Long-term snag and downed woody debris dynamics under periodic surface fire, fire suppression, and shelterwood management

Mark C. Vanderwel, Jay R. Malcolm, and Sandy M. Smith

Abstract: There are pronounced differences in the processes that act to determine the type and amount of standing and downed coarse woody debris present under partial harvesting versus other noncatastrophic disturbances. To evaluate long-term differences in snag and downed woody debris (DWD) dynamics, we developed a simulation model to project snag density and DWD volume by size and decay class in white pine (*Pinus strobus* L.) and red pine (*Pinus resinosa* Ait.) dominated stands under (*i*) a high-retention shelterwood system, (*ii*) periodic surface fire, and (*iii*) fire suppression. Snag densities under a high-retention shelterwood system were consistently lower than those in the fire-suppression and surface-fire scenarios, even if no large snags were felled at the time of harvest. Regular inputs from harvest residues were important in maintaining the total volume of DWD, but this material tended to be concentrated in a narrow range of decay classes at any given time. Preserving existing DWD at harvest was less influential than the level of inputs from harvest residues. Active measures for snag creation and staggering of harvest stages among adjacent stands may help minimize differences in the overall supply and temporal variation of coarse woody debris between managed and both naturally disturbed and old-growth stands.

Résumé : Il y a des différences prononcées entre les processus qui jouent un rôle dans la détermination du type et de la quantité de débris ligneux grossiers sur pied et au sol à la suite de coupes partielles par opposition à d'autres perturbations non catastrophiques. Pour évaluer les différences à long terme de la dynamique des chicots et des débris ligneux au sol (DLS), nous avons mis au point un modèle de simulation pour prédire la densité des chicots et le volume de DLS par classes de taille et de décomposition dans des peuplements dominés par les pins blanc et rouge (*Pinus strobus* L. et *Pinus resinosa* Ait.) et soumis à (*i*) un système de coupe progressive à forte rétention, (*ii*) des feux de surface périodiques et (*iii*) un programme de lutte contre le feu. Avec un système de coupe progressive à forte rétention, la densité des chicots était invariablement plus faible que celles associées aux scénarios de feux de surface ou de lutte contre le feu, même si aucun gros chicot n'a été abattu lors de la coupe. Les apports réguliers de résidus de coupe étaient importants pour maintenir le volume total de DLS, mais ce matériel avait tendance à être concentré dans un nombre réduit de classes de décomposition. La préservation des DLS présents au moment de la coupe avait moins d'impact que les apports de DLS provenant des résidus de coupe. Des mesures actives de création de chicots et d'étalement des stades de coupe entre peuplements adjacents pourraient aider à minimiser les différences de quantité totale et de variation temporelle entre les débris ligneux grossiers des forêts aménagées et ceux des vieilles forêts ou des forêts naturellement perturbées.

[Traduit par la Rédaction]

Introduction

In recent years, proponents of ecosystem-based forest management have advocated that managed stands should retain elements of complex stand structure, including live residual trees, dead wood legacies, and advanced regeneration (Franklin et al. 2002; Lindenmayer et al. 2006). These features may benefit species by acting as "lifeboat" habitats that maintain a semblance of mature stand conditions through time (Franklin et al. 1997) and by emulating the array of structural elements that persist after natural disturbances (OMNR 2001). However, timber harvesting differs from natural disturbances in many important respects, including the type and amount of standing and downed coarse woody debris (CWD) present following disturbance and during subsequent stand development (Niemelä 1999; McRae et al. 2001; Brassard and Chen 2006). Therefore, in assessing the effects of ecosystem-based forest management on wildlife and biodiversity values, it is important to consider the degree to which structures such as CWD differ among managed, naturally disturbed, and old-growth stands.

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Disturbance in pine stands

In Ontario, Canada, exploitative harvesting practices in the late 18th and 19th centuries have reduced the present abundance and distribution of white pine in many areas of the province (Thompson et al. 2006). Today, stands dominated by white (*Pinus strobus* L.) and red pine (*Pinus resinosa* Ait.) are managed under a high-retention uniform shelterwood system designed for successful white pine regeneration and establishment (Corlett 2004). This silvicultural system consists of four sequential management stages:

(*i*) a preparatory cut, which promotes pine crown expansion and seed production; (*ii*) a regeneration cut, which produces appropriate light levels and seedbed conditions for seedling establishment; (*iii*) a first-removal cut, which releases understorey regeneration while providing partial shade to reduce damage from the white pine weevil (*Pissodes strobi* (Peck)) and white pine blister rust (*Cronartium ribicola* J.C. Fisch.); and (*iv*) a final-removal cut, which removes the majority of remaining overstorey trees. By removing the canopy in an extended series of harvests, this silvicultural system maintains continuous overstorey cover throughout the harvest rotation.

Historically, fire has been the dominant natural disturbance agent in white and red pine forests of central Ontario's Great Lakes – St. Lawrence region. Light- to moderate-intensity surface fires are believed to have occurred every 20–40 years on fresh to dry sites, with fires capable of killing mature trees occurring at 100–200 year intervals (Heinselman 1981). Regular noncatastrophic fire disturbances are considered important to the successful regeneration of white and red pine because they create appropriate seedbed conditions for germination and limit competitive understorey vegetation (Kershaw 1993). Shelterwood management of pine-dominated stands seeks to emulate the conditions created by periodic high-intensity surface fires and, thereby, provide regeneration and habitat conditions comparable with those experienced under natural disturbances.

Aggressive fire suppression activities over the past century are believed to be responsible for a present scarcity of young white and red pine stands in Ontario (Chapeskie et al. 1989; Burgess et al. 1999). Over time, fire-management policies that lengthen the fire rotation are expected to increase the proportion of overmature and old-growth habitat across the landscape. In contrast, shelterwood management truncates the age of white and red pine stands at the length of the harvest rotation and, thereby, prevents development into an old-growth condition (although some old-growth features, such as veteran and cavity trees, are retained in managed stands). However, if this management system can maintain stand structural attributes at levels comparable with those in undisturbed stands, then loss of old-growth features may not be of concern.

Forest-management activities can have a strong influence on CWD accumulations through the removal, redistribution, and destruction of CWD during harvesting (Maser and Trappe 1984), the addition of new material from harvest residues (Fraver et al. 2002), and long-term reductions in input rate as a result of the removal of live trees (Fiedler and Morgan 2002). Although forest management guidelines are designed to mitigate negative management impacts on CWD (e.g., Naylor 1998), it is uncertain to what degree the quality and quantity of CWD in pine stands managed under a high-retention shelterwood system might differ from that in stands experiencing fire disturbances or stands in which fire is suppressed.

CWD modelling

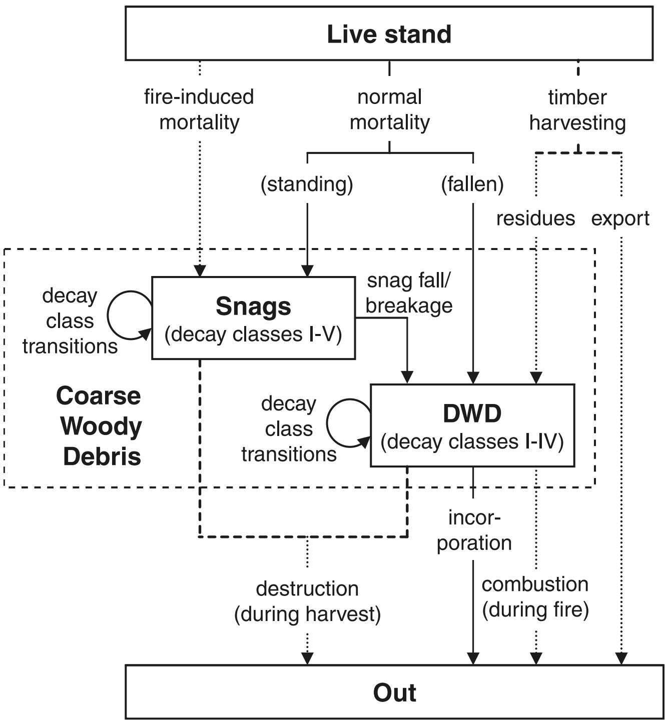
Simulation modelling is a powerful tool for investigating the long-term dynamics of CWD pools. Temporal patterns of CWD development are determined by the amount of material created and removed by disturbance, the timing of inputs from live tree mortality, and rates of CWD decomposition (Harmon et al. 1986). Early efforts adopted this process-based framework to model the long-term accumulation of CWD after fires of varying intensity (Spies et al. 1988), and after multiple rotations of clear-cut management (Spies and Cline 1988) in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests. More recently, modellers have represented different qualities of woody debris by partitioning CWD among different size and decay classes (e.g., Ranius et al. 2003; Montes and Cañellas 2006). In addition, recent CWD models have been linked to relatively sophisticated forest growth and mortality models (e.g., Wilhere 2003; Ranius et al. 2005) and have considered the effects of more elaborate management practices (Ranius and Kindvall 2004; Montes and Cañellas 2006). These innovations are well suited to investigating CWD dynamics under partial harvesting systems, such as the uniform shelterwood system, in which the live stand is expected to generate CWD throughout the rotation period.

In this paper, we developed a model of CWD dynamics that projects future accumulations of snags and downed woody debris (DWD) within specific size and decay classes over all stages of a shelterwood harvest rotation. The abundances of specific CWD resources under shelterwood management were compared with those under two alternative scenarios: one in which fire suppression allowed stands to develop in the absence of disturbance and a second in which stands were subjected to a regime of periodic light surface fires and a single intense fire. Our specific objectives were to (*i*) explore the main patterns of CWD accumulation under various noncatastrophic disturbance regimes, (*ii*) assess the expected availability of specific types of CWD at various stages of a high-retention shelterwood system relative to that in undisturbed and naturally disturbed stands, and (*iii*) evaluate the importance of hypothetically modified silvicultural practices that would vary the abundance of snags and DWD left after harvesting. These objectives were focused around the central question: how well can a high-retention shelterwood system approximate the type and amount of CWD that arises under fire-disturbance processes and in old-growth stands that escape major disturbance events?

Methods

We developed a computer model (written in the C programming language) to simulate long-term changes in the quality and quantity of CWD under fire-suppression, surface-fire, and shelterwood disturbance scenarios. Over a 200 year horizon, our simulation model calculated changes in CWD supplies at 5 year intervals through inputs from tree mortality, transitions among various states of decomposition, outputs due to advanced decomposition, and periodic impacts of fire or harvesting (Fig. 1). We used an existing distance-independent, individual tree-level growth model to simulate live-stand dynamics in each scenario; tree mortality (both autogenic and fire induced) and harvesting output from each 5 year time step were then processed as sources of CWD inputs by our model. Final output variables generated from the CWD simulations were the density of snags and volume of DWD by decay

Fig. 1. Schematic representation of the model of coarse woody debris (CWD) dynamics developed to simulate patterns of CWD accumulation. Solid lines show natural mortality and decomposition processes; broken lines show the impacts of fire and timber harvesting.



class and size class. A detailed description of individual model components follows.

Scenario descriptions

Starting conditions for model runs were based on species- and size-specific tree densities, snag densities, and DWD volumes in five pine-dominated sites in Algonquin Park, Ontario (45°53′N, 77°44′W; Table 1). In addition to white and red pine, these stands contained aspen (*Populus tremuloides* Michx. and *Populus grandidentata* Michx.), red maple (*Acer rubrum* L.), balsam fir (*Abies balsamea* (L.) Mill.), and spruce (*Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) BSP), as well as other minor species that were discarded. These sites all represented mature stands that were allocated for shelterwood management. In our simulations, we used the data from each site as an independent starting condition and averaged model output across the five replicates.

Our fire-suppression scenario allowed mature stands that were initially approximately 100 years of age to develop into an old-growth condition in the absence of major disturbances. This scenario examined CWD levels under autogenic processes alone. Succession to more shade-tolerant species gradually unfolded over the course of the simulation in this scenario.

The surface-fire scenario simulated a natural disturbance regime characterized by frequent light surface fires and an occasional intense fire. Light fires occurred at 30 year intervals, and an intense fire that initiated a new pine cohort occurred midway through the simulation (year 105). This scenario represented CWD dynamics under an idealized presettlement disturbance regime for white and red pine stands on fresh to dry sites (Heinselman 1981).

In the shelterwood scenario, stands were considered to be at the regeneration cut stage initially and were first harvested at year 5. First- and final-removal cuts were carried out at years 25 and 45, respectively. The second rotation began with a preparatory cut in year 85 followed by regeneration, first-removal, and final-removal cuts in years 105, 125, and 145, respectively. A second preparatory cut was carried out at year 185.

The 200 year time frame over which these simulations were run was long enough to capture processes of interest in this stand type but short enough to prevent nonpine species from dominating the canopy in the absence of disturbance (Martin 1959). The simulation period was well in excess of the interval between fire disturbances and spanned two complete shelterwood rotations. Decomposition times for CWD were ≤65 years (Vanderwel et al. 2006*a*; see below), so we were able follow many different cohorts of CWD from the time of tree mortality until pieces eventually left the system through decomposition. Periodic disturbances in the surface-fire and shelterwood scenarios led to convergence from different starting conditions before the end of the simulations, although there was still some variability among replicates after 200 years in the fire-suppression scenario.

Live-stand dynamics

We used the Lake States variant of the forest vegetation simulator (Dixon 2007; USDA Forest Service 2007) to simulate live-stand dynamics in each scenario, including processes of tree growth, mortality, regeneration, fire, and harvesting (Table 2). The regional form of this live-stand model was calibrated for forest conditions in Michigan, Wisconsin, and Minnesota. Although the growth and mortality equations embedded in it may not be strictly applicable to Ontario's Great Lakes – St. Lawrence region (Lacerte et al. 2004), we deemed it to provide acceptable performance for our purposes of generating CWD inputs.

CWD decomposition

All trees that died from nonfire mortality were divided among standing and fallen modes of death using treefall models presented by Vanderwel et al. (2006*a*, 2006*b*). Approximately 10%–20% of trees were expected to fall immediately upon death. New inputs of standing dead trees were distributed among five initial snag decay classes, then in subsequent years allowed to undergo transitions to later decay classes or to fall and become DWD. Snag decay class distribution after tree death, decay class transition rates, and fall rates were all derived from published snag decomposition models (Garber et al. 2005; Vanderwel et al. 2006*a*, 2006*b*). Fallen dead trees progressed through four DWD decay classes over time using decay class transition models for pine (Vanderwel et al. 2006*a*) and tolerant hardwood species (Vanderwel et al. 2008). Transitions for aspen and balsam fir DWD were modelled by the approach described in Vanderwel et al. (2006*a*) using data collected in northeastern Ontario (M. Vanderwel, unpublished data). Using these decomposition models, the ranges of half-lives for snags and

Table 1. Characteristics of pine-dominated stands in Algonquin Park, Ontario, used to parameterize initial conditions in simulation runs.

Stand No.	Age (years)*	Area (ha)	Basal area (m^2/ha)	Species composition (%)†	Snag density (no./ha)	Snag decay class‡	DWD volume (m^3/ha)§	DWD decay class‡
1	104	51	31	Pr, 53; Pw, 42	34	2.9±1.5	22	3.0±0.7
2	124	32	24	Pw, 67; Sb, 7; Al, 7	27	3.9±1.1	39	2.8±1.0
3	96	31	26	Pw, 44; At, 25; Pr, 12; Sb, 10	29	3.2±1.3	43	2.9±0.7
4	96	49	31	Pw, 65; Pr, 12; Mr, 12; Sb, 9	9	3.4±1.2	42	3.1±0.9
5	108	37	34	Pw, 66; Mr, 9; Pr, 6; Al, 5	64	3.5±1.3	24	3.0±0.9
Mean	106	40	29	Pw, 57; Pr, 18; Sb, 6; At, 5; Mr, 5	33	3.5±1.3	34	2.9±0.9

Note: DWD, downed woody debris.

*Obtained from provincial forest resource inventory (Ontario Ministry of Natural Resources, Toronto, Ont., unpublished data).

†Values are percent compositions for species comprising ≥5% of total basal area. Pr, red pine; Pw, white pine; Sb, black spruce; Al, large-toothed aspen; At, trembling aspen; Mr, red maple.

‡Values are means ± SDs.

§Total volume for decay classes 1–4.

Table 2. Description and rationale for parameters governing live-stand dynamics in the Forest Vegetation Simulator (FVS) model.

Process	Description	Rationale
Growth	Calibrated for site index of 12.4 m at age 50 years	Corresponds to moderate site productivity (Plonski 1981)
Mortality	Derived from FVS, subject to a lower bound of 0.5%/year	Approximate minimum mortality rate across temperate forests (Runkle 1985)
Regeneration	Density set through trial and error to ensure full stocking upon reaching 8 cm diameter at breast height (DBH); equivalent 200 year rates among all scenarios	Maintain ingrowth of new stems, while accounting for disturbance-related differences in timing and composition of regeneration
	Fire suppression: continuous regeneration of balsam fir, red maple, and white spruce in absence of disturbance	More shade-tolerant species; white and red pine are unable to establish without disturbance (Burgess et al. 2005)
	Surface fire: pulse of red and white pine regeneration following intense fire; no regeneration at other times	Nonfire-adapted species presumed killed by regular surface fires (Kershaw 1993)
	Shelterwood: pulse of white pine following regeneration cut; continuous regeneration of balsam fir, red maple, and white spruce at 50% of their level in the fire-suppression scenario	Light levels too low for red pine establishment (Kershaw 1993); other species impeded by white pine regeneration
Fire	Light fires kill some polewood-size trees (HSB* = 1.2 m), intense fire kills most trees <50 cm DBH (HSB = 14 m); all fire-killed trees become snags	Logistic regression model for fire mortality applied to all species (Beverly and Martell 2003)
Harvesting	Preparatory cuts: thin from below to 350 stems/ha	Silvicultural prescriptions (Corlett 2004) and retention guidelines (Naylor et al. 2004) for white pine uniform shelterwood system in Ontario
	Regeneration cuts: uniform removal of stems ≥25 cm DBH to basal area of 13 m^2/ha	Preferential removal of nonpine species at all stages
	First-removal cuts: uniform removal of 60% of all stems ≥15 cm DBH	
	Final-removal cuts: removed all stems ≥12 cm DBH, except for the 16.25 largest trees/ha	

*HSB, height of stem blackening in Beverly and Martell (2003) logistic regression model.

DWD among species were 8–30 and 13–34 years, respectively. The CWD left the system either through decomposition out of DWD decay class 4 or through combustion or destruction during a disturbance event.

Snags created as a result of fire have been found to fall at a faster rate than snags created from other agents of mortality. In our model, fall rates for burned snags were multiplied by decay class specific ratios derived from Morrison and Raphael's (1993) comparison of snag fall rates in burned and unburned plots. Fire-created snags fell 36%–135% faster than other snags using this increase in fall rates. After falling, these pieces subsequently decomposed at the same rate as other DWD.

Disturbance impacts

Combustion of existing DWD during surface fires was based on fuel consumption guidelines in jack pine (*Pinus banksiana* Lamb.) mixedwood slash (McRae 1980). This model predicts the consumption of DWD ≥7 cm diameter as a function of a fuel moisture index, which is a determinant of fire intensity. Differences in consumption rates among decay classes and sizes classes ≥7 cm were not considered. In accordance with this model, we removed 30% and 37% of all existing DWD following light and intense surface fires, respectively.

Harvesting activities both destroy existing DWD and create an influx of new material from logging slash. Existing DWD in advanced decay classes (3 and 4) has the greatest likelihood of being damaged or destroyed during harvesting, whereas that added as slash tends to be small in diameter and in sound condition (decay classes 1 and 2). Morneault et al. (2004) have reported the volume of DWD by size and decay class before and after shelterwood harvesting and site preparation in central Ontario. We estimated the amount of DWD that would be created and destroyed by harvesting, both with mechanical scarification (as would follow a regen-

Table 3. Effects of harvesting on snag density and downed woody debris (DWD) volume in the standard shelterwood scenario and two modified variants ("low" and "high" impacts).

	Standard	Low impacts	High impacts
Max. snag density following harvesting (no./ha)	15	No maximum	0
Max. DWD volume added by harvesting in regeneration cuts (m³/ha)			
Small*	14	13	15
Large†	3	2	3
Max. DWD volume added by harvesting in all other cuts (m³/ha)			
Small	26	12	40
Large	17	8	26
Class 3 or 4 DWD removed by harvesting (%)			
Regeneration cuts	30	9	51
All other cuts	24	0	71

*7.5–29.9 cm diameter.
†≥30 cm diameter.

eration cut) and without scarification (all other cuts) from their results (Table 3).

Recently harvested stands typically have fewer snags than unharvested stands because many snags are felled to comply with health and safety legislation (Naylor 1998). Field measurements indicate that stands that have received a shelterwood harvest within the past 3 years had a mean of 15 snags/ha ≥7.5 cm DBH in Algonquin Park (M. Vanderwel, unpublished data, 2003). Accordingly, if the density was >15 snags/ha prior to a harvest in our simulations, we reduced it to this level after harvesting.

Variations in harvest impacts

Parameters representing immediate harvest impacts were varied systematically to investigate long-term effects of practices that could potentially mitigate, or amplify, impacts on CWD. Removals and additions of DWD at harvest were separately varied from one standard deviation below the mean to one standard deviation above the mean (Table 3). These differences were considered to reflect the magnitude of variation in early and late decay class DWD reported by Morneault et al. (2004). The effects of retaining large (≥30 cm DBH) snags were also considered by running simulations in which no large snags were knocked down during harvesting and in which all large snags were felled (Table 3). It is unlikely that, in practice, all large snags could be retained during harvesting; however, this case served to delimit the potential range of measures for snag conservation at the time of harvesting.

Model evaluation

We evaluated our simulation model by comparing projected accumulations of CWD under shelterwood management with those observed in managed pine-dominated sites in Algonquin Park. Snags and DWD were sampled in seven sites harvested 8–16 years earlier, five sites harvested 17–25 years earlier, and nine sites that had not received a shelterwood harvest in the past 28 years (hereafter, "unharvested"). Harvested sites had most recently received a regeneration or first-removal cut, but all sites, including those classified as unharvested, had historically been subjected to strip cut or selective harvesting.

The CWD was sampled at each site within a circular area 78.5 ha in size. Sampling was carried out at each of 10–13 sampling points within this area using four variable-area plots (basal area factor 2) for snags and three 30 m line-intersect transects for DWD. Total snag density and decay class specific DWD volume were averaged across these points to obtain site-level estimates of CWD abundance. Differences in the amount of each type of CWD among the three groups of sites were analyzed by use of Kruskal–Wallis tests. Where the null hypothesis of equal group means was rejected, pairwise differences in group means were tested using Wilcoxon rank-sum tests, adjusting the familywise error rate ($\alpha = 0.05$) for multiple testing with a sequential Bonferroni correction (Quinn and Keough 2002).

Results

Live trees

With the stand growth model that we used, stands grew to a basal area of about 47 m^2/ha and remained at this level in the absence of disturbance (Fig. 2*a*). Low-intensity surface fires had very small impacts on basal area, but a more intense fire killed virtually all small-diameter trees and reduced basal area by approximately 40% (Fig. 2*b*). Under shelterwood management, basal area oscillated from lows of approximately 8 m^2/ha following first- and final-removal cuts to highs of approximately 37 m^2/ha prior to preparatory and regeneration cuts (Fig. 2*c*).

At the end of each of the 200 year simulations, species composition was 49% white pine and 7% red pine in the fire-suppression scenario (44% other species), 69% white pine and 16% red pine in the surface-fire scenario (14% other species), and 99% white pine in the shelterwood scenario (1% other species).

Snags

In the first 100 years of the fire-suppression scenario, large-diameter snag density steadily increased, whereas small-diameter snag density fluctuated (Fig. 3*a*). The density of both large and small snags declined gradually thereafter but remained above their initial levels by the end of the simulation.

Surface fires acted to create high snag densities in the short term, but these fire-origin snags tended to fall within a 10–15 year period (Fig. 3*b*). At most other times, snag densities were lower than in the fire-suppression scenario. Near the end of this simulation, very high snag densities resulted from nonfire- and fire-induced mortality within the regeneration cohort that originated from the intense fire at year 105. Large snag densities were not strongly affected by low-intensity fires but reached a sharp peak immediately following the intense fire.

During the period between preparatory and final-removal cut stages of shelterwood management, snag densities were well below levels found in the fire-suppression and surface-fire scenarios (Fig. 3*c*). Snag density increased steadily after final-removal cuts, then was sharply reduced by a preparatory cut 40 years afterward. Large snag densities were sub-

Fig. 2. Mean live basal area by diameter at breast height class over the 200 year simulation period for the (*a*) fire-suppression, (*b*) surface-fire, and (*c*) shelterwood-management scenarios. In Figs. 2*b* and 2*c*, the vertical lines show the disturbance events: LowFire, light surface fire; IntFire, intense surface fire; Reg, regeneration cut; 1stRem, first-removal cut; FRem, final-removal cut; Prep, preparatory cut.

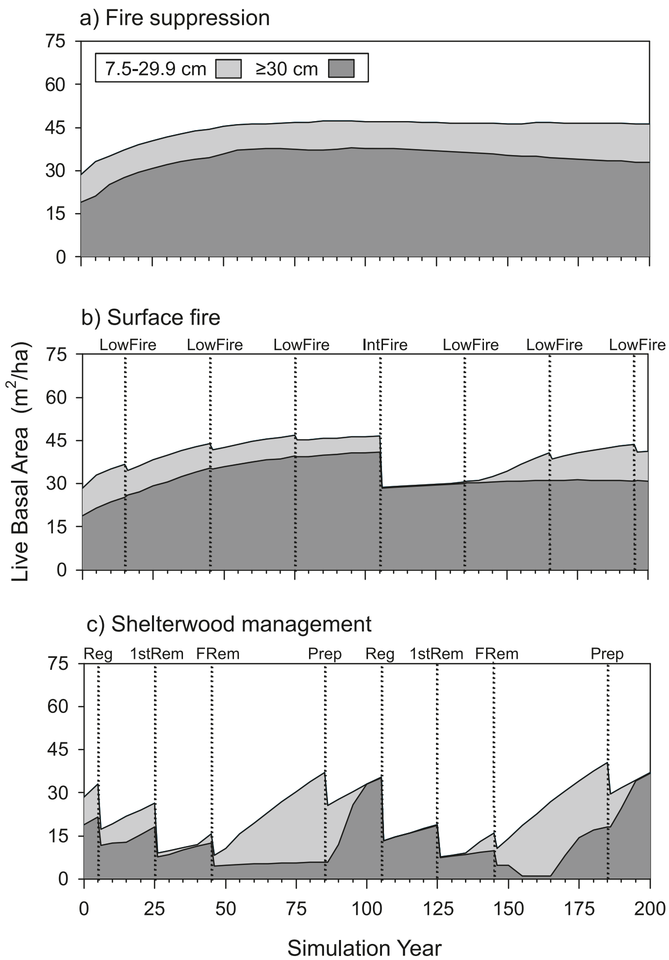
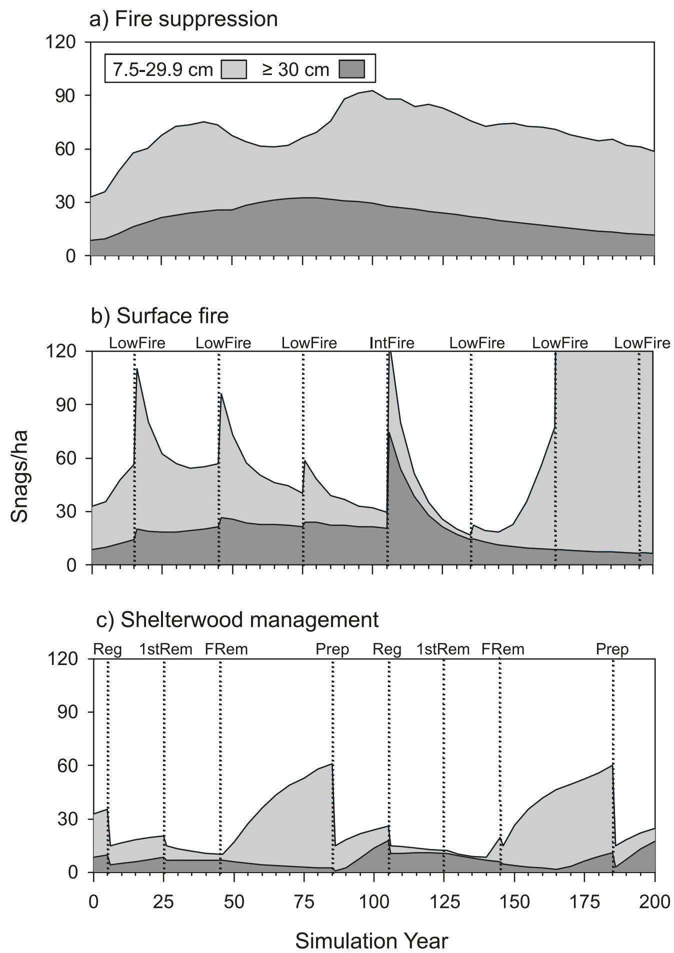


Fig. 3. Mean snag density by diameter at breast height class over the 200 year simulation period for the (*a*) fire-suppression, (*b*) surface-fire, and (*c*) shelterwood-management scenarios. Snag density in the surface-fire scenario reached a peak of 171 snags/ha in year 165, fell gradually to 122 snags/ha, and peaked at 235 snags/ha in year 195. Vertical lines show the disturbance events. See Fig. 2 for abbreviations.



stantially lower than those observed in the fire-suppression and surface-fire scenarios.

Downed woody debris

In the absence of disturbance, DWD volume increased slowly over the first 100 years of the simulation period, then steadied (Fig. 4*a*). Relatively little material (as measured by volume) was <30 cm in diameter.

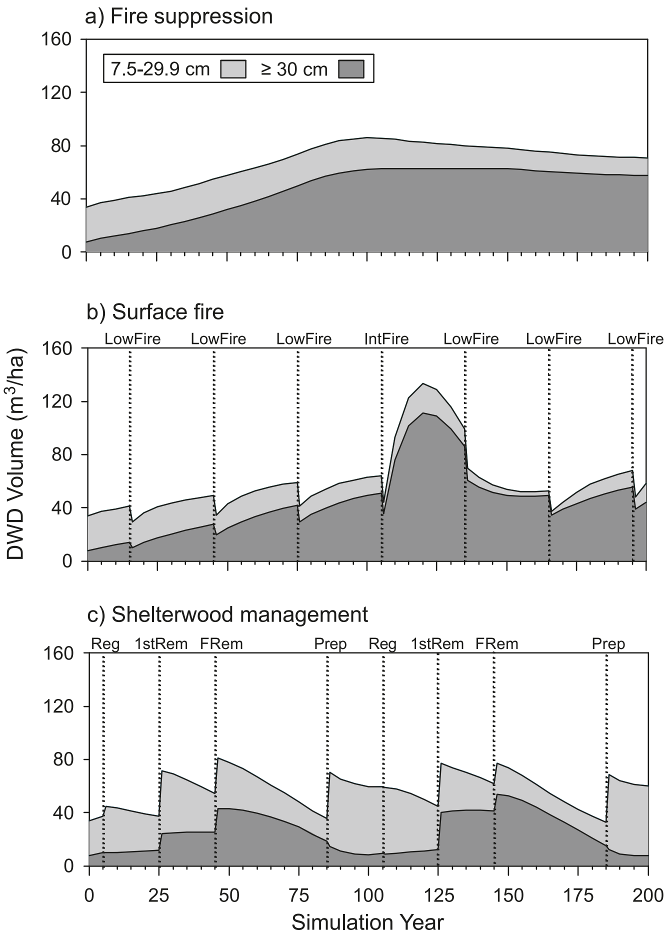
Repeated surface fires generally maintained DWD volume at lower levels than the fire-suppression scenario (Fig. 4*b*). DWD increased sharply 5–30 years after an intense fire as numerous large snags created by this fire fell to the ground. Throughout this scenario, most DWD volume was large-diameter material.

Shelterwood harvesting induced oscillations in DWD volume (Fig. 4*c*), the periodicity of which corresponded to the interval between harvests (20–40 years). Harvesting caused a strong net increase in DWD volume following preparatory, first-removal, and final-removal cuts. However, DWD volume fell steadily after these harvests. Regeneration cuts caused relatively small changes in DWD volume. On balance, DWD volume in this scenario was comparable with that in the surface-fire scenario but, at most times, was somewhat lower than in the fire-suppression scenario. Unlike the fire-suppression and surface-fire scenarios, the distribution of DWD among decay classes in the shelterwood scenario varied strongly with time since the last harvest (Fig. 5). DWD was concentrated in classes 1 and 2 for the first 10 years after each harvest and in class 3 for 15–20 years after harvest. Fluctuations of class 4 DWD were less pronounced between harvests but still showed twofold variation over a 100 year rotation.

Variation in harvest impacts

Retaining all large snags during harvesting increased median large snag density by 39%, but this level was still below that in the fire-suppression and surface-fire scenarios

Fig. 4. Mean downed woody debris (DWD) volume by diameter class over the 200 year simulation period for the (*a*) fire-suppression, (*b*) surface-fire, and (*c*) shelterwood-management scenarios. Vertical lines show the disturbance events. See Fig. 2 for abbreviations.



(Fig. 6*a*). Removing all large snags decreased median large snag density from 7 to only 2 snags/ha.

Increasing the volume of harvest residues left as DWD increased median DWD volume to a level above that in the fire-suppression scenario (Fig. 6*b*). Shortly after harvest, the relative increase in DWD volume was even greater and came to match the level that followed intense fire. Conversely, reducing the volume of harvest residues left on site decreased median DWD volume below levels in the fire-suppression and surface-fire scenarios 90% of the time. Varying the amount of decay class 3 and 4 DWD removed during harvesting had a smaller impact on median DWD volume (up to 17% difference) than varying DWD additions (35% difference).

Comparisons with observed CWD distributions

Although mean snag density varied threefold among the time since harvest groups in our field data, there was a great deal of variation among unharvested sites (range 15–270 snags/ha), and no significant differences among means were found (Table 4). Observed snag densities 8–16 years after harvesting were substantially higher than those in our shelterwood simulations; in sites harvested 16–25 years earlier, the difference was less marked. Nevertheless, the relative decrease in snag abundance following the first two harvests in our simulations (about 50%) was consistent with the relative difference in the observed means of unharvested and combined shelterwood-harvested sites.

The total volume of DWD in decay classes 1–4 did not differ significantly among the three time since harvest groups (Table 4). Differences in the volume of decay class 1 DWD were close to significant among sites that were harvested 8–16 years ago, those that were harvested 17–25 years ago, and those that were unharvested. When all harvested sites were combined, they were found to have less DWD in this decay class than unharvested sites (P = 0.041). There was significant variation in the volume of decay class 2 DWD, with sites harvested 8–16 years ago having more class 2 material than sites harvested 17–25 years ago (P = 0.005) and unharvested sites (P = 0.042). Unharvested sites also had more DWD in this class than 17- to 25-year-old harvests (P = 0.042). We found no significant variation among the three groups in the volumes of class 3 and 4 DWD. However, when combined, differences in the volume of both classes together were close to significant (P = 0.060). There was one outlying data point in each of the 17–25 year harvest and unharvested groups; removing these two sites reduced the standard deviation of their respective group means by 49% and 59%. With these sites excluded, remaining sites harvested 17–25 years ago had significantly more class 3 or 4 DWD than those harvested 8–16 years ago (P = 0.042), which in turn had more than unharvested sites (P = 0.004).

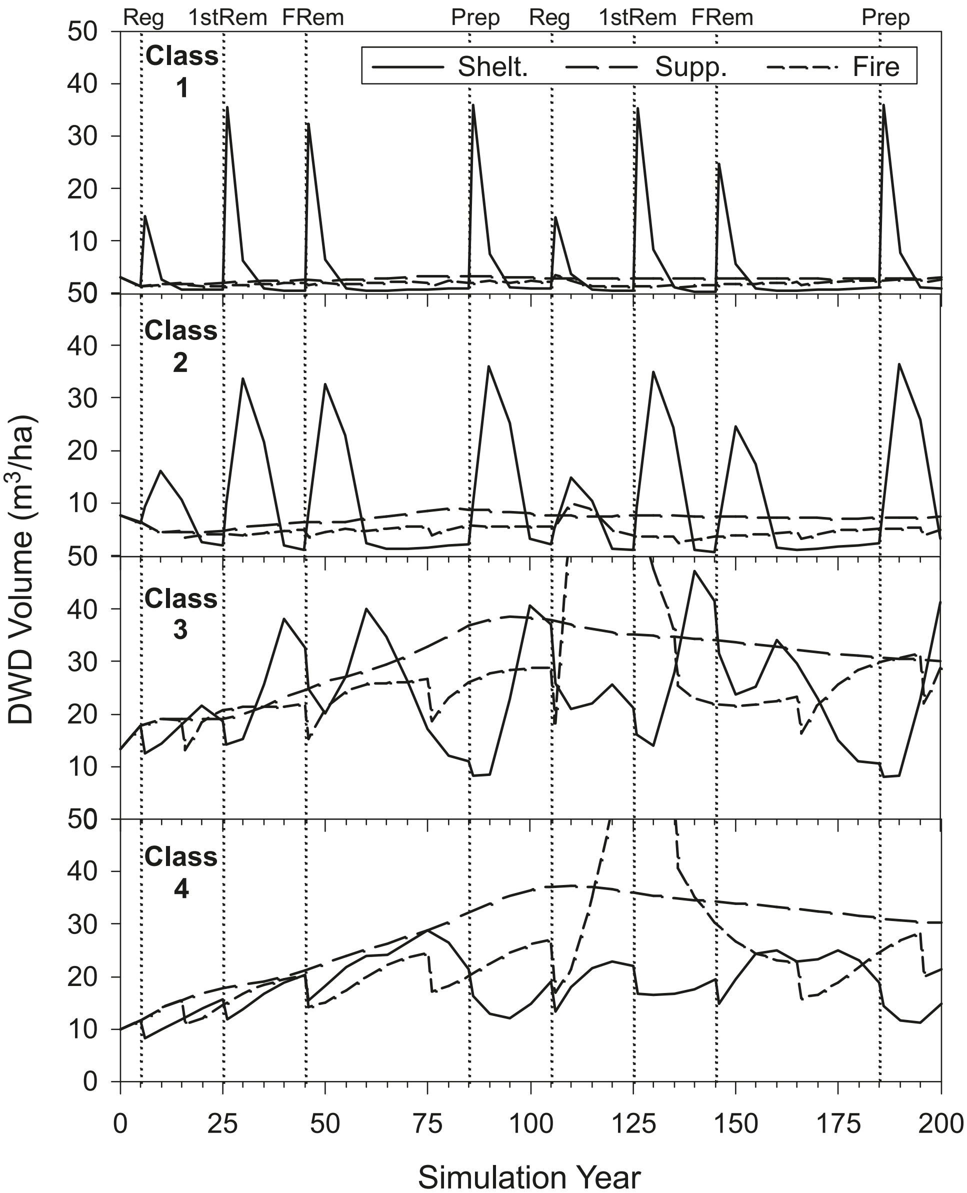
Differences in DWD volume among 8- to 16-year-old harvests (A), 17- to 25-year-old harvests (B), and unharvested sites (C) were compared with the rank of simulation volumes between the mean of 10 and 15 years after the first two harvests (A), 20 years after the first two harvests (B), and mean initial conditions before any harvesting occurred (C). In both the field-based and simulation data, the volume of decay class 1 DWD decreased in the order C > (A ≈ B), that of class 2 decreased in the order A > C > B and that of classes 3 and 4 decreased in the order B > A > C. Therefore, patterns of change in DWD abundance were consistent between the simulation results and empirical data. Overall, the mean total volume of DWD in classes 1–4 in our empirical data (58 m^3/ha) matched the median value from our shelterwood simulation (60 m^3/ha) well.

Discussion

Scenario comparisons

In our simulations, CWD dynamics under a high-retention shelterwood system showed features of management systems where the canopy is removed in a single harvest entry, as well as systems where a portion of the canopy is removed at regular intervals (Figs. 3–5). As under even-aged management where a stand may be clear-cut, regenerated, and then left to grow without intervention, DWD volume tended to increase with stand age (Sturtevant et al. 1997; Ekbom et al. 2006). This pattern was particularly evident in decay class 4, which peaked as residues from final-removal cuts became well decayed. Also, mortality processes acted to cre-

Fig. 5. Mean downed woody debris (DWD) volume within each decay class over the 200 year simulation period for the shelterwood (Shelt.) scenario (solid lines). Vertical lines show the disturbance events. See Fig. 2 for abbreviations. For comparison, long- and short-dashed broken lines show the mean volume of DWD at the corresponding points in the fire-suppression (Supp.) and surface-fire (Fire) scenarios, respectively.



ate large numbers of snags in dense young stands prior to preparatory cuts. With four harvest events over a 100 year rotation, this shelterwood system also resembled management regimes characterized by periodic partial harvesting in some respects. The distribution of DWD tended to shift among decay classes with time since last harvest, and snag densities were regularly knocked back by harvesting operations (Vanderwel et al. 2006*b*, 2008).

The shelterwood scenario supported a low density of snags compared with both the surface-fire scenario and the fire-suppression scenario. This shelterwood system reduces tree density through repeated partial harvests and lowers mortality rates by lessening competition for available light and nutrients. Both factors act to reduce snag density relative to undisturbed stands. Also, harvesting itself removes existing snags that pose a safety hazard, in contrast to fire disturbances that create many new snags by killing small-diameter trees (McRae et al. 2001). However, even if all large snags were retained at the time of harvest, median large snag densities under shelterwood management were still expected to remain below those under fire-suppression and a surface-fire regime (Fig. 6*a*).

Although shelterwood harvests decreased snag abundances, they produced a sizeable influx of DWD. Preparatory, first-removal, and final-removal cuts generated large quantities of DWD that resulted in high overall volumes at these points in the shelterwood rotation. Regeneration cuts created little DWD, because mechanical scarification operations are expected to leave less residual material intact. Standard DWD inputs from harvesting produced enough DWD to

Fig. 6. Distribution of (*a*) large (≥30 cm DBH) snag density and (*b*) downed woody debris (DWD) volume over the 200 year simulation periods in standard disturbance scenarios (Supp, fire suppression; Fire, surface fire; Shelt., shelterwood) and modified versions of the shelterwood scenario that varied the addition of DWD, the removal of DWD, or the removal of large snags at each harvest (see text for details). Horizontal lines within boxes are medians, boxes show the range from the 1st to 3rd quartile, and whiskers show the range of the 10th to 90th percentile.

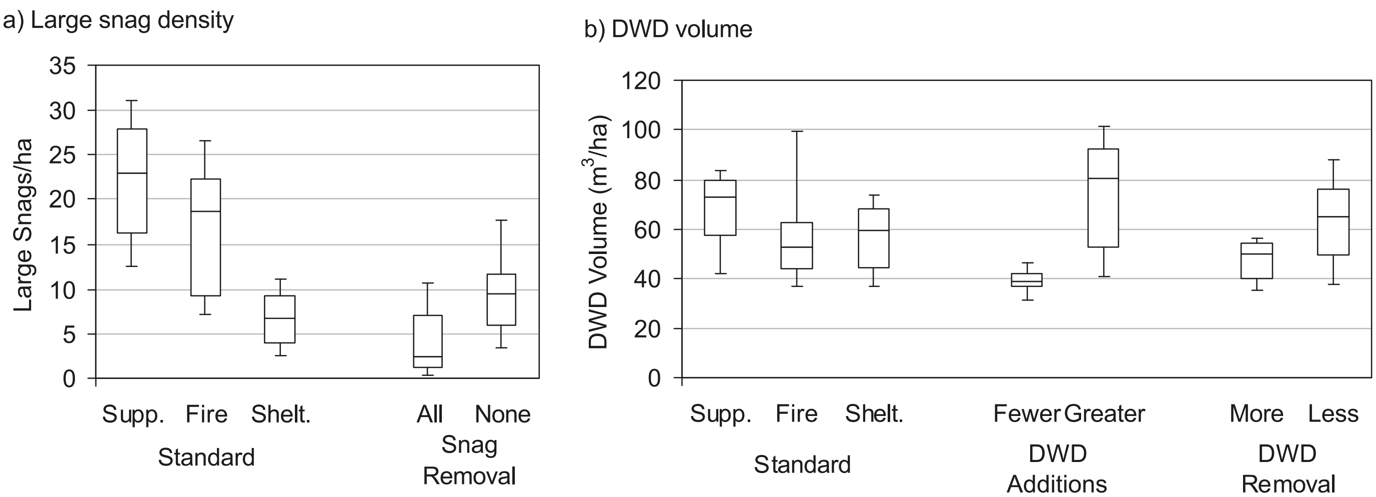


Table 4. Density of snags and volumes of downed woody debris (DWD) in each decay class of mature pine-dominated sites in Algonquin Park, Ontario.

	Harvested 8–16 years ago (*n* = 7)	Harvested 17–25 years ago (*n* = 5)	Unharvested for >28 years (*n* = 9)	Kruskal–Wallis *P* value
Snags/ha	45.6±9.8	25.0±5.2	78.2±27.6	0.252
DWD volume (m^3/ha)				
Total	61.2±3.7	59.1±7.8	54.6±4.0	0.453
Class 1	4.7±1.2	3.4±0.7	9.5±2.2	0.087
Class 2	15.9±1.8a	5.2±1.4c	10.4±1.4b	0.002
Class 3	23.6±4.1	26.4±4.5	17.0±1.4	0.262
Class 4	17.0±3.1	24.1±3.0	17.7±3.0	0.165

Note: Values are means ± SEs. Values with different letters within a row are significantly different from each other in sequential Bonferonni corrected pairwise comparisons (α = 0.05).

compensate for reduced tree and snag fall inputs and resulted in the overall volume exceeding that found in a surface-fire regime much of the time. With elevated harvest input contributions, the median volume of DWD surpassed that found under fire suppression (Fig. 6). Much of the time, however, shelterwood management produced less large-diameter DWD than was available in the fire-suppression and surface-fire scenarios. Also, unlike the fire-suppression and surface-fire scenarios, synchronous DWD inputs from harvesting cause the predominant decay state to shift among the first three decay classes over time.

Model evaluation

It should be noted that the conceptual formulation and parameter estimates incorporated into our model contain varying degrees of uncertainty. As with ecological models in general, minor changes in the model's structure or parameterization could yield plausible output that is numerically different from that presented here. Nevertheless, we believe the qualitative patterns we discuss to be robust for several reasons. Firstly, live-stand dynamics were calibrated such that they produced structural changes through time that broadly conformed to expectations (e.g., basal area, species composition, fire mortality, and harvest retention levels). Secondly, CWD decomposition parameters were based on data from published studies of these species and, therefore, are logical inductions from observed patterns. Thirdly, as described below, we evaluated our modelling results by comparing the patterns of CWD accumulation in each scenario to information available from various sources, including our own empirical data.

The projected 100 year increase in CWD in our fire-suppression scenario is consistent with the general expected pattern of accumulation during stand development (Harmon et al. 1986). Although this pattern has been observed across a number of forest types (Tyrrell and Crow 1994; Sturtevant et al. 1997), empirical data suggest that it may have limited applicability in Ontario's white and red pine forests. In a chronosequence of white and red pine dominated stands in Ontario, Carleton (2003) found that DWD volume increased linearly with age in only one of four stand productivity classes and that snag volumes declined in stands older than 150 years. Both snags and DWD appeared to peak in stands 90–125 years of age, seemingly as a result of high density-dependent mortality during the stem-exclusion phase of stand development. We found some support for this pattern for snags, which exhibited a modest decrease at about 150 years of age before later increasing. Studies in nearby parts of the United States have reported that CWD abundance increases with age to reach levels comparable with those produced by our simulation model (Tyrrell and Crow 1994; Goodburn and Lorimer 1998; Duvall and Grigal 1999). Decreases in CWD abundance over the last 100 years of our fire-suppression scenario may have resulted from a long-term compositional change to species exhibiting faster rates of decay (Spies et al. 1988).

Suitable data could not be found with which to formally evaluate CWD projections in the surface-fire scenario. In a general sense, the large pulses of snags created by fires are consistent with the type and amount of CWD found in recently burned stands (e.g., Pedlar et al. 2002). The subsequent declines in snag abundance also followed patterns of CWD accumulation observed after fire (Everett et al. 1999; Ferguson and Elkie 2003). However, in contrast to catastrophic disturbances, DWD and large snag abundances were only mildly affected by light fires at both short- and long-term time scales. According to the conceptual model of CWD dynamics developed by Hansen et al. (1991), low-intensity disturbances are not expected to affect CWD supplies, either through the addition or removal of material, to the same degree as high-intensity disturbances. Therefore, the effects of surface fires on different types of CWD in this scenario were consistent with general empirical and conceptual patterns of CWD accumulation under fire disturbances.

Although our surface-fire scenario differed from natural systems in that fires occurred at regular intervals, several important patterns emerged that aid in understanding the long-term impacts of surface fire on CWD. Firstly, surface fires produced short-lived upward spikes in snag density and downturns in DWD volume. Snag abundance fluctuated strongly through time as a result, but DWD volume was only mildly affected by light fires. Secondly, the number of snags produced by fire was related to the stage of stand development through the density of small-diameter trees. Peaks in snag abundance decreased in magnitude over the first 100 years of the simulation as small-diameter trees amounted to a lower basal area, whereas fires of the same intensity produced exceptionally high snag densities after an intense fire initiated a new cohort of regeneration towards the end of the simulation period. Lastly, the quantity and size of CWD produced was related to fire intensity. Although light surface fires can produce many small-diameter snags, the creation of large-diameter snags and high volumes of DWD require more intense fires, which occur much less frequently.

The projected decline in snag abundance under shelterwood management was not significant in our field data, even though mean snag densities in shelterwood-harvested sites were 42% and 68% below the mean for sites unharvested for at least 28 years. Failure to identify a postharvest reduction in snag density was likely attributable to high variability in snag abundance among unharvested sites. In other studies from Algonquin Park, pine stands harvested within the past decade had less than one-half as many snags as old forest: 33 versus 69 snags/ha ≥10 cm DBH, (Kingsley and Nol 1999) and 5 versus 11 snags/ha ≥25 cm DBH, (Holloway and Malcolm 2006). Thus, our projected reduction in snag abundance under shelterwood management is in agreement with the relative impacts of this silvicultural system reported by others. The higher snag densities observed in field sites compared with our model may reflect increased postharvest tree mortality from sudden changes in environmental conditions and physical damage from felling and skidding operations (Caspersen 2006). These stresses, which we did not incorporate in our simulations, could represent an important source of snag inputs to recently harvested stands.

Patterns of DWD abundance among harvested and unharvested field sites in Algonquin Park (Table 4) showed good qualitative agreement with the projections in our shelterwood scenario. The observed total volume of DWD matched that in the simulation model well, but it was somewhat more evenly distributed across the four decay classes than projected. The broader distribution across decay classes suggests that, at the site level, shelterwood harvesting may have had a smaller impact on existing CWD and future inputs than expected. Stands subjected to regeneration and first-removal cuts normally contain a number of small unharvested reserve areas that amount to 10%–15% of the stand's total area. These reserves were not included in our simulations and may account for some of the model's differences with observed stands.

Emulating natural disturbances

Coarse woody debris accumulations under a high-retention shelterwood system differed from stands in which fires were suppressed and stands experiencing periodic surface fires in three principal respects: (*i*) reduced numbers of snags, including large snags, over most of the harvest rotation; (*ii*) high abundances of early decay class DWD immediately after harvesting, followed by a lack of DWD in this condition 15 years later; and (*iii*) low amounts of large-diameter decay classes 3 and 4 DWD between preparatory and first-removal cuts. Efforts to better emulate the conditions created by natural disturbances in managed stands and landscapes, at least with respect to CWD, should seek to address these three concerns.

Snags are important for a large number of cavity-using birds and mammals (Samuelsson et al. 1994). In New Brunswick, brown creeper (*Certhia americana* Bonaparte) nests were more likely to be present in areas with at least 56 snags/ha (≥10 cm DBH) than in areas with fewer snags (Poulin et al. 2008). More generally, the abundance of cavity users has been found to be positively correlated with snag densities (Bunnell et al. 1999), implying that their populations can be limited by the availability of snags. Pinto (1998) noted that managed forests may not have as many dead and declining trees as those experiencing fire disturbances and stated that current forest-management guidelines in Ontario are designed to ensure that at least the minimum habitat requirements of cavity users are met. Ontario's guidelines specify that six living cavity trees per hectare (≥25 cm DBH) and as many snags as safety permits be retained during harvesting to meet the needs of cavity users such as the pileated woodpecker (*Dryocopus pileatus* L.; Naylor et al. 1996). Live cavity trees can provide suitable habitat for most cavity users without posing a safety hazard during harvesting operations and are expected to often develop into snags over time. Recent work suggests that about 10 snags/ha >25 cm DBH may be required to support cavity-nesting bird species at levels comparable with those in unmanaged pine-dominated stands (B.J. Naylor, Ontario Ministry of Natural Resources, Southern Science and Information Section, North Bay, Ont., unpublished data).

The median density of snags ≥30 cm DBH was 7 snags/ha in our simulations of shelterwood management. Retaining all large snags during harvesting increased this median to 9 snags/ha but would presumably pose an unacceptable risk to worker safety. If 10 large snags per hectare is taken as a rough target, our standard shelterwood simulations met this level only 10%–25% of the time (25%–50% in the full large snag retention variant). These results suggest that, if adequate habitat is to be available for snag-dependent wildlife most of the time in shelterwood-managed stands, active measures may be necessary to enhance critical snag resources. For example, creating new snags through herbicide injection or fungal inoculation after harvesting would not compromise worker safety and could greatly increase the amount of snag habitat (Brandeis et al. 2002; Jackson and Jackson 2004).

Shelterwood harvesting created large quantities of decay class 1 and 2 DWD that greatly exceeded the accumulations found in stands that were undisturbed or experienced regular surface fires. High levels of downed material from harvest residues may emulate the conditions present after other types of natural disturbances, such as a catastrophic blowdown or a major ice storm. Although harvesting events occur with much greater frequency, the large amounts of early decay class DWD they generate can be considered consistent with those occasionally produced by natural processes. In some regions, high concentrations of fresh CWD risk outbreaks of insect pests that attack and damage healthy trees. Bark beetles (Coleoptera: Scolytidae), such as the pine engraver beetle (*Ips pini* (Say)), can exhibit outbreaks following major disturbances in Ontario, but these outbreaks are not considered to pose a mortality risk for live, healthy trees (Ryall et al. 2006).

Fifteen years after harvesting, virtually no DWD was expected to occur in the early decay classes. In comparison, low amounts of DWD were consistently found in classes 1 and 2 in the fire-suppression and surface-fire scenarios. If these types of DWD are naturally uncommon, species associated with them, such as bark and wood-boring beetles (Coleoptera: Cerambycidae), should be well-adapted to using sparsely distributed resources. These organisms would be expected to have high mobility (Jonsell et al. 1999) and, thus, be able to locate supplies of suitable DWD in nearby stands if none were locally available. As such, early decay class DWD could potentially be managed at a broader scale by staggering the timing of harvests among closely grouped operating blocks.

Large-diameter DWD in decay classes 3 and 4 was particularly sparse during the period surrounding preparatory, regeneration, and first-removal cuts. These low volumes could have adverse effects on organisms such as eastern redback salamanders (*Plethodon cinereus* (Green)), whose abundance has been found to correlate with the volume of both large DWD and with that in late decay classes (Morneault et al. 2004). Several larger species, including marten (*Martes americana* (Turton)) and fishers (*Martes pennati* (Erxleben)) also utilize these types of DWD as den sites (Gilbert et al. 1997; Powell et al. 1997). Low inputs of natural-origin DWD during this period, coupled with destruction of classes 3 and 4 material during harvesting, make it difficult to maintain DWD in this condition throughout the shelterwood rotation. It may be possible to retain some of these habitat elements within small reserves in harvested stands, including internal and peninsular residual patches (OMNR 2001) and reserves around riparian areas, raptor nests, and pileated woodpecker roost trees (Naylor 1998). Otherwise, it may be possible to continuously maintain large-diameter DWD in late stages of decay by keeping adjacent groups of stands at different stages of the shelterwood rotation.

Conclusions

Under a high-retention shelterwood system, several CWD-related habitat features were modelled to be less abundant at various stages of the harvest rotation than they were under a natural fire disturbance regime. In addition, whereas our model showed that fire suppression activities lead to increased numbers of snags and amounts DWD in undisturbed stands, simulations of managed stands did not maintain large accumulations of CWD associated with old-growth conditions. Such reductions in CWD supplies have potential to adversely affect a number of species that are dependent on dead wood.

Active strategies for snag renewal may help ameliorate decreases in snag abundance under shelterwood management. Also, forest-management planning may need to make use of reserve areas and consider the timing of harvest activities among adjacent operating blocks to manage CWD habitat that cannot be continuously provided at the stand level. If properly implemented, these actions could help to minimize differences in the overall supply and temporal variation of CWD between managed and both naturally disturbed and old-growth stands over the long term.

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