (Hély et al., 2000; Cyr et al., 2007). Post-fire patches can be preserved for millennia, burning only during particularly severe fires (Ouarmim et al., 2015). In contrast, as harvest is systematic it often creates sharp edges between open and closed areas, potentially explaining the higher abundance of deadwood in post-harvest retentions compared to post-fire patches. In addition, as the post-fire residual patches and post-harvest retention patches were sampled in consecutive years, a windthrow event occurring during the sampling period could have influenced the results. So, the retention patches sampled more recently would have been affected and not the residual post-fire patches that were sampled one or two years before.

As in this study, high residual tree mortality in the first years after disturbance has been documented elsewhere in similar stand types in both managed (Hautala and Vanha-Majamaa, 2006; Lavoie et al., 2012; Urgenson et al., 2013) and natural contexts (Heikkala et al., 2014). Initial high mortality may be due to both the active recruitment of dead stems in the first five years after disturbance (Mascarúa López et al., 2006), and the fact that the remaining trees in the older patches were probably more resistant to wind (Busby et al., 2006). Moreover, given that the recent deadwood compartment has a lifespan of five to fifteen years (Angers et al., 2012), deadwood that fell immediately after the disturbance is probably no longer in the "recent" decomposition stage.

Nevertheless, in a management context, initial high mortality may be also due to the type retention, i.e., small clump, big island, and large linear separator. Old island retention patches OCi seem to continue to accumulate mortality and deadwood over time, particularly compared to old separator patches OCs that accumulate less recent deadwood. This higher recent deadwood accumulation of OCi can be due to a severe wind event occurring during the sampling period in some island patches. However, the lower proportion of recent deadwood observed in older linear retentions OCs, and the fact that they tend to have a high volume of old deadwood can be explained by both the active recruitment of deadwood during the first five years following their creation (Scott and Mitchell, 2005; Hautala and Vanha-Majamaa, 2006; Lavoie et al., 2012; Urgenson et al., 2013), and their spatial orientation (DeWalle, 1983; Ruel, 1995). The east–west orientation of the old separator patches in the cutblocks studied likely ensured that the dominant western winds did not strike the edge.

6. Conclusions and implications for forestry and conservation biology

This study displays that most post-fire residual patches produce deadwood in significant quantity and without jeopardizing their existence until the surrounding disturbed forest regenerates. In a management context, the deadwood dynamics of post-harvest remnant patches is a key element that could determine the success or failure of forestry retentions (Thorpe et al., 2008). Our results show that in managed black spruce forest, large island patches and large linear separators oriented to escape windthrow usually have a deadwood recruitment dynamics similar to those of post-fire residual patches, and when their initial stand volume is more important than the merchant commercial volume (>60 m^3/ha) they engender a significant but sustainable deadwood supply. This suggests that the selection of large retention patches in the shape of an island or a separator, with high (between 60 and 300 m^3/ha) volume should help increase the post-harvest lifespan of retention patches in black spruce forest, and simultaneously ensure quality habitat (deadwood, large trees) for several forest species while the adjacent harvested forest regenerates. The implementation of this recommendation by forest managers will allow a more sustainable management in the boreal black spruce forest. The value of this study is based partly on the fact that we evaluated and compared abundance of deadwood in post-harvest retentions with that in post-fire patches and continuous forests, and also on the presence of replicates. However, it will be important to also determine if post-harvest retention patches have structural characteristics similar to that of post-fire residual patches both in their core and edge in order to support the present results.

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