A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia* - *Picea engelmannii* forests

Johnson, E. A.1* & Greene, D. F.1,2

1Division of Ecology, Department of Biological Sciences and Kananaskis Centre for Environmental Research, University of Calgary, Calgary, Alberta, Canada T2N 1N4; 2Current address: Department of Geography, Concordia University, Montreal, Quebec, Canada H3G 4M8; *Tel. +1 403 2203570; Fax +1 289 9311

Abstract. Rates of decomposition were determined for the boles of *Pinus contorta* var. *latifolia* Engelm. and *Picea engelmannii* Parry ex. Engelm. in five lower subalpine forest stands in the Southern Canadian Rocky Mountains. Stands ranged in age from 58 to 222 yr since last fire. The date of death of standing dead and fallen boles was determined by cross-dating their ring-width patterns to stand master ring-width chronologies. Boles could be dated which had been dead for up to 35 years in a 58-yr old stand and 100 yr in a 222-yr old stand.

An empirical relationship between mass density and diameter of live trees was used to predict the mass density at death for trees already dead. The falling rate of dead standing boles was estimated from the dead bole’s time of death and whether it was standing or on the ground at the time of observation. The falling rates for both *Pinus contorta* and *Picea engelmannii* ranged from 0.020 to 0.064/yr falling with most stands in the 0.050 range. No effect of size was found on the falling rate probably as a result of the small size of the boles (< 20 cm). Because of their dry condition standing dead boles do not decompose.

An equation was developed which estimates the time a dead bole has been on the ground, given that it would have stood for some time before falling over and been subject to little decomposition during this time. Decomposition rates, using a negative exponential model, gave only marginally better $r^2$ than linear models. *Pinus contorta* had exponential decay rates from 0.0299 and 0.0171 mass density loss/yr for the most recent 15 and 25 yr in stands 58 yr old, to 0.0045 and 0.0035 mass loss/yr for the most recent 65 and 80 yr in stands 215 and 222 yr old. *Picea engelmannii* had exponential decay rates of 0.0054 and 0.0025 mass loss/yr for the most recent 20 and 65 yr in stands 99 and 215 yr old.

Keywords: Alberta; Bole decomposition; Canada; Canadian Rocky Mountains; Dead-tree fall; Dendrochronology; Forest reconstruction; Log decay; Stand history.

Introduction

The demography of dead boles in forests is determined by the population dynamics of the live trees, the rate of falling-over after death, and the decomposition rates of the standing dead and fallen boles. An understanding of dead bole demography is important in studies of decomposition, energy flow, forest fire behavior and tree demography (Harmon et al. 1986). In the lodgepole pine (*Pinus contorta* var. *latifolia*) and Engelmann spruce (*Picea engelmannii*) forests studied here, there was a non-steady input of dead boles controlled by the changing mortality rates (see Johnson & Fryer 1989). In the years immediately after the last stand-replacing fire (Fryer & Johnson 1989), large amounts of fire-killed boles fell onto the forest floor. This was followed by ca. 10 yr in which there was little dead bole input since trees were still small and mortality caused by competition for space had not started. When competition for space begins at between 20 and 30 yr after fire, it lasts for the rest of the stand’s life (an expectancy of 90 yr, cf. Johnson & Larsen 1991). The falling rate and speed of decomposition during these two periods of higher dead bole input determines the rate of decrease in the large, slow-drying forest fire fuel load and consequently the glowing combustion phase of fire behavior (Johnson in press).

The most intractable problem in studies of dead bole dynamics has been establishing the time-since-death of the boles. The common solution to this problem has been the study of chronosequences of logging debris in stands cut at different dates (e.g. Foster & Lang 1982; Fahey 1983) or the use of permanently marked and reweighed downed dead logs (e.g. Fati & Knight 1978; Grier 1978; MacMillan 1981). In both cases, the number of boles on which studies can be carried out is limited and the time-span covered by the studies is shorter than would be preferred given the slow rates of decomposition (e.g. < 0.005 mass density loss/yr ). Only in the tropics where rates of decomposition are rapid are these problems not a major handicap (e.g. 0.461 mass loss/yr, Lang & Knight 1979).

Graham & Cromack (1982) have increased the number of boles on which bole decomposition studies can be done by dating the fall and death from windthrow
and windbreak of the tree by using the scar(s) it leaves on its living neighbors. More recently, the dendrochronological method of cross-dating (Fritts 1976) has been applied to studies of bole dynamics (e.g. Marchand 1984). This technique allows investigation of dead bole dynamics without the spatial and temporal constraints of the methods discussed above.

In this study, we investigated dead bole dynamics in 58 to 222-yr old stands of lodgepole pine and Engelmann spruce in the Kananaskis Valley of Alberta. We used the dendrochronological technique of cross-dating to establish the time-since-death of all standing and fallen pine and spruce boles. In addition, we applied a series of analytical modifications to the time variable in models of the rates of decomposition (Jenny, Gessel & Bingham 1949; Olson 1963; Minderman 1968; Wieder & Lang 1982). These modifications involved two equations. The first equation (Gore, Johnson & Lo 1985) estimated the falling rate of upright dead boles given that one knows only if a tree is standing or fallen at the time of observation. The second equation estimated the time a dead bole has been on the ground, given that it would have stood for some period before falling over (falling rate estimated above) and could have been subject to a different decomposition rate during this time. This equation gave a correction factor which accounted for the variation in input of dead trees into the dead standing category.

### Study sites

The five stands (Table 1) are located in the Kananaskis River Watershed (50° 47' N, 115° 11' W) of the Canadian Rocky Mountains Front Range ca. 100 km west of Calgary, Alberta. All stands are located within a 5-km radius of each other in a lower subalpine forest of *Pinus contorta* var. *latifolia*, *Picea engelmannii* and some *Abies lasiocarpa*. The duff layer increases from approximately 5 cm in the 58-yr old stand to approximately 30 cm in the 222-yr old stand. All stands have approximately the same medium site index (14 m at 50 yr) for lodgepole pine (Anon. 1985).

The climate is continental with short, dry summers and long, cold winters. Warm dry Foehn winds interrupt winter conditions about 30 times every winter (Longley 1967). The average precipitation over a 13-yr period, at the Kananaskis Ranger Station (elevation 1463 m, 20 km north of the stands) was 340 mm from October to May and 259 mm from May to October. Average temperature in July was 13 °C and in January was –12 °C (Atmospheric Environment Service 1982). The stands are all on sandy-loam till and their soils are classified as Brunisolic Gray Luvisols (Anon.1978b).

<table>
<thead>
<tr>
<th>Stand</th>
<th>C</th>
<th>I</th>
<th>H</th>
<th>E</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (m)</td>
<td>1584</td>
<td>1798</td>
<td>1799</td>
<td>1736</td>
<td>1676</td>
</tr>
<tr>
<td>Age oldest live tree (yr)</td>
<td>58</td>
<td>58</td>
<td>58</td>
<td>99</td>
<td>215</td>
</tr>
<tr>
<td>Stand area (m²)</td>
<td>60</td>
<td>40</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Density live trees &gt; 3 cm DBH (stems /100 m²)</td>
<td>93</td>
<td>162</td>
<td>35</td>
<td>25</td>
<td>14</td>
</tr>
<tr>
<td>Relative density live trees (%):</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pinus contorta</em> var. <em>latifolia</em> boles:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. dead standing</td>
<td>23</td>
<td>27</td>
<td>7</td>
<td>11</td>
<td>13</td>
</tr>
<tr>
<td>No. dated</td>
<td>19</td>
<td>27</td>
<td>7</td>
<td>10</td>
<td>13</td>
</tr>
<tr>
<td>No. mass density</td>
<td>19</td>
<td>27</td>
<td>7</td>
<td>10</td>
<td>13</td>
</tr>
<tr>
<td>No. dead downed</td>
<td>30</td>
<td>7</td>
<td>13</td>
<td>17</td>
<td>37</td>
</tr>
<tr>
<td>No. dated</td>
<td>22</td>
<td>7</td>
<td>10</td>
<td>17</td>
<td>37</td>
</tr>
<tr>
<td>No. mass density</td>
<td>23</td>
<td>7</td>
<td>10</td>
<td>17</td>
<td>37</td>
</tr>
<tr>
<td><em>Picea engelmannii</em> boles:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. dead standing</td>
<td>0</td>
<td>0</td>
<td>14</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>No. dated</td>
<td>0</td>
<td>0</td>
<td>13</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>No. mass density</td>
<td>0</td>
<td>0</td>
<td>13</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>No. dead downed</td>
<td>6</td>
<td>0</td>
<td>6</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td>No. dated</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>No. mass density</td>
<td>5</td>
<td>0</td>
<td>6</td>
<td>8</td>
<td>5</td>
</tr>
</tbody>
</table>

* None or too few standing dead, stand not analyzed, see Methods.

### Methods

#### Field

Boles were divided into three categories: living, standing dead, and fallen (dead). Each stand in Table 1 was divided into a grid system, with 2m x 2m plots. All three categories of boles were mapped in these grids. The diameter of the base of all standing dead and fallen boles was measured and a disk 15 cm in length was cut 30 cm above the root collar. Very fragile specimens were cut using a coping or jeweler’s saw to minimize fragmentation loss. Fragile samples were wrapped with masking tape, packaged in plastic and aluminum foil and kept frozen at –10 °C.

Dead trees (fallen and standing) in these stands belonged to two groups which can be called the disturbance and self-thinning assemblages. The disturbance (fire) assemblage consisted of the trees dead before or killed by the most recent disturbance. The only trees missing would have been those that either survived the fire or were completely consumed by the fire. All stands had their origin following crown fires which killed all the pre-existing trees (Johnson & Fryer 1989). The self-thinning assemblages consisted of trees which died at different times primarily due to competition for light and space (Johnson & Fryer 1989). These trees were usually the smaller diameter individuals in the total tree.
population. In these stands mountain pine beetle (Dendroctonus ponderosae Hopk.)-killed trees were absent and wind-throw of canopy trees was very rare. This study deals only with boles from the self-thinning assemblage.

The arrangement on the ground of the disturbance and self-thinning assemblages usually allowed them to be distinguished in the dissection of the stand. In the stands of Table 1, the standing dead consisted primarily of thinning-killed individuals. Standing fire-killed boles were identified and excluded from the analysis. Standing fire-killed boles less than 5 cm were usually severely charred, boles between approximately 5 and 15 cm were lightly charred, and boles greater than 15 cm showed charring on the branches but little or no sign of charring on the boles themselves. Trees, dead before being burned generally have a cobbled surface.

Boles on the ground were found in approximate layers. The top layer of boles usually resulted from thinning deaths. Below this were trees of both the self-thinning and disturbance assemblages while on the bottom were trees of only the disturbance assemblage. In stands older than 100 yr old, the disturbance assemblages and some of the self-thinning assemblages were partly or completely buried in the duff and moss. From our observations (Fryer & Johnson 1988; Johnson & Larsen 1991), fires which killed all or most of the canopy (frontal fire intensity > 7000 kW m⁻¹) usually also ashed many of the boles already on the ground. Boles which had been burned while on the ground (not standing and subsequently falling after the fire), but not completely destroyed, could be identified by the difference between the burn pattern on the exposed wood and the portion in contact with the ground. In all cases studied, cross-dating (see below) could clarify the assemblage to which a bole belonged.

**Laboratory**

Boles of each species were identified by using wood anatomical features. Thin radial sections were pared from each basal disk and then macerated for three days at 50 °C in a solution of glacial acetic acid, distilled water, and 30% hydrogen peroxide (5: 4: 1 v/v). The macerated sections were mounted and examined under a compound microscope. The specimens of each species were identified using cross-field pits as key characteristics (Core, Cote & Day 1979; Panshin & de Zeeuw 1980). Cross-field pits could be used since the three species each belonged to a different genus. Gross anatomical features were not found to be useful.

The time of death of trees in the self-thinning assemblage was determined by the dendrochronological technique of cross-dating. Basal disks were sanded or shaved to prepare a smooth, clean surface for ring-width measurements. For old or fragile disks, we maintained stability and prevented warping by freezing in dry ice or by saturating in polyethylene glycol (molecular weight 3350). All materials used in stabilizing could be removed from the sample before mass density determination.

Two radii on each disk had the rings marked in decade intervals by pin-pricks. These decade marks were then traced between radii to see if they matched. This was the first check for locally missing or double annual rings. The second check was by cross-dating individual trees with each other. Locally missing rings sometimes occurred in injured, slow growing and old trees. In the first counts, most old trees did not give the same ages on their two radii because of missing rings. Often on close examination these missing rings could be found partially formed on another part of the disk. The measurements of ring-width were made on both radii to the nearest 0.1 mm using a Henson type ring-width measuring instrument and linked computer.

Cross-dating involved matching a ring-width series from a dead bole of unknown date of birth or death to a dated ring-width series. The dated series consisted of at least 10 trees from the same stand whose ring-widths were then averaged to form a master chronology. A master chronology was constructed for each stand. Actual cross-dating between individual boles and the stand master chronology was done visually by two investigators independently and statistically using the computer program CROSS-DATE (Baillie & Pilcher 1973).

Not all standing dead trees could be dated (Table 1). Trees with less than 15 rings often could not be cross-dated and in a few cases, decomposition, fragmentation or crushing made ring-width measurements impossible. Differential decay and loss of sapwood does not occur in these specimens.

The method of determining mass density (specific gravity) for boles follows American National Standard ANSI/ASTM D2395-69 (Anon. 1978a). Fragmentation loss was not taken into account but did not appear to be great. Bark was removed from a section of a bole and the bole was oven dried for 48 hr at 103 °C or until a constant dry mass was achieved. Mass density was determined by water immersion. The sample was coated in paraffin, re-weighed and the increase in weight used to calculate paraffin volume from its known mass density. Volume (V) of the coated sample was then determined by displacement of water. The volume of paraffin was subtracted from the total volume (V) to give the oven-dried sample volume (V). Mass density (g cm⁻³) was calculated by dividing the sample mass, M, by the sample volume, V:

\[
\frac{M}{V}
\]

A mass density of each 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.

**Estimating the time a bole has been on the ground**

Our approach to dating the time a bole has been on the ground involved two steps: (1) estimating the falling rate of dead standing trees in numbers per year (\(\phi\)), and (2) using this estimate to calculate the expected standing time of an individual dead bole, conditional on the fact that the time standing \(X_i\) is less than or equal to the time-since-death \((X)\) (cf. Gore, Johnson & Lo 1985).

Studies which have followed marked standing dead boles have found that the survival function of standing time \(S(X_i)\) is a negative exponential (Keen 1955; Cline, Berg & Wright 1980). The parameter of this distribution is \(\phi\), the rate of falling per year, and \(1/\phi\) is the average number of years a bole stands after death. The difficulty in estimating \(\phi\) is that the necessary \(X_i\) data are not observed. What is observed is the time-since-death \((X)\), and either that the tree is still standing or is already on the ground. Gore, Johnson & Lo (1985) give the maximum likelihood estimate of taking into account these limitations

\[
\sum_{i=1}^{m} X_i = \sum_{j=m+1}^{m+n} \left( \frac{X_j}{\exp(\Phi X_j) - 1} \right)
\]

where \(X_1, X_2, \ldots, X_m, X_{m+1}, \ldots, X_{m+n}\) represent the \(m+n\) boles and their time-since-death. The first \(m\) values are the time-since-death of the boles still standing and the last \(m+n\) values are the time-since-death of the boles on the ground.

One other complication, not dealt with by Gore, Johnson & Lo (1985), arises in the calculation of the expected time a bole stands \((1/\phi)\). The aforementioned estimator of \(\phi\) assumes that the input of dead boles is unchanging in time. However, the number of trees dying, which controls the input of dead boles into the standing category, is influenced by the stand history and cannot reasonably be assumed to be constant. In young stands, self-thinning deaths may produce pulses of input to the standing category and in old stands, senescence and overtopping of lodgepole pine by Engelmann spruce may cause irregular inputs of dead trees.

One possible procedure for overcoming this problem was suggested to us by M. B. Rajarshi of the University of Poona, India. Assume that the life span of a cohort of individual trees \((X_1)\) follows a negative exponential (Harper & White 1974) and that \((X_1, X_s)\) have a bivariate exponential distribution. Further, assume that if the conditional expectation of \(X_s\) given \(X_1\) is linear in \(X_1\) then the best predictor of \(X_s\) is:

\[
E(X_s) + \frac{\text{cov}(X_1, X_s)}{\text{var} X_1} \cdot \frac{\text{cov}(X_1, X_s)}{\text{var} X_1} \cdot [X_1 - E(X_1)]
\]

where \(E(X_s)\) is the expected lifespan of a tree (= mean tree age in cohort). Finally, if the dead trees’ time on the ground \((X_d)\) is independent of \((X_1, X_s)\) then \(\text{cov}(X_1, X_s + X_d) = \text{cov}(X_1, X_s)\).

Remember, \((X_1 + X_s) = X\), the time-since-death. Therefore, \(\text{cov}(X_1, X_s)\) can be estimated from the available data by computing \(\text{cov}(X_1, X_s + X_d)\).

Replacing \(E(X_s)\) in equation (2) with \(E(X_s | X_s \leq X_s + X_d)\) gives:

\[
E(X_s | X_s \leq X_s + X_d) = \frac{\text{var}X_1}{\text{var}X_1} \cdot [X_1 - E(X_1)]
\]

\[E(X_s | X_s \leq X_s + X_d)\] is the expected standing time of a dead bole conditional on the fact that the time the bole stood \((X_s)\) has to be less than or equal to the time-since-death \((X_s + X_d)\). This conditional expectation was derived by Gore, Johnson & Lo (1985) as:

\[
E(X_s | X_s \leq X_s + X_d) = \frac{\exp(-\Phi(X_s + X_d) - \Phi(X_s + X_d))}{\Phi(1 - \exp(-\Phi(X_s + X_d)))}
\]

To estimate the time a bole has been on the ground, subtract equation (3) from the time-since-death of the bole \((X)\).

**Results**

**Mass density at time of death and dead bole falling rate**

Live lodgepole pine and Engelmann spruce show a decrease in mass density with increasing diameter (Fig. 1). In both species the higher mass densities at small diameters is due to higher density core or juvenile wood (Panshin & de Zeeuw 1980). Bole density appears to be closest to the diameter class average if it is clear wood without branch stubs, scars and reaction wood. The estimated rate of falling of dead boles (\(\phi\)) is given in Table 2.

**Mass density and diameter of standing dead boles**

Fig. 2 gives the mass density of standing pine and spruce boles plotted against their time-since-death. In both the standing dead pine and spruce, there is no significant decrease in mass density with time-since-death, i.e., the slopes of the linear regression are not
Table 2. The estimated rate of falling of dead boles (E) using the method of Gore, Johnson & Lo (1985).

<table>
<thead>
<tr>
<th>Stand</th>
<th>Rate of falling (No./yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pinus contorta</td>
</tr>
<tr>
<td>C</td>
<td>0.064</td>
</tr>
<tr>
<td>I</td>
<td>0.020</td>
</tr>
<tr>
<td>H</td>
<td>0.058</td>
</tr>
<tr>
<td>E</td>
<td>0.053</td>
</tr>
<tr>
<td>A</td>
<td>0.057</td>
</tr>
</tbody>
</table>

significantly different from zero ($P > 0.05$). Except for spruce in stand H, there is also no significant relationship of diameter to mass density. In stand H, the smaller diameter spruce have higher mass densities than larger diameter boles. This is probably due to the high density core or juvenile wood (Panshin & de Zeeuw 1980) in small diameter stems established under a closed canopy.

Decomposition of boles on the ground

Both linear and negative exponential (log transformed) regressions were fitted to mass density versus estimated time-on-the-ground. The exponential regression had marginally better $r^2$ for both species in all stands and hence, only negative exponential regressions are given (Table 3) and the semilog plot of the data in Fig. 3.

The intercepts and slopes of the exponential regression for the group of five pine stands and group of two spruce stands were compared using an $F$-test for coincident lines (Zar 1974). For the pines in stand E, the slope of the exponential regression was not statistically different from zero ($P = 0.053$), all other stands were significantly different from zero ($P < 0.01$). The slopes and intercepts of stands C and H were not statistically different ($P > 0.05$), but stands A and I were statistically different from each other ($P < 0.05$) and from both stands C and H ($P < 0.001$). The slopes of the exponential regressions for spruce stand H was not significantly greater than zero ($P > 0.4$) while stand E was significantly greater than zero ($P < 0.05$). A multiple regression of mass density versus diameter and estimated time-on-the-ground for all pine and spruce stands gave no significant diameter effect ($P > 0.08$). Intercepts calculated via regressions were always significantly different from intercepts estimated using the mass density of living trees for both pine and spruce.

Table 3. Regression equations for bole mass density loss with estimated time on ground. The slope of the exponentials give the annual decay constant $k$ (cf Olson 1963). Values in parentheses are transformed intercepts. EMD = Estimated mass density at time of death.

<table>
<thead>
<tr>
<th>Pinus contorta var. latifolia</th>
<th>EMD</th>
<th>Intercept</th>
<th>Slope</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>0.574</td>
<td>$-0.509$ (0.061)</td>
<td>$-0.0171$</td>
<td>0.37</td>
</tr>
<tr>
<td>I</td>
<td>0.489</td>
<td>$-0.432$ (0.649)</td>
<td>$-0.0299$</td>
<td>0.69</td>
</tr>
<tr>
<td>H</td>
<td>0.444</td>
<td>$-0.531$ (0.588)</td>
<td>$-0.0153$</td>
<td>0.54</td>
</tr>
<tr>
<td>E</td>
<td>0.552</td>
<td>$-0.678$ (0.508)</td>
<td>$-0.0045$</td>
<td>0.16</td>
</tr>
<tr>
<td>A</td>
<td>0.547</td>
<td>$-0.567$ (0.567)</td>
<td>$-0.0035$</td>
<td>0.49</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Picea engelmannii</th>
<th>EMD</th>
<th>Intercept</th>
<th>Slope</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>H</td>
<td>0.604</td>
<td>$-0.624$ (0.536)</td>
<td>$-0.0054$</td>
<td>0.06</td>
</tr>
<tr>
<td>E</td>
<td>0.565</td>
<td>$-0.662$ (0.516)</td>
<td>$-0.0025$</td>
<td>0.43</td>
</tr>
</tbody>
</table>

Fig. 1. The decrease in mass density with increasing basal diameter of live lodgepole pine (Pinus contorta var. latifolia) and Engelmann spruce (Picea engelmannii). Bars are the standard error of the means.
and spruce boles have less than 20% moisture by dry weight. Below about 25% and above 35%, decay does not usually occur (Rayner & Todd 1979). Fahey (1983) has reported a similar lack of decay in standing dead lodgepole pine in a dry subalpine environment in Wyoming. Other researchers have also found very slow deterioration in beetle-killed and fire-killed Engelmann spruce and lodgepole pine in Colorado (Mielke 1950) and Utah (Hinds, Hawkworth & Davidson 1965). In moister habitats, decomposition of standing boles appears to be more rapid, however, the species are also different (Grier 1978; Lambert, Lang & Reiners 1980; Sollins 1982).

Because of the very slow decay of standing dead boles in dry environments, 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. At present, it appears that a negative exponential equation reasonably describes the falling rate of boles (Keen 1955; Cline, Berg & Wright 1980). This model suggests that a constant proportion of standing dead boles fall in each time interval, i.e. there is no ‘aging’ effect. An assumption like this may be reasonable when there is very little decomposition occurring in the standing dead boles, hence no changes in the ‘mortality’ (falling) schedule.

Several studies (Dahms 1949; Mielke 1950; Keen 1950; Lyon 1977; Van Sickle & Bensor 1978; Cline, Berg & Wright 1980) have found that large diameter boles stand longer than smaller diameter boles. By contrast, we did not observe a diameter effect in our boles. This may be because our boles were all small (less than 20 cm at the base) compared to the larger diameters of most of the other studies. The lower falling rates for pine in stand I and spruce in stand H suggests as yet unknown factors are allowing dead trees in these stands to remain upright longer.

Once trees are on the ground, the rates of decomposition appear to be related to stages of stand development. Fallen bole decomposition rates were higher in younger stands than older stands of pine, but not related to the size of the boles. The reason for these differences in decomposition rate is unclear. The forest floor in young stands is more open and warmer with relatively little moss cover. Old stands have forest floors which are shaded and cooler with a much thicker mat of feathermoss. Personal observation indicates that snow persists longer in the spring in older stands. We suggest that the fallen boles in older stands are wetter, cooler, and have shorter periods for decomposer activity, and that it is these factors that retard their decomposition. Limited observations made three times during the growing season on fallen boles indicated wood moisture values were greater than 55% by dry weight in stand A.
(old) and less than 35% in stand C (young).

The decomposition rates of lodgepole pine are similar to those reported by Fahey (1983). We could not find any Engelmann spruce bole decomposition rate in the literature for comparison. Our results suggest that spruce decomposes less rapidly when on the ground than pine. However, our sample size of downed spruce boles was small and subject to more variation than pine (see Fig. 3). Just as in standing dead boles, we did not find that larger diameter fallen boles had different decomposition rate than smaller diameter fallen boles.

Conclusion

Dendrochronology is a promising method in the study of dead bole dynamics. To use this method, however, confidence in the date of death is essential. The cross-dating techniques were constantly tested by comparison between investigators and by blind tests of samples of known age. Difficulty in getting enough trees in both the standing and fallen categories on which to carry out meaningful study is sometimes a problem. For example, in stand A only two standing dead spruce and five fallen spruce were found, not enough to estimate the falling rate. The number of live trees was usually correlated to the number of dead. For instance, stands C and I had few live spruce and few dead spruce while stands E and H had a large number of live spruce and reasonable numbers of dead spruce (Table 1).

Only more empirical testing of the assumptions of equations 1 and 3 will indicate their efficacy. Particularly worth testing is the assumption that the falling of dead boles follows an exponential distribution and whether the correction (equation 3) for changing dead bole input is appropriate in systems in which we have complete empirical knowledge of the falling rates.
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