Available online at www.sciencedirect.com
ScienceDirect

Forest Ecology and Management 234 (2006) 48–59

Forest Ecology and Management

www.elsevier.com/locate/foreco

An integrated model for snag and downed woody debris decay class transitions

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

Faculty of Forestry, University of Toronto, 33 Willcocks St., Toronto, Ont., Canada M5S 3B3

Received 29 November 2005; received in revised form 14 June 2006; accepted 16 June 2006

Abstract

In order to project the long-term implications of forest management for coarse woody debris (CWD) and its habitat-related ecological functions, the time frame of snag and downed woody debris (DWD) decomposition needs to be quantified. In the present study, we parameterized models of CWD decay class transitions that explicitly represent decomposition-related changes in white and red pine (*Pinus strobus*, *P. resinosa*) snags and DWD over time. Remeasurements of permanent sample plots in Ontario, Canada, were used to derive models of a tree's condition at death (standing or fallen), snag fall rates, transitions among snag decay classes, and the entry of fallen snags into DWD decay classes. DWD decay class transitions were modelled from the condition of harvest residues across a 27-year chronosequence of shelterwood-harvested stands in central Ontario, and on the quasi-equilibrium decay class distribution of DWD in a series of relatively undisturbed sites. By combining these various model components, an integrated model of CWD decay class transitions was developed to project the condition of snags and DWD pieces over time. Projections showed that white and red pine snags had median fall times of 15–20 and 30 years, respectively. DWD from trees that fell at death was projected to advance through four decay classes over a 55–60-year period, whereas DWD originating from snags was modelled to persist for up to 90 years after tree death because of slower decomposition while standing. For both snags and DWD, decay classes I and II were short–lived relative to later classes. Diameter was found to have a significant effect on DWD transitions into decay classes II and IV but not III, with projections accordingly showing smaller-sized DWD to be less abundant in class III than larger material. Incorporating CWD dynamics such as those modelled here into stand growth and mortality models would enable managers to simulate long-term changes in the quality and quantity of snags and DWD under various forest management regimes, and to evaluate the degree to which CWD-associated habitat features may be maintained over time.

Keywords: Coarse woody debris; Pine; Snags; Downed woody debris; Decomposition; Decay classes; Forest management; Shelterwood; Transition model

1. Introduction

Coarse woody debris (CWD), which consists of both standing dead trees (snags) and material that has fallen to the ground (downed woody debris, DWD), is a dynamic resource in forest ecosystems. Decomposition processes continually alter the physical and chemical structure of CWD, and as a result numerous elements of the forest biota are affected not only by the total amount of CWD, but also by its distribution across different stages of decomposition (Nordyke and Buskirk, 1991; Bader et al., 1995; Simila et al., 2003; Morneault et al., 2004). Accordingly, models of CWD inputs and decomposition are needed to assess the long-term dynamics of snags and DWD under different forest management systems, including accumulations in various decay classes over time and consequent implications for future habitat supply (Lofroth, 1998; Harmon, 2001; Jonsson and Kruys, 2001). Before such models can be developed though, a sound quantitative understanding of the temporal progression of CWD through various stages of decomposition is required.

Research on CWD decomposition has traditionally employed separate approaches for snags and downed woody debris. Studies of snag dynamics have tended to focus on fall rates and the factors affecting them (e.g., Cline et al., 1980; Lee, 1998; Huggard, 1999; Garber et al., 2005); some also have quantified rates of snag breakage (Landram et al., 2002) or progression through a series of decay classes (Raphael and Morrison, 1987; Morrison and Raphael, 1993). These analyses treat snags as discrete units whose condition can be expressed as a function of time standing. In contrast, most studies of the decomposition of downed woody debris have been based on Olson's (1963) model of plant litter decomposition, which uses an exponential decay function to

---

* Corresponding author. Tel.: +1 416 978 0142; fax: +1 416 978 3834.
E-mail address: mark.vanderwel@utoronto.ca (M.C. Vanderwel).

0378-1127/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2006.06.020

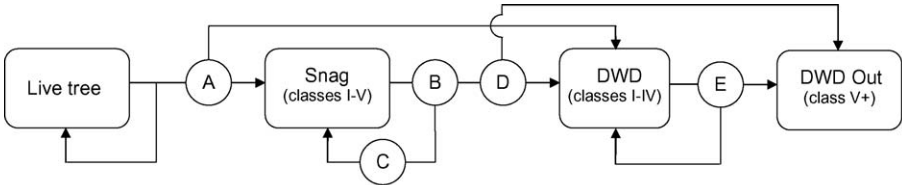

Fig. 1. Schematic illustration of the relationships among model components in the present study. Over a given time interval, trees that die are probabilistically distributed among snag decay classes and downed woody debris (A). Snags may remain standing or fall (B), and conditionally either undergo transitions among snag decay classes (C) or are distributed among DWD decay classes upon falling (D). Downed woody debris progresses through a series of decay classes (E), and here is considered to leave the system upon exiting class IV.

describe change in density over time. Extending this concept to decaying wood, many researchers have modelled the dynamics of DWD in terms of a gradual loss of density (e.g., Lambert et al., 1980; Means et al., 1985; Harmon et al., 1987; MacMillan, 1988). Some studies have also used the exponential decay model to represent the loss of volume through fragmentation (Lambert et al., 1980) or the decrease in relict CWD volume during stand development (Duvall and Grigal, 1999). Recently, Kruys et al. (2002) employed a stage-structured matrix model as an alternative framework for modelling CWD decomposition. Their approach tracks the amount of coarse woody debris within individual decay classes, and can thereby be linked with habitat studies that have long used decay classes as a measure of the changing quality of CWD (Maser et al., 1979). Kruys et al.'s (2002) approach also brings the analysis of DWD dynamics more in line with that of snags by formulating the decomposition process as a series of transitions through discrete states over time.

In the present study we analyzed the temporal progression of white and red pine (*Pinus strobus*, *P. resinosa*) CWD through different stages of decomposition, including transitions to snags and DWD following tree death, from snags to DWD, and among both snag and DWD decay classes. These components were linked together to produce a probabilistic model that describes the position (standing or downed) and condition (decay class) of individual pieces of CWD over time (Fig. 1). For snags, we modelled breakdown from the time of tree death until fall based on remeasurement data from a network of permanent sample plots in central Ontario, Canada. Although permanent plots have been used to investigate snag fall rates elsewhere (e.g., Lee, 1998), the present study is unique in presenting a detailed analysis of snag dynamics, including rates of fall, transitions among decay classes, and decay class distributions at death and at fall. For downed woody debris, decay class transitions were modelled from a 27-year chronosequence of shelterwood-harvested stands in Algonquin Provincial Park, Ontario. Several studies have previously used logging residues to quantify rates of CWD decomposition (Foster and Lang, 1982; Fahey, 1983; Erickson et al., 1985; Frangi et al., 1997), but ours is the first to apply this approach to transitions through a sequence of decay classes. Our ultimate objective in carrying out these analyses of snag and downed woody debris dynamics was to develop an integrated model that describes the progression of CWD pieces through a series of decay classes from tree death until the late stages of log decomposition.

2. Methods

2.1. Snags

2.1.1. Data

Snag data were obtained from 55 permanent sample plots in central Ontario (Fig. 2) that were established by the Ontario Ministry of Natural Resources from 1992 to 1995. These plots were remeasured once between 1997 and 2003, and were selected from among 62 remeasured plots in site regions 4E and 5E (Hills, 1959) that contained white or red pines (7 plots had no dead trees of these species and therefore contributed no snag data). Although most of the plots (43 of 55) were remeasured after 5 or 6 years, some were remeasured at 4-, 7-, or 9-year intervals.

Plots were generally dominated by white and/or red pine, with red oak (*Quercus rubra*), white birch (*Betula papyrifera*), spruce (*Picea glauca*, *P. mariana*), balsam fir (*Abies balsamea*),

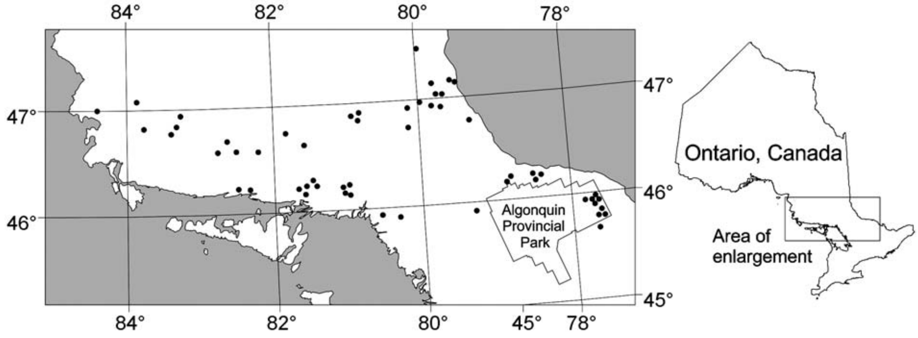

Fig. 2. Locations within central Ontario of 55 permanent sample plots used to model white and red pine snag dynamics. Actual plot positions may not be exactly as shown as some points were shifted slightly to keep symbols from overlapping.

and red maple (*Acer rubrum*) comprising less common associates. A few of the plots were dominated by trembling aspen (*Populus tremuloides*), white birch, or sugar maple (*Acer saccharum*) but still contained white and/or red pine. The great majority of these plots had an estimated age of 90–120 years and exhibited an uneven-aged structure.

Each plot consisted of three circular 400 m^2 sub-plots in which all live and standing dead trees were censused at each measurement as described in Hayden et al. (1995). Species and diameter at breast height (DBH; 1.3 m) were recorded for all trees $\geq$7.5 cm DBH, and standing or fallen dead trees were each assigned to one of five decay classes (Table 1).

Five of the plots were harvested in the interval between measurements; trees and snags in these plots that died or fell during this period were excluded from analysis, but snags that did not fall were retained. Also, there were 23 snags recorded as being in an earlier decay class at the second measurement than at the first measurement, presumably due to differences between observers in assessing decay class. To correct for these erroneous transitions, each of these snags was randomly reassigned to be in either the earlier or later decay class at both measurements. After applying these procedures, our snag data set consisted of 68 white and red pine deaths, 83 snag falls, and 343 transitions among snag decay classes.

2.1.2. Model form

We constructed a variety of transition models to represent the dynamics of snag breakdown and fall as a function of species, size, and/or decay class. Because plots were remeasured after different periods of time, it was necessary to first standardize fall and decay class transition rates to a common interval length (5 years). This was accomplished by modelling these transitions with a negative exponential function that represents a constant transition probability over time (Fox, 2001):

$$Pr = \mathrm{e}^{-\left(\beta_0+\sum_i \beta_i x_i\right)t} \tag{1}$$

where Pr is the probability of a tree or snag remaining in the original condition after t years and the expression $\beta_0 + \Sigma\beta_i x_i$ represents the exponential decay constant as a linear function of continuous and categorical predictor variables, x_i (described below). The 5-year transition probability (T_5) was then calculated as:

$$T_5 = 1 - \mathrm{e}^{-\left(\beta_0+\sum_i \beta_i x_i\right)5} \tag{2}$$

In the case of fall rates, it was relatively straightforward to apply this transition model to snags that were either standing or fallen at the time of remeasurement. For transitions among snag decay classes, the model was extended to allow transitions into multiple later decay classes between measurements. For snags in each initial decay class (except the final one, class V), a series of dichotomous transition models were constructed to represent the probabilities of advancing to each possible successive decay class. The transition probability of being in any given decay class m after 5 years, $T_5(m)$, was then calculated as:

$$T_5(m) = T_5(m^+) - T_5([m+1]^+) \tag{3}$$

where $T_5(m^+)$ is the probability of being in class m or higher after 5 years (equal to one if m is the initial decay class) and $T_5([m+1]^+)$ is the probability of being in class $m + 1$ or higher after 5 years (equal to zero if m is the final class).

This same approach was also used to model the fate of trees that died between measurements. In that analysis, a fallen state was included as the final category of the transition model so that a tree that died could be in one of five snag decay classes or in a downed position.

2.1.3. Statistical analysis

Snag fall rates were estimated according to Eq. (2) with a negative exponential regression of status (standing = 1, fallen = 0) at second measurement against the remeasurement interval, with no intercept term. This regression was implemented through a generalized linear model with a log-link function and a binomial sampling distribution. The slope of the logarithmic-scale regression line corresponded to $-\beta_0$ in Eq. (1), and represented the value of the exponential decay constant before incorporating potential effects ($-\beta_i$) of other factors as predictor variables. Differences in fall rates by DBH (log-transformed), decay class, and species were analyzed by including terms for these variables (x_i) as interaction effects with the remeasurement interval. The significance of each factor was assessed using a Type 3 likelihood-ratio test.

Transitions among snag decay classes were likewise analyzed using negative exponential regression with generalized linear models. The dichotomous transition models representing all possible transitions from a given initial snag

Table 1
Snag and downed woody debris decay class descriptions

Decay class	Description
Snags	
I	Tree is recently dead. Top is intact. Most fine branching still present. Bark is intact
II	Top is intact. Most of the fine branches have dropped. More than 50% of the coarse branches are left. Bark may begin to loosen
III	Top is intact. Fewer than 50% of the coarse branches are left. Bark may or may not have sloughed off
IV	Top is broken. No coarse branches remain. Bark may or may not have sloughed off. Height at least 6 m
V	Top repeatedly broken. No coarse branches remain. Bark may or may not have sloughed off. Height less than 6 m
DWD	
I	Wood is hard. All bark is still intact
II	Wood is hard. Bark has begun to fall off
III	Wood is soft and has some give when kicked. Usually no bark remaining
IV	Wood is substantially decayed and pieces easily slough off. Inner heartwood may be soft but is intact. Moss usually present on the outer surface
V	Wood is decayed throughout. Texture is powdery and resembles soil

decay class were not independent of each other, and thus were fit to the data simultaneously. Differences between the two pine species were considered for snags in each initial decay class by including a term for species as an interaction effect with the remeasurement interval. Likelihood-ratio tests were used to assess the significance of these added terms.

The decay class distribution of trees that died between measurements was analyzed in the same manner as snag transitions, but with the fallen state added as a sixth category. The effect of DBH (log-transformed) was considered by including a term for its interaction with the remeasurement interval, and by assessing its significance with a likelihood-ratio test. Species differences were not incorporated as there were only 13 red pine deaths.

Lastly, the entry of snags into downed woody debris decay classes was analyzed as a function of snag decay class. As the dependent variable (DWD decay class) was on an ordinal scale, we employed ordinal logistic regression under the proportional odds model (Hosmer and Lemeshow, 2000) and treated snag decay class as a continuous independent variable with equal spacing between adjacent categories (Agresti, 1996). The proportional odds model estimates a single slope parameter for the independent variable given the assumption that the effect of the predictor is the same across all levels of the response variable (Hosmer and Lemeshow, 2000). A Score test (Allison, 1999) was used to test the validity of this assumption. The effect of snag decay class was assessed for significance using a likelihood-ratio test. It was not feasible to correct for differences in remeasurement intervals; because other transitions were standardized to a 5-year interval, the model implicitly assumed that the DWD decay class at remeasurement was the same as it would have been 5 years after the first measurement.

For each of the analyses described above (snag fall, decay class transitions, position and decay class at tree death, and DWD decay class distribution at fall), 90% confidence intervals were computed for all parameter estimates using a bootstrap resampling procedure (Manly, 1997). With this approach, each of the original data sets was repeatedly sampled with replacement to generate 5000 new data sets equal in size to the original. Parameter estimates were calculated for each of these resampled data sets, and used to derive sampling distributions for the transition probabilities of interest. The 5th and 95th percentiles of these sampling distributions defined the lower and upper bounds of 90% bootstrap confidence intervals for each parameter.

Taken together, these various estimates of stage-based transitions yielded a model of snag dynamics that could project a snag's condition over time, from tree death until its entry into the DWD pool at fall.

2.2. *Downed woody debris*

2.2.1. *Data*

A model of downed woody debris decay class dynamics was developed based on the condition of harvest residues in 26 pine-dominated stands in eastern Algonquin Provincial Park. These stands ranged from 76 to 123 years of age (based on the provincial Forest Resource Inventory [Ontario Ministry of Natural Resources, *unpublished data*]) and had been harvested under the uniform shelterwood system (Pinto et al., 1998) between 1976 and 2002. Each harvest year within this range was represented by a single stand, except for 1987, which was unrepresented in the chronosequence.

In the summer of 2003, each of these stands was searched for pieces of DWD that showed evidence of a cut surface, and thus originated from trees that had presumably died and fallen during the harvesting event. The cut pieces that we found were generally in the form of tree tops, large branches, and short sections of lower boles that were left when trees were delimbed and bucked to log length. Species (where positively identifiable), diameter (minimum 7.5 cm, measured at the cut surface), and decay class (Table 1) were recorded for each piece of cut white or red pine DWD encountered.

2.2.2. *Model form*

We developed time-dependent transition models to represent the progression of DWD through a series of decay classes. A logistic model form was used to represent transitions among decay classes as a function of time since tree death:

$$Pr = \frac{1}{1 + e^{\alpha+\beta t}} \tag{4}$$

where Pr is the probability of a piece of DWD remaining in the original condition t years after being cut, and α and β are model parameters. Conversely, the complement of this function (one minus its value) represents the probability of undergoing the transition of interest between years 0 and t. With its sigmoidal shape, the logistic model allowed transition probabilities to vary over time and thus could incorporate a lag period, during which the probability of advancing to a later decay class was close to zero, over the range where the curve initially has a shallow slope. Differences in transition rates among species were not analyzed because there were too few red pine pieces sampled and because it was usually not possible to distinguish the two species when the bark was missing. The potential effects of log-transformed piece diameter, ln (D), were incorporated into the model by allowing each parameter to vary as a linear function of this continuous independent variable:

$$\alpha = \alpha_0 + \alpha_1 \ln(D) \tag{5}$$

$$\beta = \beta_0 + \beta_1 \ln(D) \tag{6}$$

For DWD to have reached a given decay class by year t, it must have already passed through each earlier decay class by this point. The transition model was thus formulated such that the complement of Eq. (4) represented the conditional probability, $Pr_c(m^+|t)$, of a piece reaching decay class m by age t, given that it had already reached class $m-1$ by then. The unconditional probability of reaching decay class m by age t, $Pr_u(m^+|t)$, was calculated as:

$$Pr_u(m^+|t) = \prod_{i=2}^{m} Pr_c(i^+|t) \tag{7}$$

After finding the unconditional probabilities of reaching each decay class in this manner, the transition probability, $T_{a\to b}(m^{+})$, of reaching a later decay class m over a given time interval since tree death, $a\to b$, could be calculated as:

$$T_{a\to b}(m^{+}) = 1 - \frac{1 - Pr_u(m^{+}|b)}{1 - Pr_u(m^{+}|a)} \tag{8}$$

where $Pr_u(m^{+}|a)$ and $Pr_u(m^{+}|b)$ are the probabilities of undergoing the transition by the start and end of the interval, respectively. Finally, the transition probability of DWD being in a specific decay class after a given time interval was calculated as the probability of reaching that class minus the probability of reaching the next higher class, as in Eq. (3).

2.2.3. Statistical analysis

Model parameters were estimated using ordinal logistic regression against time since harvest on a series of continuation-ratio logits. This analysis involved dichotomizing the decay class data to compare the probability of being in a given decay class to that of being in a later one (e.g., I versus II and higher, II versus III and higher, etc.). Because the dichotomous comparisons were independent of each other, each could be fit to the data separately without violating underlying statistical assumptions (Hosmer and Lemeshow, 2000). Generalized estimating equations using an exchangeable correlation structure were employed to account for lack of independence among samples from the same site (Quinn and Keough, 2002).

Size-dependent differences in decay class transitions were considered by including terms for log-transformed piece diameter and its interaction with time to the models. Type 3 Wald tests were used to assess the significance of these added terms (Quinn and Keough, 2002).

The above procedures enabled us to project changes in DWD decay class over time based on a piece's size and age. Too few cut pieces of DWD were found in decay class V to reliably analyze changes from decay class IV to V; an alternative approach was therefore needed to model DWD transitions out of decay class IV.

2.2.4. Transitions out of class IV

As described below, a final function was derived to represent DWD transitions out of decay class IV. We did not give further consideration to the dynamics of DWD upon reaching class V, but this exclusion was not a major concern given that material in class V constitutes only about 10% of the DWD volume in pine-dominated stands in Algonquin Provincial Park (*unpublished data*).

When input and decomposition rates of DWD are constant over time, the amount of DWD present should equal the summation of age-specific survival probabilities, multiplied by the rate of input. The survival function for decay classes I to m is equivalent to the probability of a piece not having reached class $m + 1$ by year t, as given by the complement of Eq. (7). Taking the ratio of the equations for classes I–III and I–IV, we have:

$$\frac{A_{\text{I–III}}}{A_{\text{I–IV}}} = \frac{I \times \sum_t S_{\text{I–III}}(t)}{I \times \sum_t S_{\text{I–IV}}(t)} \tag{9}$$

where $A_{\text{I–III}}$ and $A_{\text{I–IV}}$ represent the amount of DWD in classes I–III and I–IV, respectively, I is the annual rate of DWD input, and $S_{\text{I–III}}(t)$ and $S_{\text{I–IV}}(t)$ are the survival functions for DWD classes I–III and I–IV, respectively. By cancelling input rate from the equation and rearranging:

$$\sum_t S_{\text{I–IV}}(t) = \sum_t S_{\text{I–III}}(t) \times \left(\frac{A_{\text{I–III}}}{A_{\text{I–IV}}}\right)^{-1} \tag{10}$$

This shows that the function describing transitions out of class IV can be calculated in terms of the class I–III survival function, and the equilibrium proportion of DWD (excluding class V) in classes I–III.

The equilibrium decay class distribution of DWD was estimated from seven mature (80–120 years old), pine-dominated sites in Algonquin Provincial Park that had not been harvested or subjected to any major disturbances for at least 28 years. Two other undisturbed sites were discarded because they had very little class IV DWD and thus were not considered to be near equilibrium. The volume of downed woody debris, by decay class, was estimated within a 79 ha area at each of the seven sites using 450–1170 m of line intersect sampling (Van Wagner, 1968). While it is difficult to verify that 80 to 120-year-old pine-dominated stands exhibit a stable DWD decay class distribution, McGee et al. (1999) found that maturing (90–100 years old) and old-growth (>150 years old) northern hardwood stands contained approximately equal proportions of DWD volume across decay classes. This result suggests that the decay distribution of DWD has equilibrated in hardwood stands 90–100 years of age. If a similar pattern holds for pine-dominated stands, then our equilibrium assumption should be tenable.

As with the earlier DWD transitions, the transition function out of class IV, equivalent to the complement of the class I–IV survival function, was modelled as the product of a series of logistic equations (Eq. (7)). There were two unknown parameters in Eq. (10) to be quantified: namely, the intercept (α) and slope (β) parameters of the logistic function for decomposition out of class IV, given that a piece of DWD had reached this class. The slope parameter represented variability in transition ages; values close to zero indicate that transitions occur over a wide range of ages, whereas higher values signify that transitions tend to occur close to the mean age. Several studies have previously found that variability in residence time increases with decay class (Means et al., 1985; Brown et al., 1998; Kruys et al., 2002). Accordingly, the value of β was arbitrarily set at 75% of that for the transition from class III to IV. The remaining unknown parameter (the intercept term, α) was solved numerically from Eq. (10). Calculations were based on a piece diameter of 19.2 cm, which was the average diameter of DWD from the undisturbed sites in Algonquin Park.

This procedure for estimating transitions out of class IV involved a number of assumptions for which there was some uncertainty. To assess the importance of the particular values chosen, a sensitivity analysis was conducted in which different parameter values were used. The intercept term was varied by changing the proportion of DWD in classes I–III from one standard error below the mean to one standard error above the mean. The slope parameter was modified to range from 50 to 100% of that for the class III–IV transition. These values delimited a range of possible transition ages that corresponded to ''low'' and ''high'' parameter estimates.

Together with our model of transitions among the first four decay classes, the approach described above enabled us to determine the age at which a piece of DWD was expected to reach the most advanced stage of decomposition before being fully incorporated into the forest floor.

2.3. Projected dynamics of coarse woody debris

Longevity and decay class dynamics were explored by using the parameterized transition models to project the fates of (1) snags, (2) DWD from trees that fell at death, and (3) DWD from trees that died standing, over time. For snags, an initial cohort of 100 decay class I snags was followed at 5-year intervals based on estimated fall and decay class transition rates. For DWD from trees that fell and entered DWD class I at death, decay class transition models were similarly used to follow the progression through different stages of decomposition at 5-year intervals. Decay class changes of DWD from fallen snags were modelled as a function of time since death by combining the sub-models for snag falls, snag decay class transitions, transitions from snags to DWD, and DWD decay class transitions (Fig. 1). This projection of snag-derived DWD was not directly based on empirical observations, but instead integrated the various snag and DWD transitions to model the changing condition of CWD from a tree's standing death until the late stages of log decomposition.

Because DWD transition rates were age-dependent, it was necessary to assign a corresponding ''age'' to each newly-fallen piece of snag-derived DWD. Snags decompose at a different rate than DWD (Onega and Eickmeier, 1991); time since death, therefore, was not an appropriate age for the DWD transition model in this case. In a recent study, Storaunet and Rolstad (2002) found that: (1) the rate at which DWD passed through decay classes was unrelated to time spent as a snag; and (2) time since fall was a much better predictor of decay class than time since death. In accordance with these findings, DWD from fallen snags was initially assigned the mean age for the decay class that it was projected to enter (as calculated from the decay class transition models), plus 2.5 years, which assumed that it fell midway through the previous interval. Snag-derived DWD was then projected to continue through subsequent decay classes at the same rate as DWD from fallen trees.

3. Results

3.1. Snags

3.1.1. Fall rates

An initial test of the effect of DBH indicated that it was a significant factor affecting fall rates ($\chi^2 = 6.23$, d.f. = 1, $P = 0.0126$). Upon closer examination, however, this result appeared to be driven by the small number of falls among large snags (only 1 fall out of 52 snags that were >28 cm DBH). Among snags ≤28 cm, fall rates did not vary with DBH ($\chi^2 = 1.10$, d.f. = 1, $P = 0.2946$). Because it was impossible to reliably determine fall rates for these larger snags based on a single fall, the effect of DBH, though recognized to be significant, was discarded from the model.

There was no apparent difference in the two pine species' relative fall rates among snag decay classes, as shown by the lack of an interaction effect between decay class and species ($\chi^2 = 0.65$, d.f. = 4, $P = 0.9571$). After removing this term, the effects of both decay class ($\chi^2 = 11.95$, d.f. = 4, $P = 0.0177$) and species ($\chi^2 = 10.21$, d.f. = 1, $P = 0.0014$) were significant. The resulting model of white and red pine snag fall rates (Table 2) revealed that the probability of falling increased with decay class up to class IV, but then dropped markedly for snags in class V. White pine snags had a 13% lower chance of remaining standing over a 5-year period than red pine snags.

3.1.2. Decay class transitions

Decay class II red pine snags advanced to later classes faster than white pine snags ($\chi^2 = 18.54$, d.f. = 3, $P = 0.0003$), but transitions from other classes did not differ between the two species (I: $\chi^2 = 6.08$, d.f. = 4, $P = 0.1936$; III: $\chi^2 = 1.25$, d.f. = 2, $P = 0.5349$; IV: $\chi^2 = 0.01$, d.f. = 1, $P = 0.9422$). The resulting matrix of estimated transition rates (Table 3) showed that a minority of snags would remain in classes I or II after 5 years. By contrast, snags that did not fall were relatively slow to move out of decay classes III and IV.

3.1.3. Position and decay class at tree death

There was no significant effect of DBH on the position and decay class distribution of dead trees at the end of the 5-year interval in which they died ($\chi^2 = 4.91$, d.f. = 5, $P = 0.4264$).

Table 2
Five-year probabilities of snag fall for white and red pine, as calculated from a negative exponential model of fall rates based on 426 snags in central Ontario

Species	Snag decay class				
	I	II	III	IV	V
White pine	0.130 (0.076–0.194)	0.164 (0.108–0.204)	0.212 (0.145–0.256)	0.325 (0.213–0.399)	0.200 (0.131–0.251)
Red pine	0.000 (0.000–0.088)	0.039 (0.000–0.103)	0.094 (0.040–0.159)	0.224 (0.118–0.319)	0.080 (0.027–0.146)

The 90% bootstrap confidence interval of each parameter estimate is given in parentheses.

Table 3
Calculated 5-year conditional transition probabilities among decay classes of white and red pine snags in central Ontario, given that a snag had not fallen

Snag decay class 5 years later	Initial snag decay class					
	I ($n = 47$)	II		III ($n = 101$)	IV ($n = 45$)	V ($n = 62$)
		White pine ($n = 67$)	Red pine ($n = 21$)			
I	0.109 (0.032–0.194)					
II	0.368 (0.253–0.490)	0.348 (0.257–0.440)	0.234 (0.078–0.381)			
III	0.471 (0.358–0.586)	0.601 (0.506–0.694)	0.434 (0.253–0.620)	0.704 (0.630–0.775)		
IV	0.035 (0.000–0.086)	0.051 (0.013–0.092)	0.252 (0.122–0.409)	0.270 (0.200–0.340)	0.913 (0.844–0.978)	
V	0.017 (0.000–0.053)	0.000 (0.000–0.000)	0.081 (0.000–0.166)	0.027 (0.009–0.054)	0.087 (0.022–0.156)	1.000

The 90% bootstrap confidence interval of each parameter estimate is given in parentheses. Classes I, III, IV, and V are for both species combined.

Table 4
Modelled probability of fallen white and red pine snags entering downed woody debris decay classes II–V, by snag decay class

DWD decay class	Snag decay class				
	I ($n = 8$)	II ($n = 17$)	III ($n = 26$)	IV ($n = 20$)	V ($n = 12$)
II ($n = 4$)	0.162 (0.058–0.303) *0.125*	0.078 (0.019–0.140) *0.059*	0.036 (0.008–0.075) *0.000*	0.016 (0.002–0.044) *0.100*	0.007 (0.001–0.027) *0.000*
III ($n = 66$)	0.815 (0.684–0.921) *0.875*	0.871 (0.793–0.944) *0.882*	0.854 (0.785–0.927) *0.962*	0.762 (0.672–0.848) *0.600*	0.599 (0.392–0.770) *0.583*
IV ($n = 8$)	0.016 (0.003–0.041) *0.000*	0.035 (0.010–0.066) *0.000*	0.074 (0.032–0.115) *0.039*	0.140 (0.067–0.225) *0.200*	0.226 (0.102–0.382) *0.250*
V ($n = 5$)	0.007 (0.001–0.025) *0.000*	0.017 (0.003–0.042) *0.059*	0.037 (0.010–0.072) *0.000*	0.082 (0.030–0.143) *0.100*	0.169 (0.057–0.322) *0.167*

The 90% bootstrap confidence interval of each parameter estimate is given in parentheses, followed by the observed proportion in italics.

Most dead trees were found in snag decay classes I (30.9% [90% bootstrap confidence interval: 22.1–39.8%]) or II: (37.6% [28.5–47.3%]), whereas relatively few entered later snag classes (III: 9.1% [3.9–14.6%]; IV: 5.2% [1.3–9.4%]; V: 2.5% [0.0–5.2%]). Only 14.7% (8.5–21.3%) of trees were expected to fall in the same 5-year interval as they died.

3.1.4. DWD decay class distribution at fall

There were 83 snags that fell (72 white pine, 11 red pine), about 80% of which were in DWD decay class III at remeasurement. No snags ever entered DWD class I after falling. A Score test showed that the proportional odds assumption was satisfied ($\chi^2 = 3.43$, d.f. = 2, $P = 0.1804$) and that the effect of snag decay class could be represented by a single parameter. This term was highly significant ($\chi^2 = 10.88$, d.f. = 1, $P = 0.0010$), indicating that snag decay class was a good predictor of log decay class. Projections of fallen snags into DWD decay classes showed that although most snags would always enter into class III, a shift towards later classes occurred with a greater degree of snag decomposition (Table 4).

3.2. Downed woody debris

In total, 765 pieces of DWD were tallied. The majority of pieces in classes I and II were white pine, but pieces in later classes usually could not be identified to species. Piece diameter followed an approximately lognormal distribution, with a geometric mean of 19.0 cm. Likelihood-ratio tests revealed that diameter had a significant effect on transitions into class II (intercept: $\chi^2 = 40.31$, d.f. = 1, $P < 0.0001$; slope: $\chi^2 = 11.21$, d.f. = 1, $P = 0.0008$) and IV (intercept: $\chi^2 = 11.10$, d.f. = 1, $P = 0.0009$; slope: $\chi^2 = 7.27$, d.f. = 1, $P = 0.0070$), but not III (intercept: $\chi^2 = 1.62$, d.f. = 1, $P = 0.2037$; slope: $\chi^2 = 1.84$, d.f. = 1, $P = 0.1751$). Larger pieces moved into class II over a longer period of time than smaller ones. Extrapolating back to the time of harvest, more large diameter logs also appeared to enter class II directly. Smaller DWD reached class IV sooner than larger pieces on average, and did so more gradually.

When the estimated parameters (Table 5) were used to reconstruct the distribution of DWD over time, the resulting models closely matched observed distributions across decay classes (Fig. 3). DWD of the geometric mean diameter (19 cm) in classes I and II showed abrupt transitions around 3 and 10 years after death, respectively. By contrast, DWD in class III moved to the next class over a longer period of

Table 5
Parameter estimates for an ordinal logistic regression model of white and red pine downed woody debris decay class transitions

Transition	α	β
I → II+	$-7.295 + 1.888 \ln(D)$	$1.325 - 0.239 \ln(D)$
II → III+	-9.663	0.934
III → IV+	$3.882 - 2.986 \ln(D)$	$-0.076 + 0.093 \ln(D)$
IV → out	-5.584	0.149

D represents piece diameter, in cm.

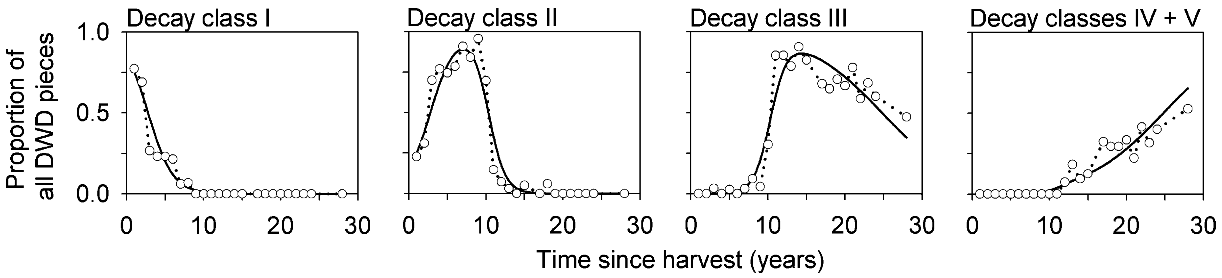

Fig. 3. Comparison of observed (open circles, dotted lines) and modelled (solid lines) decay class distributions of cut white and red pine downed woody debris over time. Modelled distributions are based on a diameter of 19 cm (the geometric mean). Observed distributions were not plotted for times since harvest of 25–27 years because very few (<5) pieces were located in these sites. Decay classes IV and V were combined because too few pieces were sampled in class V to reliably model their distribution separately from those in class IV.

time, with half expected to reach class IV within 25 years of death.

3.2.1. Transitions out of class IV

Across seven undisturbed sites, the mean (±S.E.) volume of DWD in decay classes I–III was 65% (±4%) of that in classes I–IV. Based on the assumption that these sites were at equilibrium, and on the survival function from decay classes I to III, half of the DWD of mean diameter was expected to leave class IV within 39 years of death. All but the last 5% was expected to decompose within another 19 years. Sensitivity analysis indicated that the median transition age could have reasonably ranged from 36 to 41 years, and that it might have taken an additional 15–29 years for all but the last 5% to leave this class.

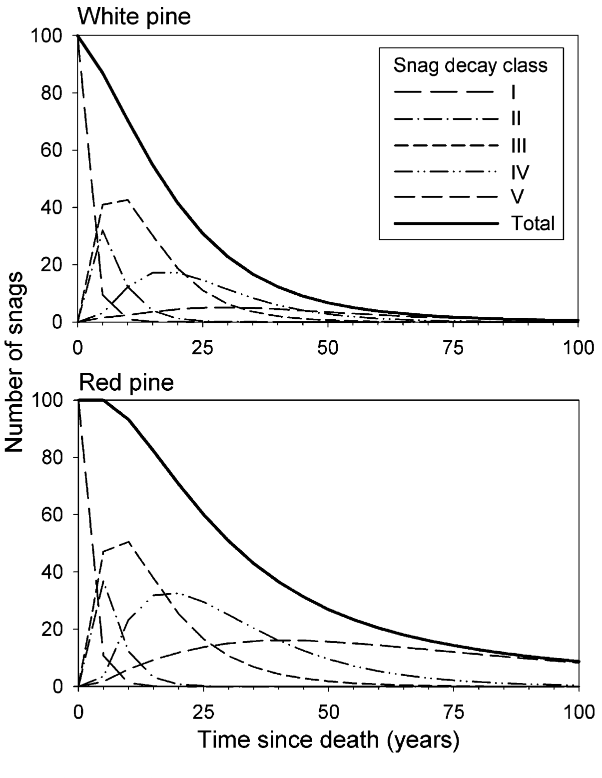

Fig. 4. Projections of snag longevity and decay class dynamics for an initial cohort of 100 newly-dead white or red pine decay class I snags.

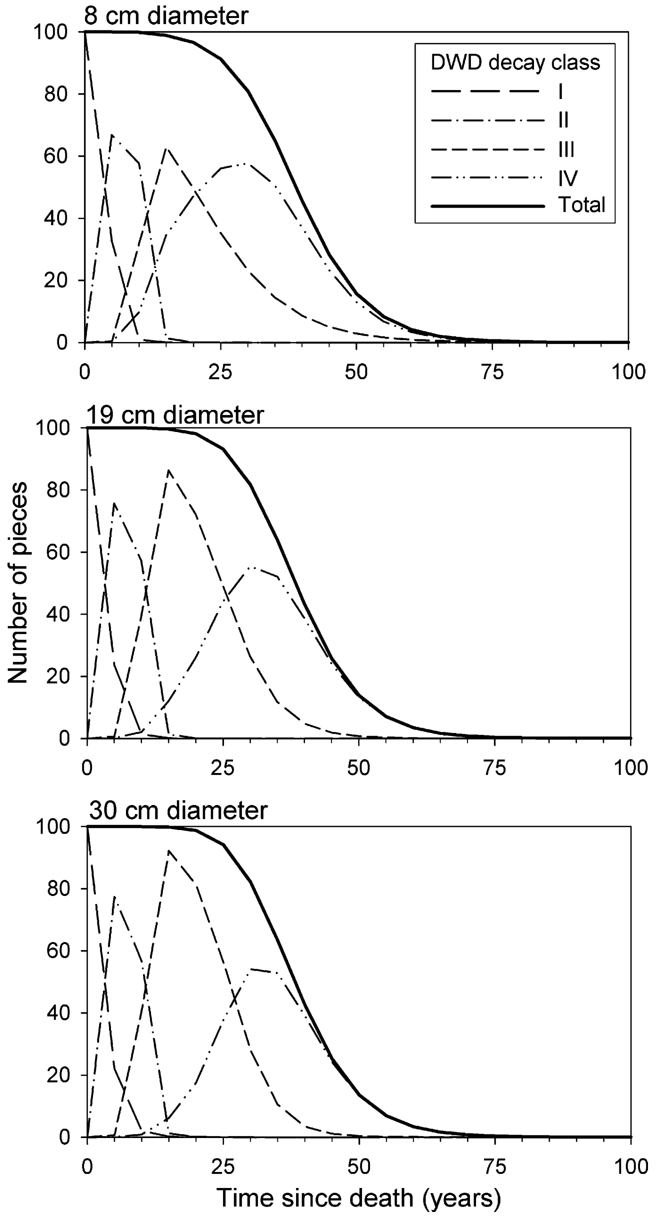

Fig. 5. Projections of downed woody debris longevity and decay class dynamics for an initial cohort of 100 newly-dead decay class I pieces originating from fallen trees. DWD pieces were considered to be lost upon exiting decay class IV.

3.3. Projected dynamics of coarse woody debris

White and red pine snags in decay classes I and II lost most of their branches in a short period, such that the majority of snags still standing after 5 years had already reached class III (Fig. 4). Snags remained in classes III and IV longer, but most that were still standing had broken and entered decay class V by age 50. At this point, 93% and 73% of white and red pine snags, respectively, had fallen. Red pine snags that reached class V fell at a slow rate, with 9% of the original cohort still standing after 100 years. Median fall times for white and red pine snags were 15–20 and 30 years, respectively.

As was observed for harvest residues, nearly all DWD was projected to reach class III within 15 years of death (Fig. 5). The strongest effects of diameter were seen in the relative abundance of decay classes III and IV. Small pieces reached class IV more quickly, and were therefore less abundant in class III than larger pieces.

Downed woody debris derived from snags (Fig. 6) exhibited several differences from DWD derived from trees that fell immediately at death (Fig. 5). Most notably, no DWD from snags was projected to enter class I, and very little was projected to occur in class II. Classes III and IV from snags both had wider age distributions than the same classes from fallen trees due to the gradual rate of input from snag falls. Correspondingly, some downed woody debris from snags (particularly red pine) could persist longer after tree death than that from fallen trees; for example, 95% of DWD from trees that fell at death would leave class IV within 55–60 years (Fig. 5), but this same proportion of snag-derived red pine DWD would not do so until at least 90 years after tree death (Fig. 6).

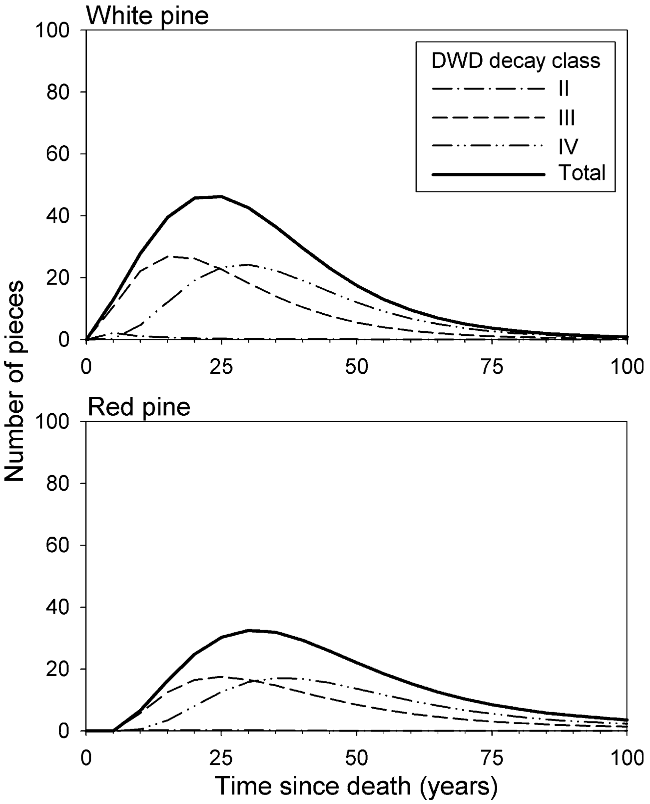

Fig. 6. Projections of downed woody debris longevity and decay class dynamics for 19 cm diameter pieces originating from an initial cohort of 100 newly-dead white or red pine decay class I snags. DWD pieces were considered to be lost upon exiting decay class IV.

4. Discussion

4.1. Interpretation of decomposition patterns

4.1.1. Standing and fallen mortality

The great majority of trees considered in the present study died standing, likely as a result of suppression. White and red pine become increasingly shade-intolerant with age (Kershaw, 1993), and have difficulty surviving under an established canopy (Chapeskie et al., 1989). As has been found in other forest types (Tyrrell and Crow, 1994; Senecal et al., 2004), wind proved to be a relatively minor agent of mortality during the interval between measurements. The predominance of standing mortality indicated that dead wood in early stages of decomposition should most commonly occur as snags rather than DWD.

4.1.2. Snag dynamics

Several studies have found that large snags tend to stand for longer than small ones (e.g., Landram et al., 2002; Garber et al., 2005). Although there were too few large snags to accurately determine their rate of fall in the present study, it was clear that snags with a DBH greater than 28 cm were less likely to fall than smaller snags. Large trees have a greater proportion of decay-resistant heartwood than smaller trees (Sellin, 1994), which may extend the time they are able to withstand the effects of fungal decay before falling. Snags less than 28 cm DBH may not have formed enough heartwood to support themselves upright, thus producing no apparent relationship between diameter and fall rate over this size range. Because the effect of snag diameter was not included in our projections of snag decomposition, the number of small snags remaining standing was probably overestimated slightly and that of large snags underestimated.

Although the permanent sample plot data used in the present study did not provide information on time since death specifically, the decay class system proved to be an effective surrogate measure that revealed changes in snag fall rate by degree of decomposition (Table 2). Fall rates increased across the first four decay classes, presumably as a result of progressive weakening of the bole through fungal decomposition. Snags in decay class V, which had broken to a height of less than 6 m, had lower fall rates than snags in the preceding class. These broken snags had a low centre of gravity and, presumably, reduced susceptibility to windthrow as a result.

4.1.3. Downed woody debris dynamics

Ninety-five percent of white and red pines that fell at the time of death were projected to pass through four decay classes within a period of 55–60 years. This was very close to the 95% breakdown time of 55 years for red pine reported by Alban and Pastor (1993), who based their estimate on an exponential decay function for wood density. Duvall and Grigal (1999) modelled the accumulation of CWD in red pine stands, and found that CWD pre-dating stand initiation should decompose, on average, by ages 15 and 90 in managed and unmanaged stands, respectively. This is a very wide range, but our estimate of decomposition time fell about 5 years from its midpoint. Both of these studies took a different approach than was used in the present study of course, making strict comparisons difficult. Nevertheless, the broad agreement among estimates suggests that our overall decomposition time for DWD was a reasonable one.

Downed woody debris in the earliest stage of decomposition (class I) was short-lived (Fig. 3). Relatively steady inputs of dead trees are therefore necessary for DWD to be continuously available in this state (Kruys et al., 2002). However, mortality is a highly variable and unpredictable event (Franklin et al., 1987). Periods with unusually low mortality may occasionally occur, leading to local breaks in the temporal continuity of DWD in the earliest decay class. By contrast, highly decayed DWD may be present over a period of several decades, and thus is expected to be less variable in time than the earlier decay classes.

Decay classes I and II both had sharply-defined transition times, and rapidly disappeared within 10 and 15 years, respectively. The transition from class III into IV occurred much more gradually, such that DWD could enter class IV anywhere from 15 to 40 (or more) years after death (Fig. 5). The latter effect was likely the result of variable decomposition rates. DWD reaches decay class IV when its sapwood becomes thoroughly decayed, a process that can vary according to the activity of decomposer organisms and on local environmental factors (Laiho and Prescott, 2004). This variability can lead to considerable overlap in the age distributions of DWD in late decay classes (Brown et al., 1998).

The decay class and age distributions of DWD from snags (Fig. 6) differed markedly from those of DWD from trees that fell at death (Fig. 5). Most notably, no snag-derived DWD was projected to enter decay class I, and a negligible volume entered class II. This was partly because most snags did not fall until they had already decomposed to some extent, and hence entered the DWD pool in later decay classes. A large majority of recently-dead snags from early decay classes also became class III DWD (Table 4). This could have been the result of decay processes that acted on snags, but not downed logs. Cavity-excavating birds, for instance, can accelerate early decomposition in snags (Farris et al., 2004). Another possibility is that trees that died standing could have been in decline for many years, during which time they may have been subjected to insects or disease that initiated the decomposition process. Trees that fell at death, on the other hand, would have been more likely to die suddenly during a windstorm. While live trees that blow down are sometimes afflicted with internal stem or root decay, these conditions would probably not affect their decay class immediately after death, which is based on external characteristics of DWD.

The age distribution of snag-derived DWD in classes III and IV extended over a longer period than the corresponding classes from fallen trees (Fig. 6). Snags created from a cohort of dead trees broke and fell over many years, and the resulting staggered DWD inputs ensured that downed wood was present over a wide range of times since tree death. The slow decomposition of snags and the variable timing of snag fall thereby appeared to extend the effective lifetime of CWD. It must be noted, however, that the snag-derived DWD projection described here hinged on certain assumptions regarding the relative decomposition dynamics of snags and downed logs. Although Storaunet and Rolstad (2002) found that the rate at which DWD moved through decay classes was unrelated to time spent as a snag, we were not able to verify this aspect of the model projection with the data available. Long-term observations of the decay class dynamics of fallen snags from permanent sample plots would be needed to address this issue definitively.

4.2. Methodological considerations

Permanent sample plots proved to be an excellent source of data for modelling the breakdown and fall of snags. Because we tracked individual snags over time, there was no need to rely upon the assumptions associated with chronosequences (Harmon and Sexton, 1996), nor correct for bias arising from measurements made at a single point in time (Kruys et al., 2002). Chronic agents involved in snag decomposition, such as fungal decay and low-to-moderate intensity wind forces, should be well-captured in the intervals between plot measurements; infrequent disturbances, such as high intensity windstorms, should be represented in the regional-scale plot network through a space-for-time substitution (Pickett, 1989). The use of permanent plots here also carried drawbacks, however. Each plot had only two measurements, which precluded the use of time-dependent transition models. A second limitation was that the year of death was not known for snags and hence time since death could not be directly incorporated as a parameter of the fall model. Fortunately, the decay class system was successful in capturing variation in fall rates and, used in concert with a matrix of decay class transition rates, allowed us to represent changes in the probability of snag fall over time.

Analyzing the decay class distributions of logging residues along a chronosequence of harvested stands was a simple and effective approach for modelling the dynamics of DWD. The detailed breakdown of times since harvest that were available allowed us to model decay class transition functions precisely. The resulting models corresponded very well with observed DWD distributions, indicating that the logistic function was an appropriate choice of model form.

If these decay class transitions are to apply to naturally-occurring DWD, we must assume that decomposition dynamics of cut pieces are equivalent to those of DWD originating from treefall or branchfall. Size-related differences might be expected, for example, because cut pieces did not include large intact fallen trees. However, the geometric mean diameter of the cut pieces we sampled (19 cm) was approximately equal to the average diameter of DWD in undisturbed sites (19.2 cm), and we also incorporated effects of diameter into our transition models. The environmental conditions created by harvesting could also have an effect on decay class transitions. Shelterwood harvesting maintained continuous canopy cover on these sites though, so we do not expect such effects to be pronounced.

A potential shortcoming of the chronosequence approach was that it was based on the observed distribution of DWD and hence did not account for material that had already decomposed completely. If some DWD had already passed through all of the decay classes, the resulting model would underestimate the transition probability at a given age. This was not likely to have been a major problem because the class IV transition function, which was derived through a different approach, indicated that only about 13% of all material (up to 18% in the sensitivity analysis) should have passed through class IV by age 28, the last year of the chronosequence. Many of these pieces could have still been available for sampling in decay class V. Thus, this potential source of error was of minor concern to us.

The transition function representing decomposition out of the fourth DWD class was parameterized based on the relative abundance of decay class IV DWD in seven undisturbed sites where the DWD pool was assumed to be at equilibrium. The steady-state condition was mainly based on the assumption of a constant input rate over time (Sollins, 1982; Ranius et al., 2004). In reality, CWD input rates often vary temporally (Franklin et al., 1987; Laiho and Prescott, 2004). We attempted to minimize the effect of this variability by using a number of mature sites that were relatively undisturbed, and by sampling DWD across a wide area within each site. We believe that a bias due to systematic changes in mortality is unlikely, as Carleton (2003) found no evidence of increasing mean DWD volume with stand age in three of four productivity classes of white and red pine-dominated stands. The standard error of the mean proportion of DWD in decay classes I–III was reasonably small in our sites, and our sensitivity analysis showed that varying the two model parameters within reasonable limits had only a modest effect on the timing of DWD decomposition out of decay class IV.

5. Management applications

The decay class transition functions defined here provide an important link between stand mortality and accumulations of coarse woody debris. By projecting backwards in time, models such as this one can be used to reconstruct past mortality from the current accumulation of CWD within a stand (Stokland, 2001). This approach can be used to determine historic patterns of mortality and assess temporal continuity of CWD, which is important to numerous CWD-dependent organisms (Grove, 2002).

Future accumulations of snags and DWD, by decay class, may also be projected by linking our transition functions with stand growth and mortality models. Individual-based models of stand dynamics are garnering increasing interest for simulating the structural development of complex stands (Groot et al., 2004). Our decay class transition model can incorporate CWD dynamics into such models by tracking the condition of dead trees through time in stand simulations. The number of snags and DWD pieces within each decay class can then be summed across the stand to determine CWD density and, in conjunction with allometric formulas (Honer et al., 1983) and decay class specific estimates of fragmentation (Harmon et al., 2000), CWD volume. Combining CWD dynamics with stand growth and mortality would enable managers to simulate long-term changes in the quality and quantity of snags and downed woody debris under a variety of silvicultural practices. Using these integrated tools, managers could investigate the potential effects of various forest management regimes on CWD, and better ensure that appropriate quantities of specific types of dead wood are available over time for CWD-associated organisms.

Acknowledgements

This research was funded by the Natural Sciences and Engineering Research Council of Canada (operating grant to J.R.M. and postgraduate scholarship to M.C.V.) and the University of Toronto Faculty of Forestry. We thank the Ontario Ministry of Natural Resources for sharing their permanent sample plot data with us, and the Algonquin Forestry Authority for logistical support. We are grateful to Brian Naylor, John Caspersen, and three anonymous referees for reviewing earlier versions of the manuscript.

References

Agresti, A., 1996. An Introduction to Categorical Data Analysis. John Wiley and Sons, New York, NY.

Alban, D.H., Pastor, J., 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. 23, 1744–1749.

Allison, P.D., 1999. Logistic Regression Using SAS System: Theory and Application. SAS Institute Inc., Cary, NC.

Bader, P., Jansson, S., Jonsson, B.G., 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol. Conserv. 72, 355–362.

Brown, P.M., Shepperd, W.D., Mata, S.A., McClain, D.L., 1998. Longevity of windthrown logs in a subalpine forest of central Colorado. Can. J. For. Res. 28, 932–936.

Carleton, T.J., 2003. Old growth in the Great Lakes forest. Environ. Rev. 11, S115–S134.

Chapeskie, D.J., Galley, D.F., Mihell, J.R., Quinn, N.W., Struik, H.H., 1989. A Silvicultural Guide for the White Pine and Red Pine Working Groups in Ontario. Ontario Ministry of Natural Resources, Toronto, Canada.

Cline, S.P., Berg, A.B., Wight, H.M., 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44, 773–786.

Duvall, M.D., Grigal, D.F., 1999. Effects of timber harvesting on coarse woody debris in red pine forests across the Great Lakes states, USA. Can. J. For. Res. 29, 1926–1934.

Erickson, H.E., Edmonds, R.L., Patterson, C.E., 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. Can. J. For. Res. 15, 914–921.

Fahey, T.J., 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* spp. Latifolia) ecosystems, southeastern Wyoming. Ecol. Monogr. 53, 51–72.

Farris, K.L., Huss, M.J., Zack, S., 2004. The role of foraging woodpeckers in the decomposition of ponderosa pine snags. Condor 106, 50–59.

Foster, J.R., Lang, G.E., 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Can. J. For. Res. 12, 617–626.

Fox, G.A., 2001. Failure-time analysis: emergence, flowering, survivorship, and other waiting times. In: Scheiner, S.M., Gurevitch, J. (Eds.), Design and

Analysis of Ecological Experiments. second ed. Chapman and Hall, NY, pp. 253–289.

Frangi, J.L., Richter, L.L., Barrera, M.D., Aloggia, M., 1997. Decomposition of *Nothofagus* fallen woody debris in forests of Tierra del Fuego, Argentina. Can. J. For. Res. 27, 1095–1102.

Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process: the causes, consequences, and variability of tree mortality. BioScience 37, 550–556.

Garber, S.M., Brown, J.P., Wilson, D.S., Maguire, D.A., Heath, L.S., 2005. Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. Can. J. For. Res. 35, 787–796.

Groot, A., Gauthier, S., Bergeron, Y., 2004. Stand dynamics modelling approaches for multicohort management of eastern Canadian boreal forests. Silva Fenn. 38, 437–448.

Grove, S.J., 2002. Saproxylic insect ecology and the sustainable management of forests. Annu. Rev. Ecol. Syst. 33, 1–23.

Harmon, M.E., 2001. Moving towards a new paradigm for dead wood management. Ecol. Bull. 49, 269–278.

Harmon, M.E., Sexton, J., 1996. Guidelines for Measurements of Woody Detritus in Forest Ecosystems. US Long-Term Ecological Research Network Office Publication 20.

Harmon, M.E., Cromack Jr., K., Smith, B.G., 1987. Coarse woody debris in mixed conifer forests, Sequoia National Park, California. Can. J. For. Res. 17, 1265–1272.

Harmon, M.E., Krankina, O.N., Sexton, J., 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Can. J. For. Res. 30, 76–84.

Hayden, J., Kerley, J., Carr, D., Kenedi, T., Hallern, J., 1995. The Ontario Growth and Yield Program Field Manual for Establishing and Measuring Permanent Sample Plots. Ontario Ministry of Natural Resources, Toronto, Canada.

Hills, G.A., 1959. A Ready Reference to the Description of the Land of Ontario and Its Productivity. Ontario Department of Lands and Forests, Maple, Ont..

Honer, T.G., Ker, M.F., Alemdag, I.S., 1983. Metric timber tables for the commercial tree species of central and eastern Canada. Canadian Forest Service Information Report M-X-140.

Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression, second ed. John Wiley and Sons, New York, NY.

Huggard, D.J., 1999. Static life-table analysis of fall rates of subalpine fir snags. Ecol. Appl. 9, 1009–1016.

Jonsson, B.G., Kruys, N., 2001. Ecology of coarse woody debris in boreal forests: future research directions. Ecol. Bull. 49, 279–281.

Kershaw, H.M., 1993. Early successional processes of eastern white pine (*Pinus strobus* L.) and red pine (*Pinus resinosa* Ait.) within the Great Lakes—St. Lawrence forest: a literature review. Ontario Ministry of Natural Resources Forest Fragmentation and Biodiversity Project Technical Report Series 8.

Kruys, N., Jonsson, B.G., Stahl, G., 2002. A stage-based matrix model for decay-class dynamics of woody debris. Ecol. Appl. 12, 773–781.

Laiho, R., Prescott, C.E., 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can. J. For. Res. 34, 763–777.

Lambert, R.L., Lang, G.E., Reiners, W.A., 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61, 1460–1473.

Landram, F.M., Laudenslayer Jr., W.F., Atzet, T., 2002. Demography of snags in eastside pine forests of California. In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.E., Weatherspoon, P., Lisle, T.E. (Technical Coordinators), Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests. USDA Forest Service General Technical Report PSW-181, pp. 605–620.

Lee, P., 1998. Dynamics of snags in aspen-dominated midboreal forests. For. Ecol. Manage. 105, 263–272.

Lofroth, E., 1998. The deadwood cycle. In: Voller, J., Harrison, S. (Eds.), Conservation Biology Principles for Forested Landscapes. University of British Columbia Press, Vancouver, Canada, pp. 185–214.

MacMillan, P.C., 1988. Decomposition of coarse woody debris in an old-growth Indiana forest. Can. J. For. Res. 18, 1353–1362.

Manly, B.F.J., 1997. Randomization, Bootstrap, and Monte Carlo Methods in Biology, second ed. Chapman and Hall, London, UK.

Maser, C., Anderson, R.G., Cromack Jr., K., Williams, J.T., Martin, R.E, 1979. Dead and down woody material. In: Thomas, J.W. (Ed.), Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. USDA Forest Service Agriculture Handbook, vol. 553, pp. 78–95.

McGee, G.G., Leopold, D.J., Nyland, R.D., 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. Ecol. Appl. 9, 1316–1329.

Means, J.E., Cromack Jr., K., MacMillan, P.C., 1985. Comparison of decomposition models using wood density of Douglas-fir logs. Can. J. For. Res. 15, 1092–1098.

Morneault, A.E., Naylor, B.J., Schaeffer, L.S., Othmer, D.C., 2004. The effect of shelterwood harvesting and site preparation on eastern red-backed salamanders in white pine stands. For. Ecol. Manage. 199, 1–10.

Morrison, M.L., Raphael, M.G., 1993. Modeling the dynamics of snags. Ecol. Appl. 3, 322–330.

Nordyke, K.A., Buskirk, S.W., 1991. Southern red-backed vole, *Clethrionomys gapperi*, populations in relation to stand succession and old-growth character in the central Rocky Mountains. Can. Field-Nat. 105, 330–334.

Olson, J.S., 1963. Energy storage and the balance of the producers and decomposers in ecological systems. Ecology 44, 322–331.

Onega, T.L., Eickmeier, W.G., 1991. Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. B. Torrey Bot. Club 118, 52–57.

Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G. (Ed.), Long-Term Studies in Ecology: Approaches and Alternatives. Springer-Verlag, New York, USA, pp. 110–135.

Pinto, F.N.L., Corlett, A.S., Naylor, B.J., Morneault, A.E., Galley, D.F., Munro, J.S., Leavey, J., 1998. Silvicultural systems. In: A Silvicultural Guide for the Great Lakes—St. Lawrence Conifer Forest in Ontario. Ontario Ministry of Natural Resources, Toronto, Canada, pp. 7.2.1–7.2.29.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.

Ranius, T., Jonsson, B.G., Kruys, N., 2004. Modeling dead wood in Fennoscandian old-growth forests dominated by Norway spruce. Can. J. For. Res. 34, 1025–1034.

Raphael, M.G., Morrison, M.L., 1987. Decay and dynamics of snags in the Sierra Nevada, California. For. Sci. 33, 774–783.

Sellin, A., 1994. Sapwood-heartwood proportion related to tree diameter, age, and growth-rate in *Picea-Abies*. Can. J. For. Res. 24, 1022–1028.

Senecal, D., Kneeshaw, D., Messier, C., 2004. Temporal, spatial, and structural patterns of adult trembling aspen and white spruce mortality in Quebec's boreal forest. Can. J. For. Res. 34, 396–404.

Simila, M., Kouki, J., Martikainen, P., 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. For. Ecol. Manage. 174, 365–381.

Sollins, P., 1982. Inputs and decay of coarse woody debris in coniferous stands in western Oregon and Washington, USA. Can. J. For. Res. 12, 18–28.

Stokland, J.N., 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecol. Bull. 49, 71–83.

Storaunet, K., Rolstad, J., 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. Can. J. For. Res. 32, 1801–1812.

Tyrrell, L.E., Crow, T.R., 1994. Dynamics of dead wood in old-growth hemlock hardwood forests of northern Wisconsin and northern Michigan. Can. J. For. Res. 24, 1672–1683.

Van Wagner, C.E., 1968. The line intersect method in forest fuel sampling. For. Sci. 14, 20–26.