

Contrasting downed woody debris dynamics in managed and unmanaged northern hardwood stands

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Abstract: The reported effects of selection silviculture on downed woody debris (DWD) vary. To investigate the processes underlying potential management impacts on DWD stocks and fluxes, we conducted a repeated census of downed wood in selection-harvested, selectively harvested, and unmanaged (old-growth) stands in central Ontario. DWD was significantly more abundant in stands harvested within the last 20 years than in stands harvested earlier, and shifted towards more advanced decay classes over the first 20 years after harvest. These results are consistent with persistence of a harvest-related DWD pulse for up to two decades in managed stands. The transition of DWD from early and middle decay classes to more advanced decay classes proceeded more slowly in managed than unmanaged stands. Species type, identity of fungal fruiting bodies, presence of a cut surface, and plot moisture class were significant predictors of variation in decay dynamics within particular decay classes; however, these factors did not account for observed differences in decay-class transitions between managed and unmanaged stands. A decay class matrix model projected DWD half-lives of 19 years for unmanaged stands and 21 years for managed stands. Over the long term, slower decay dynamics may help somewhat in maintaining relatively high DWD abundances in stands managed under selection silviculture.

Résumé : Les résultats qui ont été rapportés concernant les effets du jardinage sur les débris ligneux au sol (DLS) varient. Dans le but d'étudier les processus sous-jacents aux impacts potentiels de l'aménagement sur les stocks et les flux de DLS, nous avons effectués des relevés répétés des DLS dans des peuplements soumis à une coupe de jardinage, à une coupe d'écrémage ou non aménagés (forêt ancienne) dans le centre de l'Ontario. Les DLS étaient significativement plus abondants dans les peuplements récoltés au cours des 20 dernières années que dans les peuplements récoltés il y a plus longtemps et ont évolué vers des classes de décomposition plus avancées au cours des premiers 20 ans après la récolte. Ces résultats concordent avec la persistance d'une recrudescence des DLS reliée à la récolte pendant une période pouvant aller jusqu'à deux décennies dans les peuplements aménagés. Le passage des DLS des classes de décomposition initiale et intermédiaire vers une classe de décomposition plus avancée s'est fait plus lentement dans les peuplements aménagés que dans les peuplements non aménagés. Le type d'essences, l'identité des carpophores, la présence d'une découpe et la classe d'humidité de la placette étaient des indicateurs significatifs de la variation dans la dynamique de la décomposition dans une classe de décomposition donnée. Cependant, ces facteurs n'expliquaient pas les différences observées entre les peuplements aménagés et non aménagés dans la transition entre les classes de décomposition. Un modèle matriciel des classes de décomposition prédisait une demi-vie des DLS de 19 ans dans les peuplements non aménagés et de 21 ans dans les peuplements aménagés. À long terme, une dynamique de décomposition plus lente peut contribuer un peu à maintenir une abondance relativement élevée de DLS dans les peuplements aménagés soumis au jardinage.

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Introduction

Maintaining stocks of downed woody debris (DWD) is increasingly regarded as a necessary component of ecologically sound forest management practices (Hagan and Grove 1999; McComb and Lindenmayer 1999). In northern hardwood forests, traditional even-aged management has caused pronounced and long-lasting reductions in DWD stocks (Gore and Patterson 1986; Goodburn and Lorimer 1998;

McGee et al. 1999), and exploitive partial harvesting has induced similarly steep declines in DWD levels relative to those in old, unmanaged stands (Angers et al. 2005). Concern about negative impacts of forest management has led to the development of prescriptions aimed at retaining and renewing structural features such as DWD in managed stands (e.g., Ontario Ministry of Natural Resources 1998, 2004; Keeton 2006). In Ontario, for example, provincial forest management guidelines recommend leaving unmerchant-

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able boles on site and avoiding crushing and windrowing DWD during site preparation (Ontario Ministry of Natural Resources 1998).

In the Great Lakes – St. Lawrence Forest Region of Ontario and Quebec, uneven-aged stands dominated by shade-tolerant hardwoods are usually managed with the selection silvicultural system. Selection harvests remove trees individually, or in small groups, and aim to reduce basal areas by approximately one-third while maintaining a target size-class distribution as well as a range of tree species and habitat features (Nyland 1998; Ontario Ministry of Natural Resources 1998, 2004). Prior to the widespread implementation of the selection system in Ontario, tolerant hardwood stands were “selectively” harvested (“high-graded”), where only valuable timber was removed. Selective harvests were most commonly carried out using diameter-limit prescriptions, although unmerchantable trees larger than the diameter limit were usually retained.

Compared with more intensive practices such as clear-cutting, selection harvests are believed to have relatively minor ecological impacts; however, their influence on DWD stocks and dynamics has not been widely examined. Previous studies have found that abundances of DWD in stands subjected to selection harvests 10–15 years earlier were greater than (Doyon et al. 2005), lower than (Goodburn and Lorimer 1998), or the same as (Gore and Patterson 1986; Angers et al. 2005) abundances in unmanaged stands. These equivocal findings may be attributable to differences in the amount of downed material left by harvesting, the subsequent rates of DWD input, and (or) decomposition dynamics over time.

Downed material originating from harvesting operations, including slash and unmerchantable logs, can constitute a large DWD pulse that maintains elevated downed wood abundance in the short term (Fraver et al. 2002; Keeton 2006). If the decomposition time of DWD exceeds the interval between harvests (generally 15–25 years), then such periodic inputs could sustain a continuous abundance of DWD, albeit within a narrow range of decay stages at any given time. DWD inputs between harvests may be low because selection harvesting generally reduces densities of large-diameter trees and snags (Goodburn and Lorimer 1998; Crow et al. 2002; Angers et al. 2005; Vanderwel et al. 2006), both of which are important sources of DWD. In addition, the preferential removal of unacceptable growing stock and otherwise unhealthy trees (“low grading”) may further act to lower tree mortality rates relative to those in unmanaged stands. Although guidelines specify that a minimum number of live cavity trees should be retained to provide wildlife habitat in Ontario (Ontario Ministry of Natural Resources 1998), such trees are not guaranteed to die, fall, and become DWD before the next harvest. Reduced rates of downed wood input in managed stands may lower DWD abundance relative to that in unmanaged stands over the long term, particularly after harvest-origin material is lost through decomposition.

Selection harvesting could also impact DWD stocks through altered decomposition dynamics. Downed wood decomposition is related to substrate quality and environment (Yin 1999; Laiho and Prescott 2004), both of which can be affected directly or indirectly by harvesting activities. For

example, gaps in selection-harvested stands show increased soil temperature and water content relative to nongap areas (e.g., Peng and Thomas 2006); which can potentially expedite DWD decomposition rates. If selection practices lead to accelerated DWD decomposition, DWD residence times would be shorter, and under equivalent inputs a lower abundance of downed wood would be expected in managed stands. Conversely, selection management may slow decomposition if logging debris is less prone to decay than naturally recruited DWD, or if harvest-related changes in fungal communities reduce the activity of wood-decay organisms (Lonsdale et al. 2008). Such effects could lengthen DWD residence times in managed stands and allow the maintenance of downed wood stocks even under lower input rates.

In this study we examined stands composed of shade-tolerant hardwoods across three categories of management history: stands treated with selection harvests 2–19 years prior to sampling (for which harvest debris inputs of DWD are expected to be important), stands cut 21–43 years prior to sampling through selective harvesting (for which harvest debris will have largely decayed), and unmanaged (old-growth) stands. Our objectives were to (1) quantify and characterize DWD stocks and fluxes in tolerant-hardwood stands with different management histories, (2) determine the time course of DWD decomposition through a series of five decay classes, and (3) assess the effects of various piece- and site-level factors on decay-class transition rates. In addressing these objectives we sought to answer the following focal question: To what extent are the effects of selection silviculture on DWD stocks attributable to downed material left after harvest, variation in DWD inputs, and variation in decomposition dynamics between managed and unmanaged stands?

Materials and methods

Study site

This study was conducted in the Haliburton Forest and Wildlife Reserve, a 25 000 ha privately owned property located in central Ontario, Canada (45°13'N, 78°35'W). Haliburton Forest is located in the Great Lakes – St. Lawrence Forest Region (Rowe 1972) and is dominated by sugar maple (*Acer saccharum* Marsh.), with important components of American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.), and eastern hemlock (*Tsuga canadensis* (L.) Carrière). The mean annual temperature is 5 °C, ranging from –11 °C in January to 19 °C in July, and approximately 1000 mm of precipitation falls in an average year (Environment Canada 2002). The topography in the area undulates in the characteristic manner of Precambrian Shield landscapes. Soils are derived from granite or granitic gneiss and are generally classified as young Podzols or Brunisols. The natural disturbance regime of the region consists of frequent small-scale gap disturbances and infrequent, relatively large-scale wind events, the most recent of which occurred in 1995.

Haliburton Forest has an extensive management history, beginning with selective removal of white pine (*Pinus strobus* L.) in the mid-1800s and yellow birch during the 1940s. Despite this history, unmanaged old-growth stands remain distributed throughout the property where difficult terrain

renders stands inaccessible to harvesting machinery. More recent forest management in the Haliburton Forest employed selective harvesting from 1960 until the mid-1980s, and selection silviculture from the late 1970s onwards. We distinguish selection from selective harvesting by the use of tree marking, a practice in which individual trees are designated for harvest or retention based on criteria that include size, species, vigour, and habitat value. Tree markers follow established guidelines for maintenance of wildlife habitat, such as retention of cavity trees (Ontario Ministry of Natural Resources 2004).

Data collection

This study used a network of permanent sample plots (PSPs) established in upland hardwood-dominated stands during the summer of 2000. The PSP network consists of 23 sites, each of which contains a pair of circular 400 m² (11.3 m radius) plots in which all trees larger than 2.5 cm diameter at breast height (DBH, 1.3 m) have been measured, mapped, and tagged. Seven of the PSP sites are located in unmanaged (old-growth) stands, which were required to meet three criteria: (1) no recorded history of logging, (2) no cut stumps present, and (3) at least 1 ha in size. The remaining PSPs are located in stands that had been harvested 1 to 38 years prior to their establishment in 2000. PSP locations were selected in a manner to maximize spatial interspersion of management history.

From June to August 2001, we censused all DWD in the PSP network. In each plot, we measured and mapped all DWD pieces that fell within or intersected the outside perimeter of the PSP boundary and met a minimum size threshold of 10 cm in diameter and length. While all sampled pieces were used in piece-level analyses, pieces whose midpoint lay outside the plot boundary were later excluded from stand-level volume and frequency calculations (described below).

For each piece of DWD, we recorded diameter, length, species, and decay class. For fallen trees and snags, we measured diameters at 1.3 m from the base (DBH). When DBH was not identifiable (i.e., for fallen branches and upper boles), we measured diameter at the widest point. In cases where wood pieces were too decayed to measure around their circumference, diameters were measured horizontally with a tape measure. This technique can cause upward biases in volume estimates if pieces have collapsed and become elliptical in shape (Fraver et al. 2007). DWD pieces were identified as conifers or hardwoods and to species wherever possible. When we were not able to determine conifer–hardwood status in the field, we took a sample back to the laboratory and used wood anatomical differences, primarily the presence or absence of vessels, to determine species type.

Five decay classes were distinguished as follows (loosely based on Maser et al. 1979): (1) Wood is hard; all bark still intact. (2) Wood is hard; bark has begun to fall off. (3) Wood is soft and has some give when kicked; usually no bark remaining. (4) Wood is substantially decayed and pieces easily slough off; inner heartwood may be soft but is intact; moss usually present on the outer surface. (5) Wood is decayed throughout; texture is powdery and resembles soil. Finally, we noted the presence and identified the spe-

cies of all bracket fungi (Polyporaceae sensu lato) fruiting bodies on each piece of DWD.

We conducted a recensus from May to August 2005. No harvesting had taken place in the PSPs since their establishment, so by 2005 the stands had been harvested 6–43 years earlier. Each DWD piece was relocated using plot maps, its diameter and length were remeasured, and its decay class was reassessed. Identifying and measuring individual pieces of DWD after 4 years present some challenges (e.g., Westfall and Woodall 2007), but we minimized relocation and assessment errors by having three observers evaluate piece characteristics, including decay class, through consensus. During this census, diameters of collapsed, elliptical-shaped pieces were measured as the mean of the longest and shortest axes. This removed a possible volume bias, but rendered 2001–2005 volume comparisons difficult. We collected the same set of measurements from all new DWD pieces added to the plots between censuses. Bracket fungi were not recensused in 2005.

Each PSP was given one of three moisture class designations — dry, mesic, or wet — based on top slope, midslope, or bottom slope macrotopography, respectively. These plot-level designations were refined based on tree species composition: white pine and red oak (*Quercus rubra* L.) indicated dry sites, while red maple, spruce (*Picea* spp.), black ash (*Fraxinus nigra* Marsh.), and eastern white-cedar (*Tsuga occidentalis* L.) were indicative of wet sites. Sugar maple, beech, yellow birch, and hemlock were widely distributed across site types.

Data analysis

DWD pools and their dynamics

We calculated the volume of DWD for each plot assuming pieces were in the shape of the frustum of a neiloid (Husch et al. 2003). Taper (k) and shape (b) parameters determining the form of the neiloid were estimated by separating pieces into 10 diameter classes, then regressing the squared mean basal diameter (D_{base} , centimetres) against the 95th percentile of piece length (L_{95} , metres) using the equation

$$[1] \quad D_{\text{base}}^2 = k \times L_{95}^b$$

The resulting least-squares parameter values ($k = 0.0179$, $b = 3.7234$; $R^2 = 0.95$), along with measured lengths (L), were used to estimate end (D_{end}) and midpoint (D_{mid}) diameters for each piece. We then calculated the approximate volume (V , cubic metres) of each piece of DWD using Newton's formula:

$$[2] \quad V = \frac{\pi}{24} \times L \times (D_{\text{base}} + 4D_{\text{mid}} + D_{\text{end}}) \times 10^{-4}$$

We estimated both the volume (cubic metres per hectare) and frequency (number of pieces per hectare) of DWD in each decay class at the time of the 2001 and 2005 measurements. Data from the second measurement were also used to calculate inputs and outputs over a 4 year period. Inputs were categorized based on the structure (tree, snag) and process (breakage, cut, fall) from which they originated. Outputs were categorized as the result of either “collapse”

or “incorporation”. Collapse losses were calculated from two sources: (1) the reduction in volume between the first and second measurements for pieces still considered DWD in 2005, and (2) the volume of pieces whose large-end diameter had decreased to less than 10 cm by 2005 (i.e., no longer met our minimum size threshold). Incorporation losses were calculated using pieces from the 2001 measurement that had advanced beyond the last decay class (i.e., had become incorporated into the soil) by 2005. Twenty-five DWD pieces from the 2001 census were not remeasured in 2005 because they had been overlain by new downed wood or had been otherwise lost.

We compared stocks, inputs, and outputs of DWD among stands that had received a selection cut within the past 20 years, stands that had received a selection cut 21–43 years previously, and unmanaged stands that had never been cut. We also compared mean decay class, diameter, species type composition (conifer vs. hardwood), incidence of cut pieces, occurrence of bracket fungi, and plot moisture classes across the three management histories. Differences in numerical variables (volume, frequency, mean decay class, mean diameter) were analyzed with analysis of variance (ANOVA). Differences in categorical variables (species type composition, cut surface, bracket fungi, and moisture class) were analyzed using two-way contingency tables.

In addition to comparing DWD frequency and volume across broad management history categories, we sought to determine whether DWD stocks underwent qualitative changes in the short and medium term as a result of selection harvesting. Specifically, we examined whether the distribution of DWD among decay classes varied with time up to 20 years after harvesting. For each measurement period, the frequency of DWD in each decay class was divided by the overall stand-level DWD frequency. We then used non-linear least-squares regression to model the change in relative frequency (RF) in each decay class as a unimodal function of time since harvest (T , years):

$$[3] \quad \text{RF} = a \times b^{(T-c)^2}$$

where a , b , and c are regression model parameters. The unimodal form of this function enabled us to estimate the time after harvesting at which the relative amount of DWD in each decay class reached its peak. To assess the relative support for such unimodal changes in relative abundance versus static values through time, we also fit constant functions ($\text{RF} = k$) to the data and compared the two models using Akaike’s information criterion corrected for small samples (AIC_c). Differences in AIC_c were calculated individually for each decay class and globally for all five decay classes.

Piece-level decay-class transitions

To quantify the progressive decomposition of DWD, we derived decay-class-transition matrices that expressed the probability of moving from one decay class to another over 4 years. Log-linear models were used to examine whether transitions out of each class differed across the three classes of stand management history (stands harvested <20 years ago, stands harvested >20 years ago, unharvested stands) and across variables that could affect decomposition processes directly. The latter set of variables included species

type (conifer vs. hardwood), diameter class (<20 cm vs. ≥ 20 cm), plot moisture class (dry–mesic vs. wet, dry vs. mesic–wet), presence of a cut surface, and presence of bracket fungi (any species, species associated with deadwood only, and each of the three most common polypore species).

First, we constructed marginal-effects models (Quinn and Keough 2002) to test whether logs starting from a given decay class had different probabilities of being in subsequent decay classes at remeasurement depending on the value of one of the variables under consideration. Deviances between full and reduced models were compared with a χ^2 distribution, with degrees of freedom equal to the difference in the number of parameters, to obtain a P value for each marginal effect of interest. Because five decay classes were tested separately without prior expectations, we applied a conservative significance level of $\alpha = 0.025$ to account for the relatively large number of tests performed and to maintain an appropriate balance between type-I and type-II error rates.

In cases where both environmental and management variables had significant marginal effects on decay-class transitions, we next carried out analyses for a conditional effect of stand management history. Conditional tests determined whether an effect of management on decay-class transitions was persistent at all separate levels of the environmental factor under consideration (Quinn and Keough 2002). These tests account for the possibility that marginal effects of management may result from lack of independence with species type, diameter, moisture, cut surface, or fungi. If an effect of management was reduced or absent in this analysis (as indicated by substantially lower model deviance), we would conclude that the environmental factor considered was partly or wholly responsible for a significant marginal effect of management.

After deriving 4 year estimates for decay-class transitions, we carried out matrix projections for newly downed wood to determine the time course of decomposition through the five decay classes and the predicted half-life (time at which 50% of pieces have disappeared) of DWD. Because this stage-based matrix projection may be sensitive to errors in assessing decay class, we carried out Monte Carlo simulations, in which errors were added stochastically to the first and second decay class of each piece, to estimate 95% sensitivity limits around the projected DWD half-life. The probability distribution of decay-class errors was determined from double-blind field tests in which two observers independently assessed the decay classes of 100 DWD pieces. We further evaluated decay projections by comparing the projected mean age of DWD in each decay class to the mean age of all cut DWD pieces observed in that decay class, each of which could be dated to the previous harvest in our managed plots.

Results

DWD stocks and their dynamics

The mean volume of DWD in the sampled stands was 48.9 and 40.0 $\text{m}^3\text{-ha}^{-1}$ in 2001 and 2005, respectively (Table 1). The volume-based distribution of DWD among decay classes shifted towards later stages of decomposition over the 4 year study interval. In terms of frequency, there

Table 1. Downed woody debris stocks, 4 year inputs, and 4 year outputs in stands composed of shade-tolerant hardwoods in central Ontario.

	Volume		Frequency	
	m ³ ·ha ⁻¹	%	pieces·ha ⁻¹	%
Stocks (2001)				
Class 1	3.2	7	19.6	6
Class 2	12.3	25	78.3	23
Class 3	14.9	30	133.2	39
Class 4	13.2	27	76.1	22
Class 5	5.3	11	32.1	9
Total	48.9		339.1	
Stocks (2005)				
Class 1	0.3	1	4.3	1
Class 2	4.8	12	29.3	9
Class 3	14.6	36	83.7	26
Class 4	11.8	29	104.3	32
Class 5	8.6	22	101.1	31
Total	40.0		322.8	
Inputs				
Snag break	1.4	21	5.4	16
Snag fall	4.2	66	19.0	55
Tree break	0.1	2	1.1	3
Tree fall	0.2	3	2.2	6
Branch fall	0.2	2	2.7	8
Cut	<0.1	1	1.1	3
Unknown	0.3	5	3.3	9
Total	6.4		34.8	
Outputs				
Collapse	11.9	78	0.0	0
Below minimum size	1.1	7	31.0	61
Incorporation	1.3	8	6.5	13
Lost	1.0	6	13.6	27
Total	15.3		51.1	

was a modest decrease in DWD stocks over the 4 year period, from 339 to 323 pieces·ha⁻¹. The observed shift to later decay classes was more pronounced on a frequency basis, with 63% of all pieces residing in classes 4 or 5 by 2005. DWD inputs amounted to 6.4 m³·ha⁻¹ (34.8 pieces·ha⁻¹), most of which came from snags that fell during the 4 year interval (66% by volume or 55% by frequency; Table 1). The second most important source of DWD was input through snag breakage (21% or 16%), whereas fallen branches and live tree boles accounted for only minor inputs (2%–5% and 6%–8%, respectively). Over the same period, DWD outputs reached 15.3 m³·ha⁻¹ (51.1 pieces·ha⁻¹; Table 1). The most important output process was reduction in DWD piece size. Incorporation into the soil accounted for only 8% of all outputs by volume.

At the time of the initial measurement, there were no large differences in DWD stocks across stand management history (Table 2). By the second measurement, however, DWD frequencies were lower in stands harvested 21–43 years earlier than in sites cut 2–19 years earlier ($P = 0.040$). Volume and frequency of DWD in stands harvested >20 years earlier were only 59% and 84%, respectively, of the volume and frequency in unmanaged stands,

but high among-stand variance rendered this difference non-significant at $\alpha = 0.05$ (Table 2). Although unmanaged stands had greater snag live-tree basal areas than managed stands and greater snag basal areas than stands harvested 19–43 years earlier (Table 2), DWD inputs did not vary significantly in frequency or volume across management history categories. Likewise, DWD outputs over a 4 year period were not significantly different among management history categories (Table 2).

Mean DWD piece diameter was not perceptibly affected by stand management history. There were, however, significant differences in mean decay class, species type composition, presence of cut surface, and polypore fungi incidence among the three management histories (Table 2). Stands harvested in the past 20 years had a lower proportion of hardwood DWD than those harvested 21–43 years earlier and, in 2001, a lower mean decay class and more cut pieces than the other two management types. DWD in stands harvested 20–43 years earlier had a lower incidence of polypore fungi than DWD in unmanaged and more recently managed stands. In the 2005 census, stands harvested >20 years earlier had a lower mean decay class than unmanaged stands.

The relative frequency of DWD pieces in each decay class showed successive peaks over the first 20 years after harvest (Fig. 1). Classes 1 and 2 exhibited sharp maxima 1 and 6 years after harvesting, respectively. Decay classes 3–5 showed much more gradual changes in relative abundance over time. The relative abundance of DWD in classes 3 and 4 was highest 12 and 15 years after harvest, respectively, while class 5 DWD slowly increased in relative abundance up to 19 years after harvesting. AIC values supported constant over unimodal relative abundance models for classes 3, 4, and 5 individually, but the global AIC_c value for all five decay classes strongly supported unimodal changes in relative abundance through time ($\Delta AIC_c = -7.6$).

Piece-level decay-class transitions

Log-linear modeling revealed substantial differences in transition probabilities from decay classes 2, 3, and possibly 1 among the three stand management history categories (Table 3). DWD in these classes advanced to higher decay classes in unmanaged stands than in the two age categories of managed stands. However, within managed stands, there was no discernable difference in decomposition dynamics between stands harvested 2–19 years earlier and those harvested 21–43 years earlier. Several DWD characteristics differed between unmanaged and managed stands (Table 2), and many of these factors were likewise found to affect decay-class transition probabilities (Table 3). In decay class 1 conifer pieces decayed more quickly than hardwood pieces (mean subsequent decay class = 2.9 vs. 2.5). DWD in class 3 decayed more rapidly if it did not have a cut surface (4.0 vs. 3.4), came from wetter stands (4.2 vs. 3.8), and was not infected by the polypore fungus *Ganoderma applanatum* (4.0 vs. 3.9). In spite of these direct impacts on decay-class transitions, the effect of management history persisted when each of these categorical variables was accounted for in conditional log-linear models (Table 3). Thus the faster decomposition dynamics of DWD in old-growth stands could not be attributed to management-related differences in diameter,

Table 2. Comparison of live tree, snag, and downed woody debris characteristics in selection-managed stands harvested 2–19 years prior to the study, in selectively managed stands harvested 21–43 years prior to the study, and in unmanaged (old-growth) stands.

Stand attribute	Unit	Harvested 2–19 years prior (n=10)	Harvested 21–43 years prior (n=6)	Unmanaged (n=7)	P
Live tree basal area (2001) (m ² ·ha ⁻¹)*	Stands				
Hardwood <20 cm DBH		2.0 ±0.2	3.0±0.6	2.1±0.3	0.163
Hardwood ≥20 cm DBH		15.7±1.1a	16.7±1.5a	22.3±2.4b	0.023
Conifer <20 cm DBH		0.7 ±0.3	0.1±0.0	0.2±0.1	0.179
Conifer ≥20 cm DBH		1.9±0.8	2.0±1.0	2.9±1.1	0.729
Total		20.4±0.7a	21.7±1.6a	27.5±2.1b	0.004
Snag basal area (2001) (m ² ·ha ⁻¹)*	Stands				
Hardwood <20 cm DBH		0.3±0.1	0.3±0.1	0.2±0.1	0.576
Hardwood ≥20 cm DBH		3.5±0.7	1.7±0.5	4.6±0.7	0.053
Conifer <20 cm DBH		0.1±0.1	0.0±0.0	0.1±0.1	0.629
Conifer ≥20 cm DBH		0.3±0.3	0.2±0.1	0.8±0.6	0.425
Total		4.1±0.9ab	2.2±0.4a	5.7±0.9b	0.043
DWD stocks (2001)	Stands				
Volume (m ³ ·ha ⁻¹)		45.5±6.2	43.6±8.8	58.5±9.3	0.388
Frequency (pieces·ha ⁻¹)		368.8±23.4	291.7±41.0	337.5±25.4	0.200
DWD stocks (2005)	Stands				
Volume (m ³ ·ha ⁻¹)		41.8±5.8	28.1±4.1	47.8±5.6	0.090
Frequency (pieces·ha ⁻¹)		377.5±30.7a	254.2±31.1b	303.6±33.0ab	0.040
DWD inputs	Stands				
Volume (m ³ ·ha ⁻¹)		8.8±3.3	2.6±1.5	6.1±5.0	0.511
Frequency (pieces·ha ⁻¹)		48.8±11.7	27.1±10.9	21.4±8.1	0.174
DWD outputs	Stands				
Volume (m ³ ·ha ⁻¹)		12.5±2.4	18.2±6.2	16.9±4.8	0.583
Frequency (pieces·ha ⁻¹)		40.0±6.1	64.6±9.9	55.4±12.5	0.174
Mean DWD decay class	Pieces				
2001		2.9±0.1a	3.3±0.1b	3.2±0.1b	<0.001
2005		3.7±0.1a	3.8±0.1a	4.2±0.1b	<0.001
Mean DWD diameter (cm)	Pieces	20.4±0.5	20.1±0.9	22.3±0.9	0.093
Hardwood DWD (%)	Pieces	80a	90b	86ab	0.010
Cut DWD (%)	Pieces	15a	2b	1b [†]	<0.001
DWD with polypore fungi (%)	Pieces	32a	23b	39a	0.005

Note: Values are means ± standard errors. Values sharing a common letter within rows are not significantly different at $\alpha = 0.05$. Significant P values are shown in bold.

*Live tree and snag basal areas were measured in 1000 m² circular plots centred on the 400 m² DWD plots.

[†]Cut DWD observed in unmanaged stands represented pieces from trees felled in adjacent managed stands.

species type, presence of cut surfaces, plot moisture, or presence of bracket fungi.

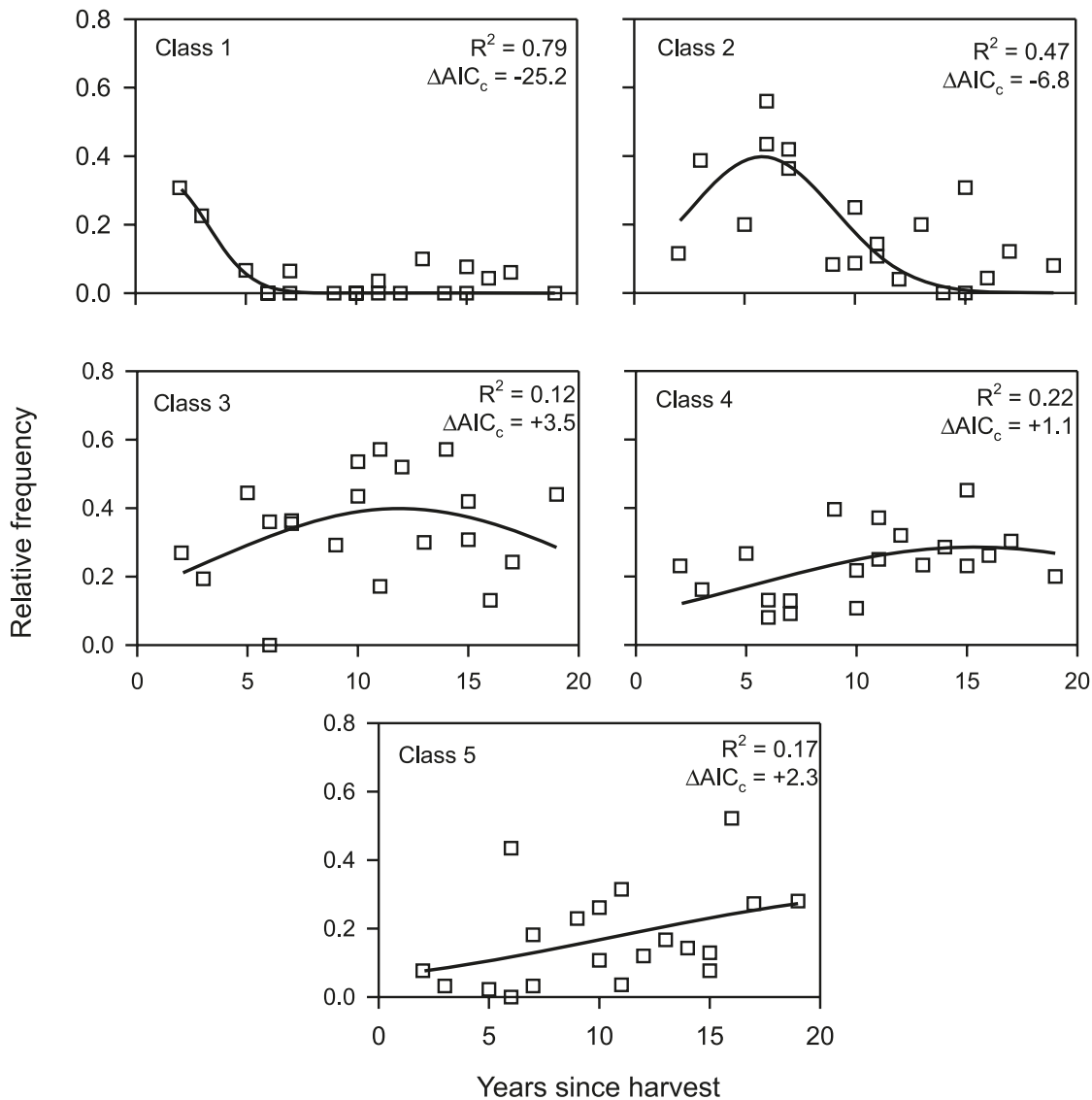
We ran separate projections of DWD dynamics for managed and unmanaged stands (Table 4, Fig. 2). In managed stands, half of all pieces were projected to leave the DWD pool about 21 years after they entered decay class 1 (a 21 year half-life). Double-blind trials indicated that independent observers had a 7% rate of disagreement in assessing decay classes; given this level of uncertainty, Monte Carlo simulations estimated the 95% sensitivity limits for DWD half-life in managed stands to be 20–22 years. In unmanaged stands, DWD moved more quickly through early decay classes and had a half-life of 19 years after entering class 1 (with estimated 95% sensitivity limits of 17–20 years). The projected mean age of DWD in each decay class in managed stands (3, 5, 9, 14, and 20 years) was between 1 and 4 years lower than the mean age of cut pieces in each of the first four decay classes (4, 8, 13, and 15 years; we only identified three cut pieces in the highest decay class). Downed wood originating from snags rather

than newly dead material commonly enters the DWD pool in decay class 2 or 3; our projections suggest that the half-life of snag-origin DWD may be 3–6 years shorter than that of live trees (the time taken to advance from class 1 to class 2 or 3).

Discussion

Our findings of (1) lower DWD frequencies in stands harvested >20 years ago, (2) shifts in the distribution of DWD pieces towards later decay classes with increasing time since harvest, (3) an increase in the mean decay class over the study period, particularly in sites harvested 2–19 years earlier, and (4) appreciable numbers of cut pieces only in stands cut 2–19 years earlier, all support the hypothesis of a harvest-associated DWD pulse. DWD decomposition dynamics were affected by environmental variables, including species type, presence of fruiting bodies of a fungus known to attack live trees, presence of a cut surface, and site moisture class. However, these factors could not account

Fig. 1. Relative frequency of downed woody debris in each decay class over the first 20 years after selection harvesting. Lines represent unimodal models fit to the data.



for the faster DWD decomposition dynamics we found in unmanaged versus managed stands.

DWD pulse from harvest

Although differences in the frequency and volume of downed wood between managed and unmanaged stands were not significant, the volume of DWD in stands cut >20 years ago averaged only 59% of DWD in unmanaged stands in 2005. Despite the fact that high interstand variation and modest replication rendered this effect non-significant ($P = 0.090$; Table 2), it is certainly ecologically important and suggests that infrequent selection harvesting may induce a decrease in DWD stocks in the long term, but not in the short to medium term. Stands that had been cut 21–43 years earlier also had 33% lower DWD frequency in 2005 than more recently harvested stands (Table 2).

Changes in the relative frequency of DWD in each decay class over the first 20 years after harvest were consistent with a harvest pulse advancing to successively later decay

classes over time (Fig. 1). In addition, the incidence of pieces with a cut surface fell from 15% to 2% in sites harvested more than 20 years previously, further supporting the notion that harvest residues contributed to DWD stocks for up to 20 years, but not more than two decades after harvesting. High levels of DWD following harvest have commonly been reported following partial harvesting (Fraver et al. 2002; Jenkins et al. 2004; Morneault et al. 2004; Bebber et al. 2005). This material tends to be below merchantable size limits and decays rapidly, rendering it less valuable than DWD from other sources. However, this is not always the case — experimental harvest prescriptions designed to enhance forest structure have specified that large trees be felled or pulled over to create large-diameter DWD (Keeton 2006), and Ontario guidelines recommend leaving large but unmerchantable tree boles on site to provide large-diameter DWD (Ontario Ministry of Natural Resources 1998). We did not find substantial or significant differences in DWD diameter across management types ($P = 0.093$; Table 2),

Table 3. Deviance of log-linear models representing marginal and conditional effects of predictor variables on downed woody debris decay class at the 2005 recensus.

	Initial decay class					
	1	2	3	4	5	All
Degrees of freedom per treatment level	4	4	3	2	1	14
Marginal effects of predictor variables on subsequent decay class						
Species group						
Hardwood vs. conifer	12.27*	7.21	0.93	1.49	1.36	23.26
Diameter class						
<20 cm vs. ≥20 cm	4.96	2.50	6.05	2.58	0.01	16.13
Polypore fungi presence						
Any fruiting bodies	9.43	3.06	3.85	5.36	0.13	21.84
Deadwood-specific species						
<i>Fomes fomentarius</i>	1.10	0.45	3.68	6.87	1.98	14.08
<i>Stereum ostrea</i> , <i>Stereum histutum</i>	2.40	2.03	3.25	0.27	0.00	7.95
<i>Ganoderma applanatum</i>	9.13	7.47	9.87*	1.21	0.96	28.64*
Cut surface						
Present vs. absent	7.32	3.77	11.94**	0.11	0.00	23.15
Moisture class						
Dry–mesic vs. wet	5.67	5.87	17.11***	5.82	0.00	34.46**
Dry vs. mesic–wet	2.85	3.03	9.44	0.94	0.20	16.46
Management history						
3-way comparison	15.55	20.89**	17.15**	3.60	0.92	58.11***
Managed vs. unmanaged	9.71	17.44**	14.06**	1.02	0.84	43.08***
Harvested 2–19 years prior vs. 21–43 years prior	5.84	3.45	3.09	3.45	0.08	15.91
Conditional effect of management history (managed vs. unmanaged) on subsequent decay class at each level of:						
Species group	9.72					
<i>Ganoderma applanatum</i> fungi	14.58					
Cut surface	12.39					
Moisture class (dry–mesic vs. wet)	14.08					

Note: Values in bold represent a significant effect at $\alpha = 0.025$ (*, $P < 0.025$; **, $P < 0.01$; ***, $P < 0.001$). In all significant pairwise effects, the first condition listed (or fungal presence) had slower decay dynamics than the second.

suggesting that selection harvests do not have a pronounced impact on DWD size in our study area.

DWD inputs and outputs

Contrary to the idea that sources of new downed wood are reduced by selection silviculture, DWD inputs were indistinguishable among stands harvested 2–19 years earlier, 21–43 years earlier, and unmanaged stands (Table 2). However, the volume and frequency of inputs during this 4 year period were inadequate to sustain observed stocks of DWD. Given our projected 19–21 year residence times (Fig. 2), 4 year inputs would need to be approximately double those we observed to support current DWD abundances. Tree mortality, and hence DWD input, is a stochastic process that varies widely over both large and small spatial and temporal scales (Harmon et al. 1986; Franklin et al. 1987). The results reported here are likely to have been influenced by a large-scale windstorm in 1995, which resulted in approximately 2000 ha of blowdown in nearby portions of the study area. While blowdown areas were not sampled, this event almost certainly resulted in a pulse of tree mortality in the sampled plots. The increase in decay class observed across our plots (particularly in unmanaged stands) likely reflects DWD from windthrown trees dating from this event. As well, below-average mortality likely occurred from 1996 to 2000

(perhaps also a result of the storm), leading to relatively low DWD inputs during the study period.

Like inputs, DWD outputs were lower than expected based on observed stocks and projected residence times. Because of differences in the methods by which diameter was measured in 2001 and 2005, volume-based outputs may be biased. Frequency-based estimates were not influenced by measurement differences and are therefore more reliable. Decay-class-transition matrices (Table 4) showed that only decay class 5 pieces had an appreciable chance of being incorporated into the soil over a 4 year period, and only about 10% of all DWD was in class 5 at the initial measurement. Accordingly, outputs through incorporation were very low over the observed interval. Existing DWD tended to decrease in diameter and length, resulting in moderate outputs both from decreases in piece volume and from pieces that fell below our minimum size threshold. Given the minor effect of decay-class transition, it is perhaps unsurprising that no differences in DWD outputs were detected among stand types (Table 2).

Lower than expected inputs and outputs in each management history category, together with changes in decay-class distribution over a 4 year period, indicate that DWD stocks in these stands were not in dynamic equilibrium, most likely as a result of persisting effects of the 1995 storm event.

Table 4. Four year decay-class-transition matrices for downed woody debris in managed (A) and unmanaged (B) stands composed of shade-tolerant hardwoods.

(A) Managed stands.					
Subsequent decay class	Initial decay class				
	1 (n=38)	2 (n=121)	3 (n=182)	4 (n=111)	5 (n=38)
1	0.026				
2	0.615	0.124			
3	0.282	0.554	0.324		
4	0.051	0.215	0.467	0.450	
5	0.026	0.107	0.209	0.514	0.553
Out	0.000	0.000	0.000	0.036	0.447
(B) Unmanaged stands.					
Subsequent decay class	Initial decay class				
	1 (n=4)	2 (n=43)	3 (n=85)	4 (n=36)	5 (n=23)
1	0.000				
2	0.000	0.023			
3	0.500	0.302	0.235		
4	0.500	0.442	0.400	0.361	
5	0.000	0.233	0.318	0.611	0.696
Out	0.000	0.000	0.047	0.028	0.304

While selection practices could affect DWD input and output processes, this was not directly observable in the relatively short study interval. Longer-term data would increase power to detect this potential effect.

DWD decomposition dynamics

Individual pieces of DWD in unmanaged stands tended to move through decay classes 1–3 faster than those from managed stands (Table 3). Decomposition rates of DWD are typically related to the characteristics of DWD pieces and the environmental conditions in which they are found (Laiho and Prescott 2004). Managed and unmanaged stands differed in several downed wood characteristics (Table 2), either because of direct or indirect harvesting impacts. We expected that such differences could account for the slower decay class 1–3 transition rates observed in managed stands.

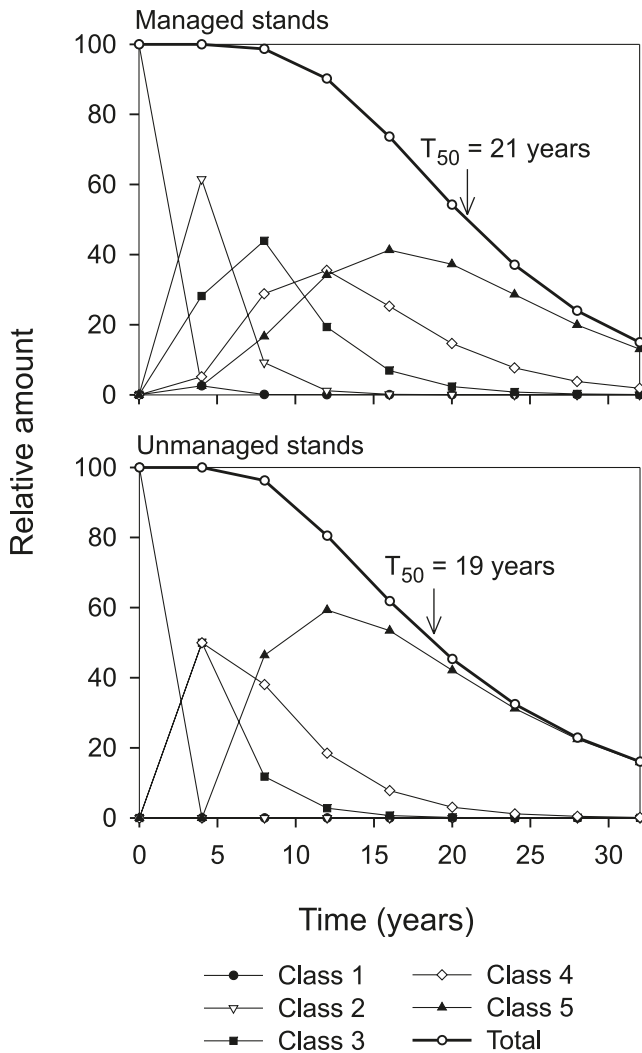
Coniferous DWD moved faster through the first decay class (Table 3), a finding we expect is a result of conifers' tendency to decay from the outside in, as opposed to the heart rotting that is common in sugar maple and other hardwoods (Hale and Pastor 1998). External decay causes faster changes in the bark and wood morphology used to identify the earlier decay classes.

Transitions out of decay class 3 were slowed by three factors: (1) location in a dry or mesic plot, (2) presence of a cut surface, and (3) presence of fruiting bodies of the polypore fungus *G. applanatum* (Table 3). The plot moisture effect reflects the fact that rates of wood decomposition increase with moisture up to the point where oxygen depletion inhibits microbial activity (Yin 1999). Cut pieces were derived from live trees and thus did not undergo decomposition before entering the DWD pool. Pieces derived from snags, which made up a large majority of the total DWD inputs (Table 1), undergo some decomposition before falling and tend to enter the DWD pool in decay class 3 (Angers et al. 2005; Vanderwel et al. 2006). Accordingly, the residence time in class 3 for most pieces of naturally recruited DWD

is expected to be shorter than for DWD pieces that were cut. Finally, we did not expect to find slower decay in DWD bearing fruiting bodies of *G. applanatum*. *Ganoderma applanatum* is a common and aggressive white-rot polypore fungus that attacks live trees. Infected trees undergo some decay before their death and often lose bark. We speculate that *Ganoderma*-infected DWD pieces may appear as decay class 3 soon after their death and then remain in this class longer than uninfected pieces. In addition, as has been hypothesized for other polypore fungi that attack live trees, it is possible that *G. applanatum* produces extracellular metabolites that inhibit colonization by other decay fungi (Niemelä et al. 1995; Renvall 1995; but see Heilmann-Clausen and Boddy 2005). A similar effect could result from changes in wood chemistry induced by *G. applanatum* during infection of sugar maple trees.

Contrary to our expectations, management history maintained a strong influence on decay dynamics even after we accounted for the effects of species group, moisture class, cut surface, and polypore fungi in our analysis (Table 3). We believe the set of piece-level variables we considered characterized the potential differences in DWD between managed and unmanaged stands well, and do not think that piece-level factors can account for the effect of management history reported here. Plot-level differences, however, were summarized only by a three-category scale of moisture classes. Although this variable affected decay class 3 transitions, it most likely did not capture all relevant environmental variation between managed and unmanaged stands. Site factors that are affected by selection silviculture include productivity (Schuler 2004), soil temperature and moisture (Peng and Thomas 2006), canopy openness (Angers et al. 2005), ground and understory cover (Crow et al. 2002), and fungal (Shuter 2002) and faunal communities (Simard and Fryxell 2003), each of which could have contributed to the different decay dynamics found in managed versus unmanaged stands.

Fig. 2. Piece-level decay-class projections of downed woody debris in managed and unmanaged stands. Arrows indicate the time required for half of all pieces to be lost (T_{50}).



Since DWD decayed faster in unmanaged stands, DWD pieces were projected to have a half-life of 19 years from the time they entered decay class 1, compared with 21 years in managed stands (Fig. 2). On average, cut pieces found in decay classes 1–4 in our managed plots were slightly older than projected by our transition matrix. Some of this difference may be attributable to slower transition rates of cut versus uncut pieces, but it remains possible that our projected decomposition times are downwardly biased by a few years. Nevertheless, they are broadly consistent with the DWD longevity others have reported for these species. For example, MacMillan (1988) found only 3 of 41 *Acer* and *Fagus* logs to be older than 25 years in an old-growth forest, and Arthur et al. (1993) determined that only about 10% of the original mass (per hectare) of DWD of these species was still present 23 years after experimental clear-felling.

Slower decay-class transitions in managed stands may partly compensate for potentially lower long-term input rates by lengthening persistence time, thereby leading to higher abundances. Decay class 2 and 3 material, in particular, was longer-lived in managed stands and therefore was expected

to have a higher relative abundance than other decay classes. This is consistent with our finding of a lower mean decay class of DWD in managed than unmanaged stands (Table 2). If unmanaged stands have proportionally higher DWD inputs from snags, which generally enter the DWD pool in a more advanced stage of decay, then the difference in mean persistence time between managed and unmanaged stands should be even more pronounced than that attributable to differences in decay-class transition rates (such an effect was not apparent in our data, however). Although small, the management-related reduction in decay-class transition rates documented here could have ecological implications. Forests in the Haliburton region are most commonly managed with 20 year intervals between stand entries, and a 21 year DWD half-life in managed stands would allow stocks of downed wood to persist throughout the harvest cycle.

Management implications

We considered three potential mechanisms that could produce differences in DWD stocks between managed and unmanaged stands composed of shade-tolerant hardwoods. There was strong evidence for the first mechanism, where selection harvesting generates a pulse of DWD that maintains DWD stocks comparable to those in unmanaged stands for up to 20 years after harvest. Lower live-tree and snag basal areas in managed stands (Table 2) suggest that harvesting reduces long-term sources of DWD, even though this effect was not apparent in observed DWD inputs over the 4 year study interval. Long-term reductions in DWD inputs are expected to lead to lower stocks in managed stands once the harvest pulse is lost. However, DWD was projected to decompose about 10% faster in unmanaged stands than in those managed under selection silviculture, an effect that partly offsets the expected reduction in long-term inputs.

Knowledge of the processes underlying changes in DWD abundance under the selection system can aid in developing practices to lessen adverse management impacts. An existing recommendation to leave unmerchantable boles on site (Ontario Ministry of Natural Resources 1998) may be sufficient to ensure that a postharvest pulse of DWD compensates for low inputs in the short to medium term. However, there is no guarantee that simply leaving unmerchantable boles will continue to be a viable strategy for DWD management as market conditions change; in particular, increasing demand for lower-quality boles as biofuel feedstock will likely lead to reduced DWD levels in managed forests unless additional efforts are made to retain some merchantable material on-site.

Maintaining sources of downed wood is critical for averting long-term DWD reductions in managed stands. Snags are the primary structures from which DWD is derived, and effective measures for snag management should accomplish this objective. Efforts to protect snags during harvesting would help to maintain both snags and DWD over the harvest rotation (Vanderwel et al. 2006). Preserving some declining live trees through harvest, as is required by current cavity-tree retention guidelines, for example (Ontario Ministry of Natural Resources 2004), would likely increase tree mortality rates in managed stands and yield DWD inputs later in a harvest rotation as well.

Our data indicated that several DWD decay-class transitions occur faster in managed than unmanaged stands, but

we were not able to attribute this to any specific piece characteristic or environmental condition. Future research should seek to verify this effect and ascertain the underlying cause of slower decay dynamics in stands managed under selection silviculture.

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