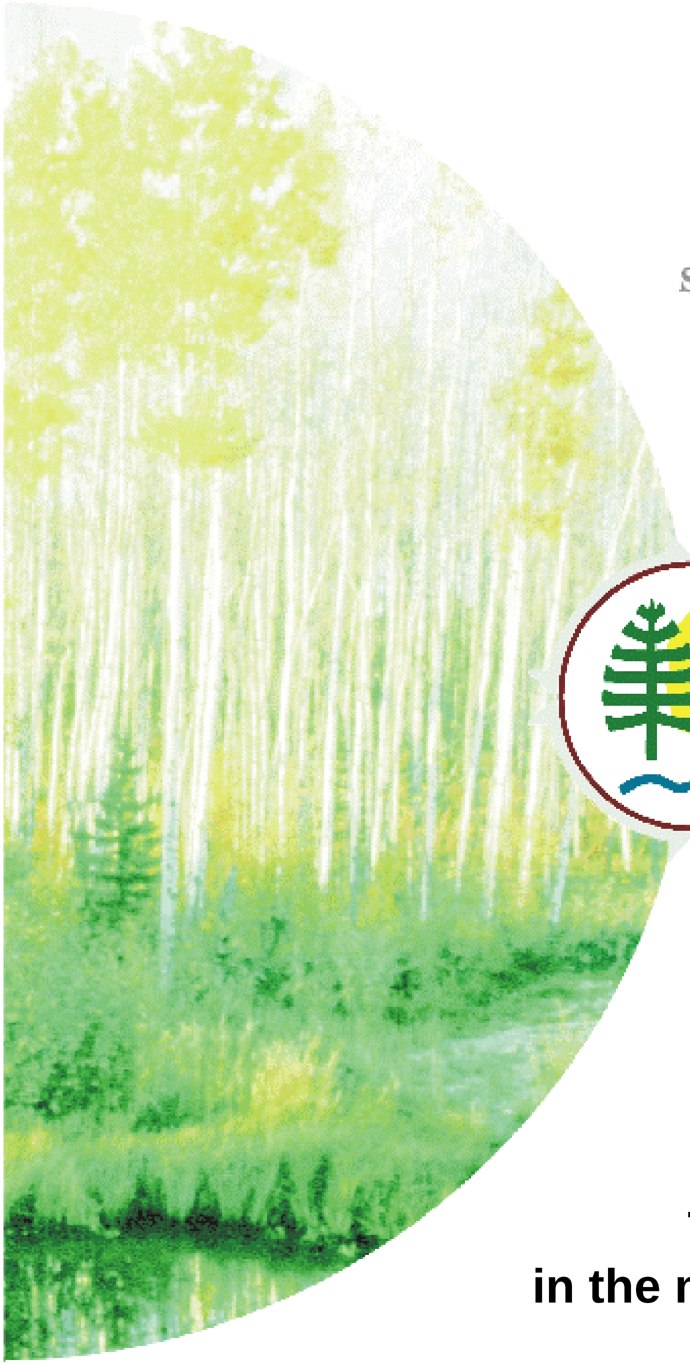

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The dead bole dynamics in the mixedwood boreal forest

by

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EXECUTIVE SUMMARY

With the emphasis in forest management on mimicking natural processes within forests, the role of dead standing and downed tree boles has become of increasing importance. Dead boles are believed to be important in ecosystem structure and function. Our results from the mixedwood boreal forest suggest that if forest managers are required to mimic the dead bole dynamics of un-managed stands they must consider that there are two types of dead boles inputs occurring nearly continuously through a stand's life time. Dead boles inputs include those from trees that are killed by the stand replacing fire, i.e. fire-killed cohort, and trees that establish after the stand-replacing fire and die before the next stand-replacing fire, i.e. post-fire cohort. Inputs of fire-killed boles are a function of the species composition and age of the pre-fire stand, while inputs from the post-fire boles are a function of the age-specific mortality rates of each tree species.

We suggest that the size distribution of dead boles left within a stand after harvest should approximate the size distribution of dead boles (from both the fire-killed and post-fire cohorts) within un-managed stands similar in age and species composition. The diameter distribution of dead boles from fire-killed and post-fire cohorts varies with stand age, and for any stand age there is wide variation in dead bole sizes. The mean bole diameter within each stand is small (mean <25.0 cm), compared to that found in many other studies.

Because the fire cycle in the boreal forest is relatively short, only a small proportion of the forest at any time is made up of old-growth stands; typically, less than 5% of the area is greater than 150 years old (Weir et al. 2000). This means that in the mixedwood boreal forest we should not expect to find large areas of old-growth forest with characteristically large quantities of dead standing and downed boles, as is often suggested.

Dead boles are believed to play an important role as a habitat for many species of organisms, and in nutrient cycling and productivity. Given that the mean dead bole diameter within each stand is relatively small, however, the importance of dead boles as habitat becomes less clear, particularly for animal species. Recent evidence also indicates that dead boles do not make a significant contribution to nitrogen and phosphorus cycling. Based on these findings, we suggest that further studies are required before animal habitat and nutrient cycling are used as a rationale for incorporating dead bole dynamics into forest management practices in the boreal forest.

INTRODUCTION

With the increasing emphasis in forest management on mimicking natural processes within forests, the role of coarse woody debris, i.e. dead standing and downed tree boles, has become of increasing importance. Dead boles are believed to be important in ecosystem structure and function, acting as a major structural feature of the forest with many crucial ecological functions. It is believed to play an important role as a habitat for many species of plants, animals, invertebrates, and fungi, and in nutrient cycling and productivity (Harmon et al. 1986).

Assessing the role of dead boles first requires an understanding of their rates of input and decomposition. Ideally, this would be accomplished by following individuals within a stand from the time of stand initiation until the next disturbance. Clearly, such measurement within forested ecosystems is difficult due to the long time span involved and the considerable temporal variation. As a result, most studies have relied on indirect measures, usually involving a chronosequence of stands representing different stages of stand development or age. Many studies have quantified dead bole inputs over the course of stand development by measuring the quantity (mass/volume/basal area) of dead boles over a chronosequence of stands, assuming that the changes in the quantity of dead boles over stands represents the same changes one would see within each stand if it was followed through time. Unfortunately, this assumption is never validated and consequently, conclusions from these studies are limited.

Decomposition rates have been indirectly examined by subjectively classifying tree boles into decay classes using visible structural characteristics that correlate with the degree of decay (e.g. Harmon et al. 1987; Hunter 1990). Decay class is then used as an index of time and the changes in mass across decay class is used as a measure of decomposition rate. Such a subjective classification must assume that the changes in characteristics across decay class represents the same changes one would see through time. Unfortunately, this assumption is never validated and consequently, conclusions from these studies are also limited.

Some studies have directly measured dead bole inputs and decomposition over a limited time span of 10-15 years (e.g. Laiho and Prescott 1999). Within permanent plots, inputs have been quantified by collecting and measuring inputs, while decomposition rates have been quantified by destructively re-sampling boles. By assuming a constant decomposition rate, the past and future rates of decomposition are then extrapolated (e.g. Laiho and Prescott 1999). The advantage of this approach is that rates can be measured directly without using either the chronosequence assumption or a subjective classification system. However, conclusions that extrapolate beyond the measured interval may be limited if the assumption of constant rates is not validated.

What is missing in many of these studies is a clear understanding of the processes controlling the inputs and decomposition of dead boles. The demography of dead boles is clearly determined by the population dynamics of trees, i.e. recruitment and mortality rates, the falling rate of the trees after they die, and the decomposition rates of the standing and fallen dead tree boles. The objective of this study is to examine the processes controlling the inputs of dead boles within a stand over time. We investigated the dead bole dynamics within upland stands in the southern mixedwood boreal forest of Saskatchewan. Using cross-dating techniques, we established the time of death of all standing, downed, and buried tree boles. We estimated their falling and decomposition rates using the methods of Johnson and Greene (1991).

SUMMARY OF DATA ANALYSIS

Data for the present study were collected from within 15 of the stands sampled in the local population dynamics study of Gutsell and Johnson (2000). The selection of stands was based on the distributions of five dominant upland tree species along the moisture and nutrient gradients (Bridge and Johnson 2000), and time-since-fire (Weir et al. 2000). Jack pine and black spruce dominated stands were located top to mid-slope on glaciofluvial hillslopes, while trembling aspen and white spruce dominated stands were located top to bottom-slope on glacial till hillslopes. Time-since-fire of stands ranged from 32 years to 154 years.

Each stand (up to 40 m × 40 m) was divided into a 2 m × 2 m grid and all live and dead standing stems were mapped. All downed dead boles were mapped, including their locations and horizontal positions relative to other downed trees lying over or under them. For each standing and downed bole, the species, height, and diameter at base were recorded. All buried dead boles were excavated and mapped. Species was recorded and height and diameter at base were measured. All sapling and tree stumps were excavated to locate the root collar. Cross-dating techniques were used to determine the date of recruitment and mortality of each of the dead individuals. A section 15 cm in length was cut 30 cm above the root collar of each individual to determine mass density.

Within each stand we examined two types of dead bole inputs: 1) trees from the pre-fire stand that are killed by the stand replacing fire, and 2) trees that establish after the stand-replacing fire and die within the period between stand initiation and the next stand-replacing fire. For convenience we will refer to these as fire-killed boles and post-fire killed boles, respectively (Figure 1). Fire-killed tree boles were distinguished from post-fire killed boles by their position in the stand (standing, fallen, buried), and state of decomposition given the age of the stand. Within young stands (<20 years), fire-killed boles are charred and either standing or fallen, and visibly distinct from the newly emergent post-fire seedlings and saplings. In stands 20 to 80 years of age, most fire-killed boles are lying on the ground and are buried (at least partially) within the soil organic layer, while post-fire killed boles are either standing or downed (and not buried). Compared to post-fire killed boles, which are more intact, fire-killed boles are characteristically very decomposed (crumbly) as stand age increases. In general, within stands 80 to 125 years old fire-killed boles were completely buried within the soil organic layer and very decomposed, while post-fire killed boles were clearly visible and either standing, downed, or partially buried. Within stands older than 125 years, few fire-killed boles could be detected, while most post-fire killed boles >5 cm diameter that died within the most recent 50 years could be detected.

The method of determining mass density (specific gravity) for boles followed American National Standard ANSI/ASTM D2395-69 (Anonymous 1978). Bark was removed from each 15 cm section and oven dried for 48 hrs, or until a constant mass was achieved. Sample mass density was determined using the dry weight and volume of each 15 cm sample. To determine sample volume, each sample was coated in paraffin, immersed in water, and then re-weighed. The increase in weight was used to calculate paraffin volume from its known mass density. Volume of the coated sample was then determined by displacement of water. The volume of paraffin was subtracted from the total volume to give the oven-dried sample volume. Mass density (g· cm-3) was calculated by dividing the sample mass by the sample volume.

The mass density of each dead bole at its time of death was estimated using the diameter of each dead bole and determining the mass density for that diameter from the relationship of density to diameter in living trees. To estimate the time a dead bole has been on the ground we used the methods of Johnson and Greene (1991). The approach involved two steps: first, the falling rate of dead standing trees (number per year) was estimated, and then this estimate was used to calculate the expected standing time of an individual dead bole, conditional on the fact that the time standing is less than or equal to the time since death (cf. Gore et al. 1985).

The size distribution of fire-killed trees at any time is dependent on the species composition and age of the fire-killed stand. In jack pine - black spruce stands, the mean diameter distribution of jack pine is greater than the mean for black spruce. In trembling aspen - white spruce - balsam fir stands, the mean diameter distribution of aspen is generally greater than white spruce, which is greater than balsam fir. All species have a very wide range of dead boles sizes at any time. In all stands, a greater mean diameter distribution indicates higher early growth rates, rather than a difference in age. Differences between species in the mean diameter distribution is greatest in young stands and decreases as stands age, since growth rate differences occur only within the first 1-metre of growth (Gutsell and Johnson 2000).

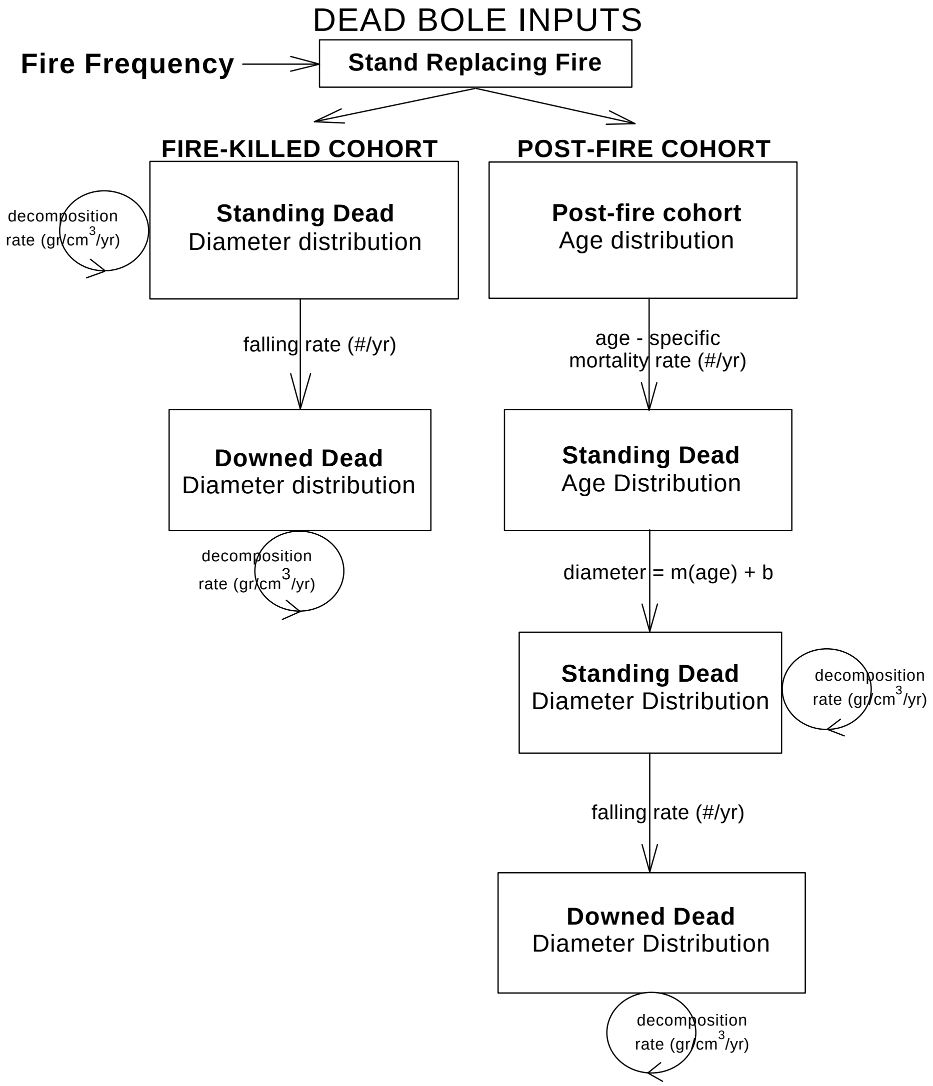

Figure 1: Conceptual model of dead bole dynamics in the mixedwood boreal forest.

The rate at which fire-killed trees fall to the ground, i.e. the falling rate (number per year), is dependent on tree size and the amount of duff consumed by the stand replacing fire (see Miyanishi and Johnson 2000). In general, the falling rate of trees increases with increasing tree size, primarily because larger trees are subject to higher wind speeds, given that wind speed within a forest increases with height. The consumption of duff, i.e. the soil organic layer, by smoldering combustion also affects the falling rates since it removes the organic layer around the base of each tree, exposing most of a tree’s supportive roots (Miyanishi and Johnson 2000). Even in moderate duff consumption conditions, duff is consumed around the base of tree boles because this is where duff moisture is lowest (Miyanishi and Johnson 2000). As duff consumption increases, these consumed areas around tree boles increase in size, exposing an increased proportion of the supportive root system of a tree. Compared to an intact forest, a fire-killed forest will have a much higher falling rate because wind speeds are higher in forests with leafless trees, and because duff consumption exposes a tree's supportive root system. As a result, most fire-killed trees fall to the ground within the first 10-15 years after the stand-replacing fire.

The decomposition rate, i.e. the rate of mass loss, of fire-killed boles is dependent on bole mass density (g· cm-3), which is in turn related to tree size. With increasing tree size, mass density decreases and the decomposition rate increases. Consequently, larger trees have a higher decomposition rate. In these forests, the decomposition rate of both standing and downed fire-killed boles is relatively low such that fire-killed dead boles can be found within stands as old as 125 years. Fire-killed jack pine and black spruce boles (8.5 - 10 cm basal diameter) were detected within stands up to 125 years, while trembling aspen and white spruce fire-killed boles (4 - 30 cm) were detected within stands up to 110 years. It appears that fire-killed dead boles are rarely considered in studies of dead boles because most fire-killed trees fall to the ground within the first 10 - 15 years after a stand replacing fire and quickly become buried by the build-up of organic matter.

The dead bole inputs from individuals that recruit after the stand replacing fire, i.e. post-fire killed boles, are primarily those individuals that recruit within the first 5 to 7 years after fire. Gutsell and Johnson (2000) showed that all species recruit within the first 5 to 7 years after fire and these individuals eventually form the canopy. Individuals that recruit after this initial period suffer high rates of mortality. They live for only short periods of time and rarely reach one meter in height.

The age distribution of standing dead post-fire individuals at any time is estimated from the total number of individuals recruited in the first 5 to 7 years after fire and their age-specific mortality rate. Charron (1998) found that individuals recruiting in the first few years are grouped into one cohort because their early age-specific mortality rate is independent of the year of establishment. All species suffer very high age-specific mortality rates within the first five years after fire (Charron 1998). Given that these individuals are small seedlings, however, most decompose and disappear within the first year after death.

In jack pine - black spruce mixed stands the age-specific mortality rate of jack pine decreases after the first five years until 10 to 35 years after fire when mortality increases (often called thinning mortality). Consequently, there are high inputs of small diameter (range of 1.6 cm to 9.1 cm basal diameter) dead standing dead jack pine boles throughout this period (3.3 cm ± 0.18; mean ± se). Black spruce has relatively low and constant mortality after the first five years until it reaches 60 - 75 years, when it reaches the canopy of jack pine. Both jack pine and black spruce have increased mortality during this period, resulting in a second significant period of standing dead bole inputs. The range in size of jack pine individuals dying during this time is 3 to 18.7 cm (8.85 cm ± 0.81), while the range in size of black spruce is 3 to 9.3 cm (5.78 cm ± 0.19).

Age-specific mortality of jack pine and black spruce decreases again after this period until individuals reach 100 to 130 years, when mortality increases again. The range in size of jack pine individuals dying during this time is 9.8 to 20.2 cm (15.5 cm ± 1.95), while the range in size of black spruce is 12.5 to 20.3 cm (16.4 cm ± 15.2). Beyond 130 years, the mortality rate of jack pine decreases, while the mortality of black spruce continues at a low but relatively constant rate, with dead bole inputs ranging in size from 7.1 to 33.4 cm (19.0 cm ± 10.25). Given the short fire cycle within the boreal forest, typically less than 5% of stands survive beyond 150 years.

In trembling aspen - white spruce - balsam fir mixed stands the age-specific mortality rate of trembling aspen decreases after the first five years and maintains a relatively low and constant mortality rate until 40 to 75 years when white spruce reaches the canopy of aspen. Both trembling aspen and white spruce have increased mortality during this period, resulting in a period of significant standing dead bole inputs. The range in size of aspen individuals dying during this time is 4.6 to 37.0 cm (14.5 ± 9.33), while the range in size of white spruce is 2.1 to 46.8 cm (8.4 cm ± 0.93). Age-specific mortality of both species decreases again after this period until individuals reach 100 to 120 years, when mortality increases again. The range in size of aspen individuals dying during this time is 10.5 to 37.3 cm (22.0 cm ± 3.13), while the range in size of white spruce is 11 to 40.4 cm (24.7 cm ± 6.49). There were too few post-fire balsam fir dead boles to give meaningful estimates of dead bole inputs. Given the short fire cycle within the boreal forest, typically less than 5% of stands survive beyond 150 years.

The falling rate of standing dead trees from the post-fire cohort is dependant on tree size. In general, the falling rate of trees increases with increasing tree size, primarily because larger trees are subject to higher wind speeds given that wind speed within a forest increases with height. Small dead boles often remain standing because they exist within the understorey where wind speeds are relatively low, and their small size means that they are affected little by drag. Few dead boles of any species were found standing after death for longer than 65 years. Compared to the fire-killed cohort, the falling rate of the post-fire cohort is much lower since no duff is consumed and wind speeds are relatively lower within an intact forest.

The decomposition rate of the post-fire cohort of standing and downed boles is related to a tree's mass density, which is in turn related to tree size. The decomposition of dead standing trees is marginally lower than that for downed trees. However, the decomposition rate of both is so low that most dead boles are present in the stand until the next stand replacing fire. The slow (sometimes, non-existent) decomposition of standing dead boles in our stands is likely a result of boles drying out as they stand dead, which significantly reduces decomposer activity. Other studies using similar species have found similar results (e.g. Johnson and Greene 1991; Fahey 1983). Because of the very slow decay of standing dead boles, the amount of time a dead bole stands before falling to the ground must be taken into account so that the decomposition rate of fallen boles is not underestimated.

MANAGEMENT APPLICATIONS

With the increasing emphasis in forest management on mimicking natural processes within forested ecosystems, dead standing and downed tree boles are increasingly becoming incorporated into sustainable forest management policy. If foresters are required to mimic the dead bole dynamics of un-managed stands they must consider that inputs occur nearly continuously throughout a stand's lifetime and that there are two types of dead bole inputs into stands. Dead boles inputs include those from trees that are killed by the stand replacing fire, i.e. fire-killed cohort, and trees that establish after the stand-replacing fire and die before the next stand-replacing fire, i.e. post-fire killed cohort. Inputs of fire-killed boles are a function of the species composition and age of the pre-fire stand at the time of the fire, while inputs from the post-fire stand are a function of the age-specific mortality rates of each tree species. Fire-killed boles are added to the system as standing dead boles at the time of the stand-replacing fire, and as downed dead boles within 15-20 years after fire. Post-fire killed boles are added to the standing dead cohort nearly continuously from stand initiation until the next stand replacing fire, with at least three significant periods of increased inputs. Post-fire killed standing dead boles become downed dead boles within 50 years of their death.

We suggest that the size distribution of dead boles left within a stand after harvest should approximate the size distribution of dead boles within un-managed stands similar in age and species composition. In each stand, the history of dead bole inputs must be taken into account and thus inputs from both the pre-fire stand and the post-fire stand must be included.

The diameter distribution of boles killed by the stand replacing fire, i.e. fire-killed cohort, depends on the species composition and age of the stand before it was killed by fire. Generally, a wide range of sizes of fire-killed dead boles can be found in stands as old as 125 years. Consequently, fire-killed boles must be included in the management plan of harvested stands up to 125 years of age. It must be remembered that the age distribution of fire-killed stands should approximate the age distribution of live stands on the landscape.

The diameter distribution of boles that die within the life span of the post-fire stand, i.e. post-fire killed cohort, varies with stand age. For any stand age there is also a wide variation in the sizes of both standing and fallen dead boles. For example, in stands 70 years of age, jack pine dead boles range in diameter from 3 cm to 19 cm (8.9 cm±0.81), black spruce ranges from 3 cm to 9.3 cm (5.8 cm±0.19), trembling aspen ranges from 5 cm to 37 cm (14.5 cm±9.33), and white spruce ranges from 2 cm to 47 cm (8.4 cm±0.93). In stands 100 to 130 years of age, jack pine dead boles range from 9.8 to 20.2 cm (15.5 cm ± 1.95), black spruce ranges from 12.5 to 20.3 cm (16.4 cm ± 15.2), trembling aspen ranges from 10.5 to 37.3 cm (22.0 cm ± 3.13), and white spruce ranges from is 11 to 40.4 cm (24.7 cm ± 6.49). Notice that in both 70 year old and 120 year old stands there is a wide range of sizes of dead boles but the mean diameter for all species is relatively small (mean of all species <25.0 cm basal diameter) compared to that found in many other studies in the boreal forest (e.g. Hely et al. 2000).

It is commonly believed that old-growth stands once covered a large percentage of the landscape and that this should be reflected in forest management practices in terms of the range of stand ages harvested. However, because the fire cycle in the boreal forest is relatively short, only a small proportion of the forest at any time is made up of old-growth stands; typically, less than 5% of the area is greater than 150 years old (e.g. Weir et al. 2000). This means that in the boreal forest we should not expect to find large areas of old-growth forest with characteristically large quantities of dead standing and downed boles, as is often suggested. Instead, we should expect a wide range of stand ages and a dead bole size distribution that varies accordingly. As we have shown, the mean size of dead boles increases slowly as stands age and the sizes of dead boles at any time are highly variable.

Dead boles are believed to play an important role as a habitat for many species of plants, animals, invertebrates, and fungi (Harmon et al. 1986). In the boreal forest, there appears to be some evidence that large dead boles in old-growth stands serve as habitat for many species of organisms. However, given that the mean diameter of dead boles is relatively small (<25 cm in most stands), the importance of dead boles as habitat becomes less clear, particularly for animal species. Consequently, we suggest that further studies are required before animal habitat is used as a rationale for incorporating dead bole dynamics into forest management practices in the boreal forest.

Dead boles are also believed to play an important role in nutrient cycling and productivity (Harmon et al. 1986) however, the evidence for this in the boreal forest is unclear. In fact, recent studies within permanent plots have demonstrated that dead boles within similar forests (subalpine coniferous forests) do not make a significant contribution to nitrogen and phosphorus cycling (Laiho and Prescott 1999; Busse 1994). Boles with low initial nitrogen and phosphorus contents tend to be net importers of nitrogen and phosphorus, suggesting that wood decay fungi may be competing with live vegetation for limiting nutrients. Consequently, it appears that the rationale for incorporating dead bole dynamics into forest management practices in the boreal forest should not be based on nutrient cycling.

CONCLUSIONS

The dynamics of dead boles in the boreal forest is determined by the species composition and age of the stand killed by fire, i.e. fire-killed cohort, and the population dynamics, falling rates, and decomposition rates of the trees killed after stand initiation, i.e. post-fire killed cohort. Our results suggest that if forest managers are required to mimic the dead bole dynamics of un-managed stands they must consider both types of dead boles inputs.

We suggest that the size distribution of dead boles left within a stand after harvest should approximate the size distribution of dead boles (both fire-killed and post-fire killed) within un-managed stands similar in age and species composition. The diameter distribution of dead boles from fire-killed and post-fire cohorts varies with stand age, and for any stand age there is wide variation in dead bole sizes. The mean bole diameter within each stand is relatively small (mean <25.0 cm), compared to that found in many other studies.

Because the fire cycle in the boreal forest is relatively short, only a small proportion of the forest at any time is made up of old-growth stands; typically, less than 5% of the area is greater than 150 years old (Weir et al. 2000). This means that in the mixedwood boreal forest we should not expect to find large areas of old-growth forest with characteristically large quantities of dead standing and downed boles, as is often suggested.

Dead boles are believed to play an important role as a habitat for many species of organisms, and in nutrient cycling and productivity. However, evidence from our study and other recent studies suggest that further studies are required before animal habitat and nutrient cycling are used as a rationale for incorporating dead bole dynamics into forest management practices in the boreal forest.

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